1   Synthesizing multiple data types for biological conservation using integrated population models

2

3   Elise F. Zipkin[a,b*] and Sarah P. Saunders[a]

4

5   [a] Department of Integrative Biology, Michigan State University, East Lansing, MI 48864 USA

6

7   [b] Ecology, Evolutionary Biology, and Behavior Program, Michigan State University, East

8   Lansing, MI 48864 USA

9

10   [*] Corresponding author, Email: ezipkin@msu.edu, Phone: 517-884-8039

11

12   Short title: Integrated population models for conservation

13

14   Keywords: Bayesian analysis, capture-recapture data, integrative modeling, management, state-

15   space model, threatened species

16

17   Type of article: Review

18

19   Statement of authorship: EFZ and SPS jointly conceived of the idea for this review and

20   participated in all aspects of writing.

21

22 **Abstract**

23 Assessing the impacts of ongoing climate and anthropogenic-induced change on wildlife

24 populations requires understanding species distributions and abundances across large spatial and

25 temporal scales. For threatened or declining populations, collecting sufficient broad-scale data is

26 challenging as sample sizes tend to be low because many such species are rare and/or elusive. As

27 a result, demographic data are often piecemeal, leading to difficulties in determining causes of

28 population changes and developing strategies to mitigate the effects of environmental stressors.

29 Thus, the population dynamics of threatened species across spatio-temporal extents is typically

30 inferred through incomplete, independent, local-scale studies. Emerging integrative modeling

31 approaches, such as integrated population models (IPMs), combine multiple data types into a

32 single analysis and provide a foundation for overcoming problems of sparse or fragmentary data.

33 In this paper, we demonstrate how IPMs can be successfully implemented by synthesizing the

34 elements, advantages, and novel insights of this modeling approach. We highlight the latest

35 developments in IPMs that are explicitly relevant to the ecology and conservation of threatened

36 species, including capabilities to quantify the spatial scale of management, source-sink

37 dynamics, synchrony within metapopulations, and population density effects on demographic

38 rates. Adoption of IPMs has led to improved detection of population declines, adaptation of

39 targeted monitoring schemes, and refined management strategies. Continued methodological

40 advancements of IPMs, such as incorporation of a wider set of data types (e.g., citizen science

41 data) and coupled population-environmental models, will allow for broader applicability within

42 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 & 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

3

66   within time frames for appropriate management actions (Taylor *et al.* 2007; Mosnier *et al.* 2015).

67   As a result, understanding the population dynamics of threatened species, and indeed most

68   species, is typically either inferred through independent local-scale studies (Thogmartin *et al*.

69   2007; Rushing *et al.* 2016) or achieved through large-scale niche modeling of distribution data

70   that is correlative with limited power to elucidate underlying mechanisms (Kearney & Porter

71   2009; Buschke *et al.* 2015). Emerging integrative modeling approaches that combine multiple

72   data sources across spatio-temporal scales into a single analysis provide a foundation for

73   overcoming these problems and allow research to scale from local biological processes to

74   regional-level patterns, where management occurs (Pacifici *et al.* 2017).

75   In this paper, we review integrated population models (IPMs), an approach to combine

76   multiple data types in a unified analysis to study the dynamics of animal populations. We

77   compiled and collated peer-reviewed articles, textbook chapters, and government technical

78   reports on IPMs that were relevant to biological conservation. Our paper builds on reviews by

79   Schaub and Abadi (2011) and Maunder and Punt (2013), both of which focus on taxa-specific

80   IPMs. Literature was searched through Google Scholar and ISI Web of Knowledge, using terms

81   such as: 'integrated population model' and 'integrative model', coupled with 'biological

82   conservation' and 'population management'. We also checked the bibliographies of relevant

83   papers to identify further pertinent literature. We outline the key components of IPMs, synthesize

84   the advantages of this approach for improved biological conservation and ecological inference,

85   and highlight the latest theoretical and technical developments in IPMs that are explicitly

86   relevant to the ecology and management of threatened species. We conclude with a perspective

87   on several potential avenues of IPM advancement related to the fields of ecology and

88   conservation science.

2. The power of integrated population models

89

90   Integrative modeling generally refers to the incorporation of multiple (1) data types on a single

91   target population, (2) analytical models or methods, or (3) predictions from multiple theories into

92   a model, thus 'integrating' several pieces of information into a single modeling framework. The

93   combined analysis of all available information allows for an understanding of processes

94   underlying ecological and demographic responses to environmental variability (Brown &

95   Collopy 2013; Grace *et al.* 2016; Fletcher *et al.* 2016). Conclusions that are inferred from

96   independent analyses can be hindered by an inability to accurately account for error in parameter

97   estimates (Schaub & Abadi 2011), spatio-temporal correlations in covariate effects (Lieury *et al.*

98   2015), and possible biases in trend estimates (Tempel & Gutiérrez 2014). Integrative modeling

99   has the potential to resolve these issues by incorporating all available data into a single analysis

100 and thus properly accounting for spatio-temporal variation and uncertainty in parameter

101 estimates (Dorazio 2014; Grace *et al.* 2016).

102   Integrated population models (IPMs) are a well-developed subset of integrative models in

103 which the analysis of the joint likelihood of two or more datasets allows for simultaneous

104 estimation of population abundance and the processes leading to population change. IPMs

105 provide an approach for addressing issues of sparse or fragmentary population data by

106 incorporating multiple data types (e.g., census, productivity, telemetry) into a single, dynamic

107 model of the target population (Fig. 1; Schaub & Abadi 2011). IPMs typically include the unified

108 analysis of data on population abundance, trajectory, or structure (e.g., census, count, and/or

109 occupancy data) and demographic parameters (e.g., productivity data, capture-recapture data,

110 dead recovery data; Besbeas *et al.* 2002; Abadi *et al.* 2010a; Schaub & Abadi 2011). The use of

111 IPMs in animal ecology began in the early 2000s (Besbeas *et al.* 2002; Besbeas *et al.* 2003;

5

112 Brooks *et al.* 2004; reviewed in Schaub & Abadi 2011), although variations of these models

113 were used in fisheries research and management as early as the 1980s (Fournier & Archibald

114 1982; reviewed in Maunder & Punt 2013). Fisheries IPMs have generally focused on stock

115 assessment to determine harvest quotas and are not examined here (except as they may pertain to

116 the conservation of a particular species). However, early work on integrated fisheries modeling

117 greatly advanced previous population assessment approaches, which relied on independent data

118 summaries of disparate stock data (Maunder & Punt 2013). These primary methodological

119 advances paved the way for subsequent inclusion of increasingly diverse data types and

120 development for additional taxa (Catchpole *et al.* 1998; Gauthier & Lebreton 2004).

121   A key feature of IPMs is the ability to model a population's underlying dynamics

122 including important life history elements by explicitly accounting for the processes that lead to

123 population changes over time (e.g., birth/death and immigration/emigration; Besbeas *et al.* 2002;

124 Brooks *et al.* 2004; Schaub *et al.* 2007). The objective of IPMs is to incorporate as much

125 mechanism as possible to estimate a population's trajectory and assess the primary factors

126 causing changes in abundance and demographic rates (Schaub & Abadi 2011). By incorporating

127 all available data on a population, IPMs overcome limitations of traditional independent analyses

128 (Véran & Lebreton 2008; Tempel *et al*. 2014; Hostetler *et al.* 2015) and allow for (1) the

129 simultaneous estimation of demographic parameters and population trajectories, while

130 standardizing the error structure across different data types and accounting for multiple sources

131 of uncertainty (Besbeas *et al.* 2002; Schaub & Abadi 2011); and (2) the direct linking of

132 variation in population abundance to changes in stage-specific vital rates and covariate effects

133 (Johnson *et al.* 2010; Mosnier *et al.* 2015).

134   The hierarchical structure of IPMs separates the underlying (and unobservable)

135   ecological mechanisms from the observation process, allowing for disentanglement of process

136   variation from sampling variation (Gould & Nichols 1998, Besbeas *et al*. 2002). This is typically

137   done in IPMs through a state-space formulation, which assumes that abundance may be over- or

138   under-counted (de Valpine & Hastings 2002; Schaub & Abadi 2011). The importance of

139   accounting for potential biases due to imperfect detection during sampling has been

140   demonstrated repeatedly in studies estimating the population dynamics and trends of species

141   (e.g., Royle *et al*. 2005; MacKenzie *et al*. 2009, Nichols *et al*. 2009). Failure to accurately

142   account for the sampling process can lead to misleading or even erroneous inferences on

143   population status (Ruiz-Gutiérrez & Zipkin 2011; Guillera-Arroita *et al*. 2014). It is especially

144   important to consider the sampling methodology for situations in which detection varies spatially

145   or through time, as well as in cases where it is important to know the absolute size of a

146   population, such as in conservation applications (e.g., population viability analysis).

147   Unfortunately, many data collection protocols do not allow for explicit estimation of detection

148   probabilities (e.g., non-replicated point counts, species checklist programs). IPMs provide an

149   approach for incorporating such data types even if it is not possible to estimate detection at every

150   site or with every data collection technique, leading to unbiased inference of both demographic

151   rates and population trends.

152

153   **3. Components of integrated population models**

154   IPMs are built according to three general steps (Fig. 2; Brooks *et al.* 2004; Schaub *et al.* 2007;

155   Schaub & Abadi 2011). First, one develops a population model linking abundance and

156   demographic rates that captures the important life history features of the target species. This is

157 typically a stage- or age-structured matrix projection model (i.e., Lefkovitch matrix or Leslie

158 matrix, respectively) where the population size of each stage/age class is assumed to be a

159 function of the population size in the previous year and the demographic rates (Caswell 2001).

160 The population model describes the relevant recruitment, survival, and immigration processes

161 that reflect dynamics and can include density-dependence and stochasticity in stage transitions.

162 Demographic stochasticity, which tends to be important in small populations, is modeled by

163 assuming that changes in abundance occur probabilistically rather than through deterministic

164 equations (e.g., using the binomial distribution to estimate the number of individuals that survive

165 between time steps; Melbourne & Hastings 2008). Environmental covariates (Rhodes *et al.*

166 2011) and/or random effects (Fieberg *et al.* 2010; Tempel & Guitiérrez 2014) can be added using

167 standard approaches and link functions. The complexity of the population model depends on the

168 questions of interest, the intricacies of the organism's life cycle, as well as the quality and

169 quantity of available data.

170 Next, the likelihoods of each dataset are formulated to estimate the parameters (e.g.,

171 survival, fecundity, and population size) defined in the population model. The likelihood

172 functions, which are specified independently for every data type, describe the probability of an

173 observed outcome (i.e., the data) conditional on particular parameter values. For example,

174 capture-recapture data can be analyzed using Cormack-Jolly-Seber models, which generally

175 utilize a multinomial likelihood to estimate survival and capture probabilities (Lebreton *et al.*

176 1992; Kéry & Schaub 2012; Schaub *et al.* 2015). A state-space likelihood, one in which the true

177 demographic process is modeled separately from the observation process, is often used for time-

178 series data types (e.g., count data) and can be specified using random sampling noise (de Valpine

179 & Hastings 2000) or through known sampling processes (e.g., imperfect detection; Péron *et al.*

180   2012). It is essential that the component likelihoods for the different data types have at least

181   some parameters in common (Fig. 1); this is the mechanism by which information is shared

182   across datasets in an IPM.

183   Finally, the joint likelihood of all datasets combined is specified, typically by multiplying

184   the individual component likelihoods defined in the second step. Thus, in addition to the

185   assumptions of each of the component likelihoods, an implicit assumption of IPMs is

186   independence among likelihoods and datasets (Mosnier *et al.* 2015; Weegman *et al.* 2016). In the

187   strictest sense, this implies that animals seen in one data type are not observed in other datasets,

188   although this rarely occurs in practice (Schaub & Abadi 2011). It is important to evaluate the

189   potential effects on parameter estimates if the independence assumption is violated. Lack of

190   independence among datasets can lead to overconfidence in parameter estimates in the form of

191   inflated precision. Abadi *et al.* (2010a) simulated data with varying levels of independence and

192   found that a lack of independence had minimal impacts on parameter accuracy in an IPM using

193   census, capture-recapture, and productivity data. Yet, this result may not hold true for every data

194   type combination and IPM structure. Recent IPM development has focused on approaches that

195   do not require independent datasets (Chandler & Clark 2014, Lee *et al.* 2015) and this remains an

196   area of active research.

197   Once the joint likelihood is specified, the IPM is analyzed to estimate parameter values.

198   The hierarchical structure of IPMs naturally lends them to Bayesian analysis (Lee *et al.* 2015),

199   although the joint likelihood can be analyzed using either frequentist (e.g., maximum likelihood)

200   or Bayesian frameworks (Schaub & Abadi 2011). Bayesian analysis has become a common

201   method for describing uncertainty in fisheries and wildlife management (Walsh *et al.* 2015) and

202   facilitates the inclusion of additional information in the form of prior distributions. Prior

9

203   distributions can be developed from previous studies on different populations or similar species,

204   as well as meta-analyses or expert opinion (Gelman *et al.* 2014; McCaffery & Lukacs 2016).

205   Using an IPM in a Bayesian framework allows for the most efficient use of the available data

206   and the best possible description of uncertainty, and is the most rigorous method for

207   incorporating parameter and demographic uncertainty in forward projections (Hoyle & Maunder

208   2004; Lee *et al.* 2015).

209

210   **4. Integrated population models as a tool for conservation**

211   To successfully manage populations for conservation purposes, it is necessary to track changes in

212   demographic parameters, identify vital rates having the greatest influence on population growth,

213   as well as determine the factors driving spatial and temporal variation in those key rates and

214   whether or not those relationships are stationary (Nichols *et al.* 2011, Shoemaker & Akçakaya

215   2015). IPMs are especially valuable in the study of declining or small populations because gains

216   in accuracy and parameter precision are most apparent in complex models with large numbers of

217   parameters, as is often the case for conservation-focused projects encompassing multiple

218   interacting threatening processes (Rhodes *et al.* 2011). Increased precision is especially

219   important in cases where the objective is to evaluate temporal patterns in parameter estimates

220   and/or detect significant population trends, including subtle declines (Abadi *et al.* 2010a). As

221   such, IPMs are well-suited for wildlife conservation research, providing a powerful tool for

222   holistic analyses on threatened populations, as exemplified by a number of recent applications

223   (Supplementary material: Table A1). Below we discuss a number of conceptual and practical

224   advances made possible through the development of IPMs.

225

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 & Collopy 2012; 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 & 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

249   (Abadi *et al.* 2010b). However, estimates of immigration can also reflect any systematic biases in

250   other vital rates and should be interpreted with caution when explicit data on movement are

251   unavailable. Parametrizing an IPM such that the number of immigrants is a random number

252   (centered on an expected mean value) rather than as a rate (dependent on population size, which

253   can lead to unrealistically high estimates) may help with estimating immigration, particularly in

254   small populations (Schaub & Fletcher 2015). Assessing the amount of immigration into a

255   population can help identify whether a local population is a sink and how it might be managed

256   effectively. For example, Schaub *et al.* (2010) found that a population survey of eagle owls

257   (*Bubo bubo*) indicated that abundance was stable. However, using an IPM that combined the

258   survey data with data from radio-tracking, age-at-death, and productivity, the authors found that

259   the population was actually a sink, highly dependent on immigration for stability. Additional

260   studies have demonstrated a similar contribution of immigration to population stability and

261   temporal variation in population growth (Schaub *et al.* 2010; Brown & Collopy 2013; Schaub *et*

262   *al.* 2013; Altwegg *et al.* 2014; Tempel & Gutiérrez 2014), whereas other populations of

263   conservation concern are growing or maintaining stability without reliance on high immigration

264   rates (Demerdzhiev *et al.* 2015).

265   Extending IPMs to multi-state systems (e.g., multiple sites, disease states, breeding

266   conditions) can provide a more precise and nuanced understanding of results by enabling

267   inference on patterns of condition-dependent demographic rate parameters. In particular, multi-

268   site IPMs allow for estimation of dispersal at the landscape level, yet capture-recapture data need

269   only be collected at a subset of sites within the species' range (McCrea *et al.* 2010; Péron *et al.*

270   2010). This advancement has important implications for determining the optimal spatial scale for

271   conservation; understanding temporary emigration; and identifying locations with the highest

272   reproductive success and/or survival, information that can be used to prioritize locations for

273   management interventions.

274

275   *4.2. Population synchrony within metapopulations*

276   Population synchrony, or coincident changes in the size of local populations, is a common

277   ecological phenomenon exhibited by many taxa including insects, molluscs, birds, amphibians,

278   and mammals (reviewed by Liebhold *et al*. 2004). Synchronous dynamics over a species' range

279   can be critical in conservation as it increases the extinction risk of spatially structured

280   populations (Harrison & Quinn 1989). However, little is known about the relative effects of

281   demographic rates on synchrony because of difficulties obtaining data, estimating rates

282   independently for all populations, and making spatial comparisons (Jorgensen *et al.* 2016). An

283   IPM framework is particularly advantageous for analyzing data from geographically-distinct

284   populations because it is possible to handle differing sampling protocols and survey periods

285   among sites (Schaub *et al.* 2015), enabling conservation management to scale from a single

286   population to an entire metapopulation or species. Using an IPM, relevant demographic rates

287   from all study areas within a metapopulation can be estimated concurrently by partitioning

288   sources of variation in population growth rates using covariates and random effects. In a

289   spatially-structured IPM of a barn swallow (*Hirundo rustica*) metapopulation, Schaub *et al.*

290   (2015) decomposed the variation in population growth and demographic rates into global and

291   local temporal components using random effects and examined population synchrony in

292   parameters using post-hoc correlations. It is also possible to assess synchrony by explicitly

293   estimating the variance and covariance structure in vital rates among local populations to make

294   inferences on correlations directly within a model (Péron & Koons 2012). Determining both the

295 degree and causes (e.g., specific environmental and/or demographic drivers) of synchrony within

296 metapopulations provides an opportunity to adjust management strategies accordingly. Recent

297 IPM developments have expanded these approaches to a multi-species context, facilitating

298 enhanced understanding of how changing community dynamics, and synchrony among species,

299 may impact a target species (Lahoz-Monfort *et al.* 2017). Methodological approaches for

300 quantifying synchronous patterns in population parameters fill a significant knowledge gap in

301 understanding how metapopulations react to long-term changes in the environment and can be

302 used to improve predictions of future environmental scenarios.

303

304 *4.3. Density effects on population dynamics*

305 Accurate understanding of how populations are regulated often requires evaluation of the effect

306 of density on different age or stage classes. Density dependence is an important ecological

307 concept and determining how it operates is crucial to evaluating how populations persist in

308 complex ecological systems and to developing effective management plans (Stubbs 1997).

309 Despite numerous methods for studying density dependence in wild populations (reviewed in

310 Lebreton & Gimenez 2013), many approaches do not assess the effect of density on multiple

311 demographic parameters simultaneously while accounting for errors incurred during the

312 sampling process. The state-space framework within IPMs can overcome this shortcoming

313 whereby the effects of density can be incorporated on individual parameters - not just on

314 population growth - while simultaneously accounting for uncertainty in the data due to

315 stochasticity and detection biases (Gamelon *et al.* 2016). The additional data included in the

316 model as a result of the IPM approach allow these parameters to become identifiable. Abadi *et*

317 *al*. (2012) developed an IPM to assess of the effect of density dependence on demographic

14

318 parameters (and thus overall population growth rate) and revealed negative effects of density on

319 adult survival of red-backed shrikes (*Lanius collurio*). Model simulations demonstrated

320 improved precision in estimates of density-dependent relationships as compared to a regression

321 model, providing a framework for understanding the mechanisms by which populations are

322 regulated. This approach could be further extended to assess non-linear density dependence,

323 delayed density dependence, Allee effects, as well as density dependence at the population level

324 using a derived population growth rate parameter.

325

326 *4.4. Data collection priorities*

327 The charismatic nature of many threatened species (e.g., birds of prey, top predatory taxa, iconic

328 migrants) leads to disproportionate attention and monitoring by different entities, including

329 professional researchers, public administrators, and volunteers (Tenan *et al.* 2012). In some

330 cases, spatially-extensive data, typically in the form of population counts (e.g., aerial surveys,

331 regional censuses), are collected by conservation organizations or government programs (e.g.,

332 North American Breeding Bird Survey) while independent researchers simultaneously collect

333 more intensive (but spatially-limited) data types, such as capture-recapture and productivity data.

334 The involvement of multiple stakeholders with differing goals and protocols can lead to a

335 relative wealth of data, albeit with heterogeneous data types. For instance, regional-scale count

336 surveys (e.g., lek counts) are frequently the most extensive information available for sage-grouse

337 (*Centrocercus minimus*, *C. urophasianus*), a threatened species in the western United States;

338 however, these data are minimally informative of vital rates and do not account for imperfect

339 detection during sampling (Walsh *et al.* 2004; Kelling *et al.* 2015). Recent data collection efforts

340 on the sage-grouse have consequently focused on obtaining intensive, short-term demographic

341   data, allowing for development of an IPM to rigorously estimate population growth rates as well

342   as survival and fecundity (Davis *et al.* 2014). IPMs compensate for diversity in data collection by

343   reducing biases inherent in a single dataset and providing more precise estimates of demographic

344   rates than can be obtained from separate analyses (Hoyle & Maunder 2004; Oppel *et al.* 2014;

345   Harris *et al.* 2015). Yet, the caliber of individual datasets ultimately determines the quality of

346   inference, and integrated modeling techniques cannot remove inherent biases within a dataset. As

347   with all analyses, careful consideration of sampling protocols, potential biases of data collection,

348   and *a priori* biological hypotheses are necessary for high quality inference within an IPM

349   framework.

350   From a management perspective, the incorporation of multiple data types into a single

351   analysis can reveal data collection priorities that would otherwise be unclear from separate

352   analyses. For example, if population estimates from an IPM are substantially different than those

353   from annual census data, it is possible that count data alone may be unreliable for obtaining

354   accurate population estimates because of missing information. In such cases, allocating resources

355   to the supplementary collection of individual-based demographic data (e.g., capture-recapture,

356   productivity, and/or telemetry data) would likely contribute to more precise estimation of

357   population trends and critical parameters compared to an exhaustive population census (Lee *et*

358   *al.* 2015). Coupling IPMs with simulations of several data types can help in the assessment of the

359   relative inferential value of different data sources, a useful exercise for evaluating potential

360   adjustments in field data collection efforts.

361

362   *4.5. Conservation efficacy*

363   IPMs can elucidate the efficacy of conservation actions relative to natural population processes.

364   Several studies have used IPMs to investigate the extent to which management actions (e.g., nest

365   box installation, predator control, supplementary feeding) have contributed to population

366   recovery through improvements in demographic rates (Altwegg *et al.* 2014; Demerdzhiev *et al.*

367   2015; Lieury *et al.* 2015). Distinguishing between various factors that contribute to population

368   change consequently allows for the prioritization of conservation actions. For example, Altwegg

369   *et al.* (2014) found through analysis of an IPM that immigration was the most important driver of

370   growth in an urban population of peregrine falcons (*Falco peregrinus*), more so than recruitment,

371   even with the aid of nest box deployment. These results revealed the critical importance of

372   protecting falcon populations in remote environments to the successful maintenance of the urban

373   population and the welfare of the species as a whole.

374

375   **5. Areas of advancement: extensions of integrated population models**

376   Initial IPM development within wildlife ecology focused on combining annual census data with

377   capture-recapture data (Besbeas *et al.* 2002; Brooks *et al.* 2004). Over the last decade, IPMs have

378   expanded to include many additional data types. Although the foundations of IPMs are well

379   developed, novel uses continue to spur technical advancements and expand their applicability

380   within ecology. Below we highlight several advancements that are particularly relevant for

381   conservation applications of IPMs.

382

383   *5.1. Retrospective and prospective analyses*

384   Estimates of demographic rates and population size and structure obtained from IPMs can be

385   used in subsequent analyses to gain a deeper understanding of the reasons for past population

386   changes (i.e., retrospective analyses; Szostek *et al.* 2014; Abadi *et al.* 2017) and to predict future

387   population trajectories (i.e., prospective analyses; Oppel *et al.* 2014). IPMs allow for correlation

388   assessment between annual estimates of demographic parameters with population growth rates to

389 quantify the impact of demography (Figure 3a&b; Schaub *et al.* 2013). The strength of the

390 correlation between population growth and demographic rates indicates the magnitude with

391 which temporal variation in a given demographic parameter contributes to the temporal variation

392 of population growth (Robinson *et al.* 2014; Schaub *et al.* 2013; Szostek *et al.* 2014; Tempel *et*

393 *al.* 2014). This approach is particularly useful in the study of populations that never reach a

394 stable steady state because of non-stationary environmental conditions, and can be combined

395 with formal methods for assessing transient dynamics (e.g., Koons *et al.* 2016, Koons *et al.*

396 2017). Evaluating the transient dynamics of populations is notoriously difficult, but it is

397 especially important for threatened species inhabiting areas that experience significant climate

398 and/or habitat changes (e.g., locations undergoing invasion; Ezard *et al.* 2010).

399 IPMs are particularly well-suited for enabling predictions of future population sizes

400 (Figure 3c&d). Analysis in a Bayesian framework aids predictions as posterior sampling can be

401 used to obtain a full assessment of all uncertainties involved in forecasts (Kéry & Schaub 2012;

402 Gelman *et al.* 2014; Servanty *et al.* 2014). The posterior distributions of the predicted future

403 population sizes can be used to compute population-level extinction probabilities or population

404 prediction intervals (i.e., intervals that include the projected unknown population size at a

405 specified future time with a given probability or confidence level), both typical components of

406 population viability analyses (Servanty *et al.* 2014). Model results generated from IPMs can be

407 adjusted to predict population sizes and extinction probabilities under different management

408 scenarios that may alter various demographic rates (Duarte *et al.* 2017, Saunders *et al.* In

409 review). In Figure 3d, we simulate results from an IPM of a hypothetical passerine population to

410 estimate changes in extinction probabilities under conditions that either increase productivity by

411 20% (e.g., through nest predation control) or reduce temporal variability in adult survival by

18

412   50% (e.g., through removal of competitors and/or primary predators), as compared to no

413   management (example and code taken from unpublished work by M. Schaub & M. Kéry).

414   Conducting this type of exercise helps identify the most practical strategy for maintaining

415   population persistence into the future.

416

417   *5.2. Spatially explicit IPMs*

418   Development of IPMs using spatially explicit capture-recapture data (Efford *et al.* 2009; Royle *et*

419   *al.* 2013) extends the utility of conventional IPMs by (1) accounting for spatial variation in

420   demographic, movement, and detection parameters and (2) enabling the ability to make spatially-

421   explicit predictions of abundance or vital rates (Chandler & Clark 2014). The basis of the

422   spatially explicit IPM is a spatial point process describing the number and locations of

423   individuals in a population during the initial time period, and the variation in abundance (and

424   density) over time as a function of death, recruitment, and movement (i.e.,

425   immigration/emigration). Both capture-recapture and survey (either count or detection-

426   nondetection) data can be modelled conditional on the point process (Chandler & Royle 2013;

427   Royle *et al.* 2013), thus avoiding the conventional and restrictive requirement that these two

428   datasets be independent.

429   Like non-spatial IPMs, the spatially explicit IPM can account for process variation and

430   observer error when predicting population size under future environmental conditions. Unlike

431   classic IPMs, which are unable to account for individual heterogeneity in vital rates and

432   detection probability (Abadi *et al*. 2013), the spatially explicit IPM fully accommodates

433   spatially-induced individual heterogeneity in demographics and capture or detection

434   probabilities, increasing accuracy of parameter estimates and expanding the framework's utility

19

435 (Chandler & Clark 2014). The model provides a straightforward means of predicting abundance

436 or density in unsampled regions and time periods, and can be used to map and project species

437 distributions and vital rates at broad spatio-temporal scales. This spatial point process framework

438 avoids the problems associated with scaling up continuously-varying measures such as density or

439 movement, which can introduce bias in non-spatial models (Melbourne & Chesson 2005). These

440 advantages are particularly beneficial in conservation-related projects where logistical and

441 financial constraints frequently prevent survey coverage across a species' entire range (or over

442 long time periods), yet inference is required at a broad scale for range-wide management

443 decisions.

444

445 *5.3. Environmental uncertainty*

446 Uncertainty surrounding ecological responses to environmental factors should be incorporated

447 into population assessments as environmental stochasticity can play a significant role in the

448 viability of a population, particularly for threatened species (Kanno *et al.* 2015). Existing

449 demographic projection models assess the effects of future environmental conditions on

450 population trends, but often fail to rigorously integrate uncertainty around both demographic and

451 environmental processes (Crone *et al.* 2013; but see Gauthier *et al.* 2016). This can lead to

452 erroneous predictions, particularly if there is uncertainty about how future environmental

453 scenarios may affect demographic parameters (Coulson *et al.* 2001). Oppel *et al.* (2014)

454 developed an approach to incorporate environmental variation into IPMs to explicitly account for

455 both environmental and demographic stochasticity in a single modeling framework, providing a

456 comparatively more realistic assessment of population viability under unknown future

457 environmental conditions. The fundamental idea is to draw future values of environmental

458   variables from probability distributions to simulate environmental uncertainty (Heard *et al.* 2013)

459   and to then use the results in combination with IPM parameter estimates (and their full

460   uncertainties) to project population trends (Oppel *et al.* 2014). Although incorporating both

461   demographic and environmental stochasticity into models can result in considerable uncertainty

462   surrounding population projections (Jenouvrier 2013), the wider credible (or confidence)

463   intervals represent a more realistic assessment of future population viability.

464

465   *5.4. Two-sex IPMs*

466   Typical IPMs are female-based models (i.e., only female life history is specified for the state

467   process) that frequently do not account for mate availability, differing sex ratios, or polygamy

468   among individuals (Schaub & Abadi 2011; but see Véran & Lebreton 2008). Yet, two-sex

469   models are required when vital rates significantly differ between males and females, males are

470   the limiting sex in the population, or when life history characteristics vary by sex such that

471   modeling the dynamics of a single sex is inadequate (Gerber & White 2014; Shyu & Caswell

472   2016). Even in cases when demographic rates are similar between the two sexes, incorporating

473   data from males can lead to overall improved inference on female vital rates simply because of

474   the additional data (Péron & Koons 2012). Recent IPM advancements allow for the investigation

475   of population dynamics and quantification of cause-specific mortality rates in non-monogamous

476   species, enabling the use of IPMs in a new suite of mating systems (Tenan *et al.* 2016). In this

477   framework, the state process is specified using a two-sex population model, in which the annual

478   number of breeding individuals is determined by explicitly modeling the probability that males

479   and females breed (i.e., access to reproduction) as a function of the availability of opposite-sex

480   individuals (Jenouvrier *et al.* 2010). Many carnivores have polygamous mating systems and mate

481 availability can play an important role in population viability, especially when populations are

482 small (Gerber & White 2014). Large terrestrial carnivores are a highly endangered group of

483 species; the advent of the two-sex IPM extension, which contains a nonlinear mating function

484 (Tenan *et al.* 2016), offers an opportunity to expand the use of IPMs into a much broader set of

485 at-risk species.

486

487 *5.5. Technical advancements: goodness-of-fit assessments*

488 Goodness-of-fit evaluations for IPMs are typically either not conducted or they are done in an *ad*

489 *hoc* fashion (Abadi *et al.* 2010b; Schaub & Abadi 2011). A newly proposed approach, motivated

490 by Bayesian *p*-values and using calibrated simulation, offers the first potential evaluation

491 procedure of IPMs (Besbeas & Morgan 2014). For each component dataset, a discrepancy

492 measure determines whether the model fits the data well, or either over- or under-predicts the

493 outcome as compared to simulated data generated from the estimated model parameters.

494 Different goodness-of-fit discrepancy measures can be used to highlight various aspects of fit

495 and multiple discrepancy measures can be used in tandem to evaluate more complex integrated

496 models, such as one that includes density dependence on productivity (i.e., the productivity

497 parameter is related to population size through a threshold dependence). Besbeas & Morgan

498 (2014) illustrate the performance of their goodness-of-fit metric using capture-recapture data and

499 count data, assessing the utility of different discrepancy measures (e.g., Freeman-Tukey

500 discrepancy measure, Pearson chi-square statistic) for each data type. Their comprehensive

501 approach adopts a common evaluation procedure for all components of an IPM and establishes a

502 consistent criterion that researchers can use when conducting model selection. Model fit is

503 notoriously difficult to assess in hierarchical models and remains an area of active research

22

504 (Hooten & Hobbs 2015). For example, Carvalho *et al*. (2016) evaluated the efficacy of several

505 recently-proposed diagnostic tests (e.g., residuals analysis, catch-curve analysis) in identifying

506 model misspecification in both the observation and system dynamics components of integrated

507 stock assessments. The authors found that residual analyses were the best detector of

508 misspecification of the observation model while age-structured production models were best at

509 detecting misspecification of the system dynamics model (Carvalho et al. 2016). A similar

510 comparison of commonly-used diagnostic tests (e.g., Bayesian *p*-values) for IPM component

511 models could help identify appropriate methods for assessing both model fit and model selection

512 within IPMs.

513

514 **6. The future of integrated population models**

515 We foresee several potential avenues of IPM advancement related to the fields of ecology and

516 conservation science, which we highlight below while providing suggestions for future modeling

517 efforts.

518

519 *6.1. Inclusion of citizen science data*

520 IPMs have the potential to address complex conservation questions at unprecedented scales using

521 widely-collected volunteer data. Citizen science data are well-suited to integrated modeling

522 because their wide geographic distributions of volunteers can provide much richer datasets than

523 are typically available (Sauermann & Franzoni 2015), and the prevalence of these programs has

524 surged in the last few years (Pimm *et al*. 2014). The full potential of citizen science has yet to be

525 realized as the vast majority of such data have not been included in any research (Theobald *et al*.

526 2015). Problems due to variable effort over time, lack of random sampling, and informal

527 protocols continue to present challenges. Several statistical techniques have recently been

528   employed to account for these biases, especially methods that use random effects and

529   hierarchical structures (Fink *et al.* 2010; Sauer & Link 2011; Kelling *et al.* 2015; Barrows *et al.*

530   2016; Saunders *et al.* 2017). IPMs have the potential to advance these methods even further by

531   appropriately combining datasets while accounting for errors across multiple citizen science

532   programs. For example, the use of eBird detection-nondetection data

533   (www.ebird.org/content/ebird) or count data from the Breeding Bird Survey

534   (www.pwrc.usgs.gov/bbs/index.cfm) in an IPM framework (i.e., with local-scale capture-

535   recapture data) has the potential to reveal large-scale population trends, shifts in species niches,

536   and/or the varying importance of demographic processes across spatial and temporal scales

537   (Sauer & Link 2011; Sullivan *et al.* 2014). Ahrestani et al. (2016) recently used an IPM

538   framework to combine two broad-scale avian citizen science datasets (Breeding Bird Survey and

539   Monitoring Avian Productivity and Survivorship) to assess population trends and latent

540   recruitment of gray catbird (*Dumetella carolinensis*) and wood thrush (*Hylocichla mustelina*). It

541   is possible that other data types, including citizen-reported mortality data such as car collisions

542   with wildlife (RoadKill: www.adventurescience.org/ roadkill.html) and bird-window collisions

543   (Project BirdSafe: www.mn.audubon.org/project-birdsafe; Project Safe Flight:

544   www.nycaudubon.org/project-safe-flight), can be used in conjunction with planned surveys to

545   help inform population dynamics (Loss *et al.* 2015), although additional model development is

546   needed.

547

548   *6.2. Incorporation of unmarked data types into demographic estimates*

549   Capture-recapture or other "marked" data types (e.g., dead recovery data) are the typical sources

550   for demographic analyses (Lebreton *et al.* 1992). However, recently developed approaches for

551 modeling unmarked data within a population dynamics framework provide a promising avenue

552 for estimating parameters such as survival, fecundity, and even immigration from only count and

553 detection-nondetection data (Dail & Madsen 2011; Zipkin *et al.* 2014b; Rossman *et al.* 2016).

554 Time series data can be modeled according to a Markovian process whereby individuals remain

555 in the population through a stochastic survival process and are gained to the population either via

556 recruitment or immigration (Dail & Madsen 2011). A crucial feature of these data are repeated

557 observations at each step in the time series (i.e., repeated sampling during periods of closure),

558 which allow for estimation of the detection process separately from the underlying state process

559 (Royle 2004). Incorporating these new models for time series or census data within an IPM

560 framework would lead to greater accuracy and precision of demographic rates and population

561 trends (Zipkin *et al.* 2017). Stage-structured (Link *et al.* 2003) and seasonally segregated (Link

562 & Sauer 2007) count data are especially useful because they can allow for estimates of both

563 population abundance and demographic parameters, similar to those obtained from capture-

564 recapture data (Zipkin *et al.* 2014a, b). Many rare and/or threatened species have available only

565 limited capture-recapture data or none at all; the ability to estimate demographic parameters

566 using only unmarked data offers the potential to expand integrative modeling approaches to less

567 invasive and intensive sampling methodologies.

568

569 *6.3. Coupled population-environment modeling*

570 Integrated population modeling is an ideal analytical platform for coupled population-

571 environment models that are designed to project population trajectories under forecasts of future

572 conditions (e.g., climate, land-use changes). Although a growing number of studies have linked

573 climate-dependent demographic models to climate simulations (Jenouvrier *et al.* 2012; van der

574   Meer *et al.* 2016; Gauthier *et al.* 2016), this has not yet been done using IPMs, likely because

575   most population models are parameterized from a single dataset. Uncertainties in climate

576   modeling scenarios have been described extensively (Hawkins & Sutton 2009), but methods for

577   combining uncertainties from both climate and integrated models have not yet been attempted

578   (other than with random environmental noise, e.g., Oppel *et al.* 2014). Developing an approach

579   that links future environmental scenarios with integrated models is crucial to deriving accurate

580   projections of population change (Ehrlén & Morris 2015), and properly accounting for sources of

581   uncertainty and potential variation.

582

583   **7. Conclusions**

584   Monitoring the consequences of anthropogenic alterations is increasingly urgent as changing

585   environmental and climate conditions continue to modify the population dynamics of species

586   worldwide. Record species losses have hastened efforts to identify extinction risks and

587   ameliorate the ultimate causes of decline (Pimm *et al.* 2014), but methodological and statistical

588   advancements often lag behind the pace necessary to enact management decisions.

589   Characterizing population dynamics and trends at broad spatial scales can be challenging, as it is

590   difficult to measure all relevant parameters, and data on those that are measured may be

591   representative of only a sample of the population (Robinson *et al.* 2014). Yet the spatial and

592   temporal scope of ecological research and conservation efforts has expanded greatly over the last

593   few decades (e.g., Fink *et al.* 2010; Robinson *et al.* 2014; Loss *et al.* 2015), requiring ever more

594   efficient data collection and analytical methods. Collection of demographic data, which are

595   necessary to understand mechanistic changes in population dynamics, is complicated when the

596   population of conservation concern is rare, sparsely distributed, or includes life stages that are

597   difficult to observe in the field (Harris *et al.* 2015; Mosnier *et al.* 2015). The development of

598   IPMs and their recent application to threatened and declining populations overcomes many

599   drawbacks associated with classical modes of inference, and has advanced our ability to

600   investigate environmental and demographic drivers of population change as well as more

601   accurately estimate trends.

602   The key strength of IPMs is that each sub-model borrows information from other sub-

603   models, making use of all available data from a study system, leading to the best possible

604   inference on a target population (Schaub & Abadi 2011). Although IPMs can be complex and

605   beyond the expertise of some ecologists and conservation practitioners, the software for their

606   implementation is freely available (e.g., R, JAGS, BUGS, NIMBLE, Julia, C++, INLA, ADMB)

607   and example code for typical models can be found online (e.g., Kéry & Schaub 2012, Chapter

608   11). More user-friendly tutorials and how-to papers, especially within a Bayesian framework,

609   would enable a wider audience to become familiar with IPMs and their implementation. IPMs

610   should be broadly adopted for conservation-focused projects with multiple data sources,

611   including those with data types not typically incorporated (e.g., citizen science programs),

612   because IPMs can be used to better understand and detect population declines (Schaub *et al.*

613   2010; Mosnier *et al.* 2015), prioritize populations of conservation concern (Altwegg *et al.* 2014),

614   enhance monitoring schemes (Tempel *et al.* 2014), and adjust management strategies (Johnson *et*

615   *al.* 2010; Demerdzhiev *et al.* 2015). These capabilities are improving recovery for threatened and

616   declining species worldwide, and have the potential to continue to do so with further method

617   development and application.

618

619   **Acknowledgements**

27

629   **References**

630   Ahrestani, F.S., Saracco, J.F, Sauer, J.R., Pardieck, K. & Royle, J.A. (2016). An integrated

631   population model for bird monitoring in North America. *Ecol. Appl.,* doi: 10.1002/eap.1493.

632   Abadi, F., Barbraud, C. & Gimenez, O. (2017). Integrated population modeling reveals the

633   impact of climate on the survival of juvenile emperor penguins. *Global Change Biol.* 23,

634   1353-1359.

635   Abadi, F., Botha, A. & Altwegg, R. (2013). Revisiting the effect of capture heterogeneity on

636   survival estimates in capture-mark-recapture studies: does it matter? *PLoS One*, 8, e62636.

637   Abadi, F., Gimenez, O., Arlettaz, R. & Schaub, M. (2010a). An assessment of integrated

638   population models: bias, accuracy, and violation of the assumption of independence.

639   *Ecology,* 91, 7-14.

640   Abadi, F., Gimenez, O., Ullrich, B., Arlettaz, R. & Schaub, M. (2010b). Estimation of

641   immigration rate using integrated population models. *J. Appl. Ecol.,* 47, 393-400.

642   Abadi, F., Gimenez, O., Jakober, H., Stauber, W., Arlettaz, R. & Schaub, M. (2012). Estimating

643   the strength of density dependence in the presence of observation errors using integrated

644   population models. *Ecol. Modell.,* 242, 1-9.

645   Alroy, J. (2015). Current extinction rates of reptiles and amphibians. *Proc. Natl. Acad. Sci.*

646   *USA,* 112, 13003-13008.

647   Altwegg, R., Jenkins, A. & Abadi, F. (2014). Nestboxes and immigration drive the growth of an

648   urban peregrine falcon Falco peregrinus population. *Ibis,* 156, 107-115.

649   Baillie, S.R., Sutherland, W.J., Freeman, S.N., Gregory, R.D. & Paradis, E. (2000).

650   Consequences of large-scale processes for the conservation of bird populations. *J. Appl. Ecol.*

651   37, 88-102.

652 Barrows, C.W., Hoines, J., Vamstad, M.S., Murphy-Mariscal, M., Lalumiere, K. & Heintz, J.

653   (2016). Using citizen scientists to assess climate change shifts in desert reptile

654   communities. *Biol. Conserv.,* 195, 82-88.

655 Besbeas, P., Freeman, S.N., Morgan, B.J.T. & Catchpole, E.A. (2002). Integrating mark–

656   recapture–recovery and census data to estimate animal abundance and demographic

657   parameters. *Biometrics,* 58, 540-547.

658 Besbeas, P., Lebreton, J.D. & Morgan, B.J.T. (2003). The efficient integration of abundance and

659   demographic data. *Appl. Stat.* 52, 95-102.

660 Besbeas, P. & Morgan, B.J. (2014). Goodness-of-fit of integrated population models using

661   calibrated simulation. *Methods Ecol. Evol.,* 5, 1373-1382.

662 Brooks, S.P., King, R. & Morgan, B.J.T. (2004). A Bayesian approach to combining animal

663   abundance and demographic data. *Anim. Biodivers. Conserv.,* 27, 515-529.

664 Brown, J.L. & Collopy, M.W. (2013). Immigration stabilizes a population of threatened cavity-

665   nesting raptors despite possibility of nest box imprinting. *J. Avian Biol.,* 44, 141-148.

666 Buschke, F.T., Brendonck, L. & Vanschoenwinkel, B. (2015). Simple mechanistic models can

667   partially explain local but not range-wide co-occurrence of African mammals. *Global Ecol.*

668   *Biogeogr.,* 7, 762-773.

669 Cardinale, B.J., Duffy, E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, C., *et al*. (2012).

670   Biodiversity loss and its impact on humanity. *Nature,* 486, 59-67.

671 Carvalho, F., Punt, A.E., Chang, Y.-J., Maunder, M.N. & Piner, K.R. (2016). Can diagnostic

672   tests help identify model misspecification in integrate stock assessments? *Fish. Res.* doi:

673   10.1016/j.fishres.2016.09.018.

674 Caswell, H. (2001). *Matrix population models*. John Wiley & Sons, Ltd.

675   Catchpole, E.A., Freeman, S.N., Morgan, B.J.T. & Harris, M.P. (1998). Integrated

676   recovery/recapture analysis. *Biometrics,* 54, 33-46.

677   Chandler, R.B. & Clark, J.D. (2014). Spatially explicit integrated population models. *Methods*

678   *Ecol. Evol.,* 5, 1351-1360.

679   Chandler, R.B. & Royle, J.A. (2013). Spatially explicit models for inference about density in

680   unmarked or partially marked populations. *Ann. Appl. Stat.,* 7, 936-954.

681   Coulson, T., Mace, G.M., Hudson, E. & Possingham, H. (2001). The use and abuse of population

682   viability analysis. *Trends Ecol. Evol.,* 16, 219-221.

683   Crone, E.E., Ellis, M.M., Morris, W.F., Stanley, A., Bell, T., Bierzychudek, P., *et al.* (2013).

684   Ability of matrix models to explain the past and predict the future of plant populations.

685   *Conserv. Biol.,* 27, 968-978.

686   Dail, D. & Madsen, L. (2011). Models for estimating abundance from repeated counts of an open

687   metapopulation. *Biometrics,* 67, 577-587.

688   Davis, A.J., Hooten, M.B., Phillips, M.L. & Doherty Jr., P.F. (2014). An integrated modeling

689   approach to estimating Gunnison sage-grouse population dynamics: combining index and

690   demographic data. *Ecol. Evol.,* 4, 4247-4257.

691   Demerdzhiev, D., Stoychev, S., Dobrev, D., Spasov, S. & Oppel, S. (2015). Studying the

692   demographic drivers of an increasing Imperial Eagle population to inform conservation

693   management. *Biodivers. Conserv.,* 24, 627-639.

694   de Valpine, P. & Hastings, A. (2002). Fitting population models incorporating process noise and

695   observation error. *Ecol. Monogr.*, 72, 57-76.

696   Dorazio, R.M. (2014). Accounting for imperfect detection and survey bias in statistical analysis

697   of presence-only data. *Glob. Ecol. Biogeogr.* 23, 1472-1484.

31

698   Duarte, A., Pearl, C. A., Adams, M. J. and Peterson, J. T. (2017). A new parameterization for

699   integrated population models to document amphibian reintroductions. *Ecol Appl.*

700   doi:10.1002/eap.1564

701   Duarte, A., Weckerly, F.W., Schaub, M. & Hatfield, J.S. (2015). Estimating golden-cheeked

702   warbler immigration: implications for the spatial scale of conservation. *Anim. Conserv.,* 19,

703   66-74.

704   Edgar, G.J., Bates, A.E., Bird, T.J., Jones, A.H., Kininmonth, S., Stuart-Smith, R.D., *et al*.

705   (2016). New approaches to marine conservation through the scaling up of ecological data.

706   *Ann. Rev. Mar. Sci.,* 8, 435-461.

707   Efford, M.G., Borchers, D.L., & Byrom, A.E. (2009). Density estimation by spatially explicit

708   capture–recapture: likelihood-based methods. In *Modeling demographic processes in marked*

709   *populations* (pp. 255-269). Springer US.

710   Ehrlén, J. & Morris, W.F. (2015). Predicting changes in the distribution and abundance of

711   species under environmental change. *Ecol. Lett.,* 18, 303-314.

712   Ezard, T.H., Bullock, J.M., Dalgleish, H.J., Millon, A., Pelletier, F., Ozgul, A., & Koons, D.N.

713   (2010). Matrix models for a changeable world: the importance of transient dynamics in

714   population management. *J. of Appl. Ecol.*, 47, 515-523.

715   Fieberg, J.R., Shertzer, K.W., Conn, P.B., Noyce, K.V. & Garshelis, D.L. (2010). Integrated

716   population modeling of black bears in Minnesota: Implications for monitoring and

717   management. *PLoS ONE,* 5, e12114. doi:10.1371/journal.pone.0012114.

718   Fink, D., Hochachka, W.M., Zuckerberg, B., Winkler, D.W., Shaby, B., Arthur Muson, M., *et al*.

719   (2010). Spatiotemporal exploratory models for broad-scale survey data. *Ecol. Appl.,* 20,

720   2131-2147.

721 Fletcher, Robert J., McCleery, R.A., Greene, D.U. & Tye, C.A. (2016). Integrated models that

722   unite local and regional data reveal larger-scale environmental relationships and improve

723   predictions of species distributions. *Lands. Ecol.,* 31, 1369-1382.

724 Fournier, D. & Archibald, C.P. (1982). A general theory for analyzing catch at age data. *Can. J.*

725   *Fish. Aquat. Sci.* 39, 1195-1207.

726 Gamelon, M., Grøtan, V., Engen, S., Bjørkvoll, E., Visser, M.E. & Sæther, B-E. (2016). Density

727   dependence in an age-structured population of great tits: identifying the critical age classes.

728   *Ecology* 97, 2479-2490.

729 Gauthier, G. & Lebreton, J.-D. (2004). Population models for greater snow geese: a comparison

730   of different approaches to assess potential impacts of harvest. *Anim. Biodivers. Conserv.* 27,

731   503-514.

732 Gauthier, G., Péron, G., Lebreton, J.-D., Grenier, P. & van Oudenhove, L. (2016). Partitioning

733   prediction uncertainty in climate-dependent population models. *Proc. R. Soc. B.,*

734   DOI: 10.1098/rspb.2016.2353.

735 Gelman, A., Carlin, J.B., Stern, H.S. & Rubin, D.B. (2014). Bayesian Data Analysis, 3rd ed. Eds:

736   A. Gelman, J.B. Carlin, H.S. Stern, D.B. Dunson, A. Vehtari, and D.B. Rubin. Chapman &

737   Hall Press, Boca Raton, FL.

738 Gerber, L.R. & White, E.R. (2014). Two-sex matrix models in assessing population viability:

739   when do male dynamics matter? *J. Appl. Ecol.,* 51, 270-278.

740 Gould, W. R., & Nichols, J. D. (1998). Estimation of temporal variability of survival in animal

741   populations. *Ecology*, 79, 2531-2538.

742   Grace, J.B., Anderson, T.M., Seabloom, E.W., Borer, E.T., Adler, P.B., Harpole, W.S., *et al*.

743   (2016). Integrative modelling reveals mechanisms linking productivity and plant species

744   richness. *Nature*, 529, 390-393.

745   Guillera-Arroita, G., Lahoz-Monfort, J.J., MacKenzie, D.I., Wintle, B.A. & McCarthy, M.A.

746   (2014). Ignoring imperfect detection in biological surveys is dangerous: a response to 'fitting

747   and interpreting occupancy models'. *PLoS ONE*, *9*, e99571.

748   Harris, W.E., Combe, F.J. & Bird, S. (2015). Using integrated population modelling in

749   conservation monitoring: a case study in the common dormouse (*Muscardinus*

750   *avellanarius*). *Folia Zool.,* 64, 330-336.

751   Harrison, S. & Quinn, J.F. (1989). Correlated environments and the persistence of

752   metapopulations. *Oikos,* 56, 293-298.

753   Hawkins, E. & Sutton, R. (2009). The potential to narrow uncertainty in regional climate

754   predictions. *Bull. Am. Meteorol. Soc.,* 90, 1095-1107.

755   Heard, G.W., McCarthy, M.A., Scroggie, M.P., Baumgartner, J.B., Parris, K.M. & Burgman, M.

756   (2013). A Bayesian model of metapopulation viability, with application to an endangered

757   amphibian. *Divers. Distrib.,* 19, 555-566.

758   Hooten, M. B., & Hobbs, N. T. (2015). A guide to Bayesian model selection for ecologists. *Ecol.*

759   *Monogr.*, 85, 3-28.

760   Hostetler, J.A., Scott Sillett, T. & Marra, P.P. (2015). Full-annual-cycle population models for

761   migratory birds. *Auk,* 132, 433-449.

762   Hoyle, S.D. & Maunder, M.N. (2004). A Bayesian integrated population dynamics model to

763   analyze data for protected species. *Anim. Biodivers. Conserv.,* 27, 247-266.

764   Jenouvrier, S. (2013). Impacts of climate change on avian populations. *Glob. Change Biol.,* 19,

765   2036-2057.

766   Jenouvrier, S., Caswell, H., Barbraud, C. & Weimerskirch, H. (2010). Mating behavior,

767   population growth, and the operational sex ratio: a periodic two-sex model approach. *Amer.*

768   *Nat.,* 175, 739-752.

769   Jenouvrier, S., Holland, M., Stroeve, J., Barbraud, C., Weimerskirch, H., Serreze, M. *et al*.

770   (2012). Effects of climate change on an emperor penguin population: analysis of coupled

771   demographic and climate models. *Global Change Biol.,* 18, 2756-2770.

772   Johnson, H.E., Scott Mills, L., Wehausen, J.D. & Stephenson, T.R. (2010). Combining ground

773   count, telemetry, and mark–resight data to infer population dynamics in an endangered

774   species. *J. Appl. Ecol.,* 47, 1083-1093.

775   Jorgensen, J.C., Ward, E.J., Scheuerell, M.D., & Zabel, R.W. (2016). Assessing spatial

776   covariance among time series of abundance. *Ecol. Evol.*, 6, 2472-2485.

777   Kanno, Y., Letcher, B.H., Hitt, N.P., Boughton, D.A., Wofford, J.E.B. & Zipkin, E.F. (2015).

778   Seasonal weather patterns drive population vital rates and persistence in stream fish. *Glob.*

779   *Change Biol.,* 21, 1856-1870.

780   Kearney, M. & Porter, W. (2009). Mechanistic niche modelling: combining physiological and

781   spatial data to predict species' ranges. *Ecol. Lett.,* 12, 334-350.

782   Keith, S.A., Webb, T.J., Böhning-Gaese, K., Connolly, S.R., Dulvy, N.K., Eigenbrod, F., *et al.*

783   (2012). What is macroecology? *Biol. Lett.,* 8, 904-906.

784   Kelling, S., Fink, D., La Sorte, F.A., Johnston, A., Bruns, N.E. & Hochachka, W.M. (2015).

785   Taking a 'Big Data' approach to data quality in a citizen science project. *Ambio,* 44, 601-611.

786 Kéry, M., & Schaub, M. (2012). Bayesian population analysis using WinBUGS: a hierarchical

787   perspective. Academic Press.

788 Koons, D. N., Arnold, T. W. & Schaub, M. (2017). Understanding the demographic drivers of

789   realized population growth rates. *Ecol. Appl.* 10.1002/eap.1594.

790 Koons, D. N., Iles, D. T., Schaub, M. & Caswell, H. (2016). A life-history perspective on the

791   demographic drivers of structured population dynamics in changing environments. *Ecol.*

792   *Lett.*, 19, 1023–1031.

793 Lahoz-Monfort, J. J., Harris, M. P., Wanless, S., Freeman, S. N., & Morgan, B. J. (2017).

794   Bringing it all together: multi-species integrated population modelling of a breeding

795   community. *J. Agric. Biol. Environ. Stat.*, 22, 140-160.

796 Lebreton, J.-D., Burnham, K.P., Clobert, J. & Anderson, D.R. (1992). Modeling survival and

797   testing biological hypotheses using marked animals: a unified approach with case

798   studies. *Ecol. Monogr.,* 62, 67-118.

799 Lebreton, J.-D. & Gimenez, O. (2013). Detecting and estimating density dependence in wildlife

800   populations. *J. Wildl. Manag.,* 77, 12-23.

801 Lee, A.M., Bjørkvoll, E.M., Hansen, B.B., Albon, S.D., Stien, A., Sæther, B-E., *et al*. (2015). An

802   integrated population model for a long-lived ungulate: more efficient data use with Bayesian

803   methods. *Oikos,* 124, 806-816.

804 Lefcheck, J.S., Byrnes, J.E.K., Isbell, F., Gamfeldt, L., Griffin, J.N., Eisenhauer, N., *et al*.

805   (2015). Biodiversity enhances ecosystem multifunctionality across trophic levels and

806   habitats. *Nat. Commun.,* 6, 6936-6942.

807 Liebhold, A., Koenig, W.D. & Bjørnstad, O.N. (2004). Spatial synchrony in population

808   dynamics. *Annu. Rev. Ecol. Evol. Syst.* 35, 467-490.

809   Lieury, N., Gallardo, M., Ponchon, C., Besnard, A. & Millon, A. (2015). Relative contribution of

810   local demography and immigration in the recovery of a geographically-isolated population of

811   the endangered Egyptian vulture. *Biol. Conserv.,* 191, 349-356.

812   Link, W.A., Royle, J.A., & Hatfield, J.S. (2003). Demographic analysis from summaries of an

813   age-structured population. *Biometrics*, 59, 778-785.

814   Link, W.A., & Sauer, J.R. (2007). Seasonal components of avian population change: Joint

815   analysis of two large-scale monitoring programs. *Ecology*, 88, 49-55.

816   Lomba, A., Pellisier, L., Randin, C., Vicente, J., Moreira, F., Honrado, J., *et al*. (2010).

817   Overcoming the rare species modelling paradox: a novel hierarchical framework applied to

818   an Iberian endemic plant. *Biol. Conserv.,* 143, 2647-2657.

819   Loss, S.R., Loss, S.S., Will, T. & Marra, P.P. (2015). Linking place-based citizen science with

820   large-scale conservation research: A case study of bird-building collisions and the role of

821   professional scientists. *Biol. Conserv.,* 184, 439-445.

822   MacKenzie, D.I., Nichols, J.D., Seamans, M.E. & R.J. Gutiérrez. (2009). Modeling species

823   occurrence dynamics with multiple states and imperfect detection. *Ecology,* 90, 823-835.

824   Maunder, M.N. & Punt, A.E. (2013). A review of integrated analysis in fisheries stock

825   assessment. *Fish Res.* 142, 61-74.

826   McCaffery, R. & Lukacs, P. M. (2016). A generalized integrated population model to estimate

827   greater sage-grouse population dynamics. *Ecosphere,* 7:e01585. 10.1002/ecs2.1585.

828   McCrea, R.S., Morgan, J.T., Gimenez, O., Besbeas, P., Lebreton, J.-D. & Bregnballe, T. (2010).

829   Multi-site integrated population modelling. *JABES,* 15, 539-561.

830   Melbourne, B.A. & Chesson, P. (2005). Scaling up population dynamics: integrating theory and

831   data. *Oecologia,* 145, 178-186.

832   Melbourne, B.A. & Hastings, A. (2008). Extinction risk depends strongly on factors contributing

833   to stochasticity. *Nature*, 454, 100-103.

834   Mora, C., Aburto-Oropeza, O., Ayala Bocos, A., Ayotte, P.M., Banks, S., Bauman, A.G., *et al.*

835   (2011). Global human footprint on the linkage between biodiversity and ecosystem

836   functioning in reef fishes. *PLoS Biology,* 9:e1000606.

837   Mosnier, A., Doniol-Valcroze, T., Gosselin, J.-F., Lesage, V., Measures, L.N. & Hammill, M.O.

838   (2015). Insights into processes of population decline using an integrated population model:

839   The case of the St. Lawrence Estuary beluga (*Delphinapterus leucas*). *Ecol. Model.,* 314, 15-

840   31.

841   Nichols, J.D., Koneff, M.D., Heglund, P.J., Knutson, M.G., Seamans, M.E., Lyons, J.E., Morton,

842   J.M., Jones, M.T., Boomer, G.S. & Williams, B.K. (2011). Climate change, uncertainty, and

843   natural resource management. *The J. Wildl. Manage.*, 75, 6-18.

844   Nichols, J.D., Thomas, L., & Conn, P.B. (2009). Inferences about landbird abundance from

845   count data: recent advances and future directions. In *Modeling demographic processes in*

846   *marked populations* (pp. 201-235). Springer US.

847   Oppel, S., Hilton, G., Ratcliffe, N., Fenton, C., Daley, J., Gray, G., *et al*. (2014). Assessing

848   population viability while accounting for demographic and environmental

849   uncertainty. *Ecology,* 95, 1809-1818.

850   Pacifici, K., Reich, B.J., Miller, D.A., Gardner, B., Stauffer, G., Singh, S., McKerrow, A. and

851   Collazo, J.A. (2017) Integrating multiple data sources in species distribution modeling: a

852   framework for data fusion. *Ecology*, 98, 840-850.

853   Pardikes, N.A., Shapiro, A.M., Dyer, L.A. & Forister, M.L. (2015). Global weather and local

854   butterflies: variable responses to a large-scale pattern along an elevational gradient. *Ecology,*

855   96, 2891-2901.

856   Péron, G., Crochet, P.-A., Doherty, P.F. & Lebreton, J.-D. (2010). Studying dispersal at the

857   landscape scale: efficient combination of population surveys and capture-recapture data.

858   *Ecology,* 91, 3365-3375.

859   Péron, G., & Koons, D. N. (2012). Integrated modeling of communities: parasitism, competition,

860   and demographic synchrony in sympatric ducks. *Ecology*, 93, 2456-2464.

861   Péron, G., Nicolai, C. A. & Koons, D. N. (2012). Demographic response to perturbations: the

862   role of compensatory density dependence in a North American duck under variable harvest

863   regulations and changing habitat. *J. Anim. Ecol.*, 81, 960–969.

864   Pimm, S.L., Jenkins, C.N., Abell, R., Brooks, T.M., Gittleman, J.L., Joppa, L.N., *et al*. (2014).

865   The biodiversity of species and their rates of extinction, distribution, and

866   protection. *Science,* 344, 1246752.

867   Platts, P.J., Garcia, R.A., Hof, C., Foden, W., Hansen, L.A., Rahbek, C., *et al*. (2014).

868   Conservation implications of omitting narrow-ranging taxa from species distribution models,

869   now and in the future. *Divers. Distrib.,* 20, 1307-1320.

870   Rhodes, J.R., Fei Ng, C., de Villiers, D.L., Preece, H.J., McAlpine, C.A. & Possingham, H.P.

871   (2011). Using integrated population modelling to quantify the implications of multiple

872   threatening processes for a rapidly declining population. *Biol. Conserv.,* 144, 1081-1088.

873   Robinson, R.A., Morrison, C.A. & Baillie, S.R. (2014). Integrating demographic data: towards a

874   framework for monitoring wildlife populations at large spatial scales. *Methods Ecol. Evol.,* 5,

875   1361-1372.

876   Rossman R., Yackulic C., Saunders S.P., Reid J., Davis R., and Zipkin E.F. (2016). Dynamic *N-*

877   *occupancy* models: estimating demographic rates and local abundance from detection-

878   nondetection data. *Ecology*, 97, 3300-3307.

879   Royle, J.A. (2004). N-mixture models for estimating population size from spatially replicated

880   counts. *Biometrics*, 60, 108-115.

881   Royle, J.A., Chandler, R.B., Sollman, R. & Gardner, B. (2013). *Spatial capture-*

882   *recapture.* Academic Press, Oxford, United Kingdom.

883   Royle, J.A., Nichols, J.D. & Kéry, M. (2005). Modelling occurrence and abundance of species

884   when detection is imperfect. *Oikos,* 110, 353-359.

885   Ruiz-Gutiérrez V. & Zipkin, E.F. (2011). Detection biases yield misleading patterns of species

886   persistence and colonization in fragmented landscapes. *Ecosphere*, 2, art6 doi:10.1890/ES10-

887   00207.1.

888   Rushing, C.S., Ryder, T.B. & Marra, P.P. (2016). Quantifying drivers of population dynamics for

889   a migratory bird throughout the annual cycle. *Proc. Biol. Sci.,* 283, 10.1098/rspb.2015.2846.

890   Sauer, J.R. & Link, W.A. (2011). Analysis of the North American breeding bird survey using

891   hierarchical models. *Auk.* 128, 87-98.

892   Sauermann, H. & Franzoni, C. (2015). Crowd science user contribution patterns and their

893   implications. *Proc. Natl. Acad. Sci. USA,* 112, 679-684.

894   Saunders S.P., Cuthbert F.J., and Zipkin E.F. *In review*. Evaluating population viability and

895   efficacy of conservation management using integrated population models. *J. Appl. Ecol.*

896   Saunders S.P., Ries L., Oberhauser K.S., Thogmartin W.E., and Zipkin E.F. 2017. Local and

897   cross-seasonal effects of climate and land-use on migratory monarch butterflies. *Ecography,*

898   doi 10.1111/ecog.02719.

899   Schaub, M. & Abadi, F. (2011). Integrated population models: a novel analysis framework for

900   deeper insights into population dynamics. *J. Ornithol.,* 152, 227-237.

901   Schaub, M., Aebischer, A., Gimenez, O., Berger, S. & Arlettaz, R. (2010). Massive immigration

902   balances high anthropogenic mortality in a stable eagle owl population: Lessons for

903   conservation. *Biol. Conserv.,* 143, 1911-1918.

904   Schaub, M. & Fletcher, D. (2015). Estimating immigration using a Bayesian integrated

905   population model: choice of parameterization and priors. *Eviron. Ecol. Stat.,* 22, 535-549.

906   Schaub, M., Gimenez, O., Sierro, A. & Arlettaz, R. (2007). Use of integrated modeling to

907   enhance estimates of population dynamics obtained from limited data. *Conserv. Biol.,* 21,

908   945-955.

909   Schaub, M., Jakober, H. & Stauber, W. (2013). Strong contribution of immigration to local

910   population regulation: evidence from a migratory passerine. *Ecology,* 94, 1828-1838.

911   Schaub, M., von Hirschheydt, J. & Grüebler, M.U. (2015). Differential contribution of

912   demographic rate synchrony to population synchrony in barn swallows. *J. Anim. Ecol.,* 84,

913   1530-1541.

914   Servanty, S., Converse, S.J., & Bailey, L.L. (2014). Demography of a reintroduced population:

915   moving toward management models for an endangered species, the whooping crane. *Ecol.*

916   *Appl.*, 24, 927-937.

917   Shoemaker, K.T. & Akçakaya, H.R. (2015). Inferring the nature of anthropogenic threats from

918   long-term abundance records. *Conserv. Biol.,* 29, 238-249.

919   Shyu, E. & Caswell, H. (2016). A demographic model for sex ratio evolution and the effects of

920   sex-biased offspring costs. *Ecol. Evol.,* 6, 1470-1492.

921   Sullivan, B.L., Aycrigg, J.L., Barry, J.H., Bonney, R.E., Bruns, N., Cooper, C.B., *et al.* (2014).

922   The eBird enterprise: an integrated approach to development and application of citizen

923   science. *Biol. Conserv.,* 169, 31-40.

924   Stubbs, M. (1977). Density dependence in the life-cycles of animals and its importance in K-and

925   r-strategies. *Jour. Anim. Ecol.*, 46, 677-688.

926   Szostek, K.L., Schaub, M. & Becker, P.H. (2014). Immigrants are attracted by local pre-breeders

927   and recruits in a seabird colony. *J. Anim. Ecol.,* 83, 1015-1024.

928   Taylor, B.L., Martinez, M., Gerrodette, T. & Barlow, J. (2007). Lessons from monitoring trends

929   in abundance of marine mammals. *Mar. Mamm. Sci.,* 23, 157-175.

930   Tempel, D.J., Peery, M.Z. & Gutiérrez, R.J. (2014). Using integrated population models to

931   improve conservation monitoring: California spotted owls as a case study. *Ecol. Model.,* 289,

932   86-95.

933   Tenan, S., Adrover, J., Navarro, A.M., Sergio, F. & Tavecchia, G. (2012). Demographic

934   consequences of poison-related mortality in a threatened bird of prey. *PLoS ONE,* 7, e49187.

935   Tenan, S., Iemma, A., Bragalanti, N., Pedrini, P., Barba, M., Randi, E., Groff, C. & Genovart, M.

936   (2016). Evaluating mortality rates with a novel integrated framework for nonmonogamous

937   species. *Conserv. Biol.*, 30, 1307-1319.

938   Theobald, E., Ettinger, A.K., Burgess, H.K., DeBey, L.B., Schmidt, N.R., Froehlich, H.E., *et al.*

939   (2015). Global change and local solutions: Tapping the unrealized potential of citizen science

940   for biodiversity research. *Biol. Conserv.,* 181, 236-244.

941   Thogmartin, W.E. & Knutson, M.G. (2007). Scaling local species-habitat relations to the larger

942   landscape with a hierarchical spatial count model. *Landscape Ecol.,* 22, 61-75.

943   Van der Meer, S., Jacquemyn, H., Carey, P.D. & Jongejans, E. (2016). Recent range expansion

944   of a terrestrial orchid corresponds with climate-driven variation in its population dynamics.

945   *Oecologia,* 181, 435-448.

946   Véran, S. & Lebreton, J. (2008). The potential of integrated modelling in conservation biology: a

947   case study of the black-footed albatross (*Phoebastria nigripes*). *Can. J. Stat.,* 36, 85-98.

948   Walsh, D.P., White, G.C., Remington, T.E. & Bowden, D.C. (2004). Evaluation of the lek-count

949   index for greater sage-grouse. *Wildl. Soc. Bull.,* 32, 56-68.

950   Walsh, D.P., Dreitz, V.J. & Heisey, D.M. (2015). Integrated survival analysis using an event-

951   time approach in a Bayesian framework. *Ecol. Evol.,* 5, 769-780.

952   Weegman, M.D., Bearhop, S., Fox, A.D., Hilton, G.M., Walsh, A.J., McDonald, J.L., *et al.*

953   (2015). Integrated population modelling reveals a perceived source to be a cryptic sink. *J.*

954   *Anim. Ecol.,* 85, 467-375.

955   Wilson, S., Gil-Weir, K.C., Clark, R.G., Robertson, G.J. & Bidwell, M.T. (2016). Integrated

956   population modeling to assess demographic variation and contributions to population growth

957   for endangered whooping cranes. *Biol. Conserv.,* 197, 1-7.

958   Zipkin, E.F., Sillett, T.S., Grant, E.H.C., Chandler, R.B., & Royle, J.A. (2014a). Inferences from

959   count data using multi-state population models: a comparison to capture-recapture

960   approaches. *Ecol. and Evol.*, 4, 417-426.

961   Zipkin, E.F., Thorson, J.T., See, K., Lynch, H.J., Campbell Grant, E.H., Kanno, Y., *et al.*

962   (2014b). Modeling structured population dynamics using data from unmarked individuals.

963   *Ecology,* 95, 22-29.

964   Zipkin, E.F., Rossman, S., Yackulic, C., Wiens, J.D., Thorson, J.T., Davis, R.J., and Grant,

965   E.H.C. (2017) Integrating count and detection/nondetection data to model population

966   dynamics. *Ecology*, 98, 1640-1650.

Figure Legends

968 **Figure 1.** Graphical depiction of a hypothetical integrated population model showing the

969 potential for different data sources to contribute to shared inference on demographic parameters

970 and population abundance. Four common types of population data are shown; all data types

971 shown are not required in an IPM and other data types can be incorporated. Demographic

972 parameters are represented with purple rectangles, observation parameters with green rectangles,

973 and data are symbolized with blue diamonds. Arrows demonstrate the dependences between

974 nodes. Sub-models are represented by dotted yellow rectangles and titled with the typical data

975 type and model structure. Node notations: n_a = number of adults assessed for reproduction, n_0 =

976 number of juveniles produced, f = per-capita recruitment rate, ω = immigration rate, s_1 = first-

977 year survival probability, s_j = juvenile survival probability (for individuals older than one), s_a =

978 adult survival probability, y = population count data, σ^2 = observation error on count data, N =

979 true population abundance, t = telemetry data, p_t = encounter rate for telemetry data, d =

980 recovery rate of dead individuals, m = capture-recapture data, p_m = capture probability for

981 marked individuals. Figure adapted from Schaub & Abadi 2011.

982

983 **Figure 2.** The process for developing an integrated population model for conservation

984 applications. IPMs jointly analyze data on population size and demographic parameters. A

985 variety of data input types can be used in IPMs, including (1) telemetry or radio-tracking data,

986 (2) productivity/fecundity data, (3) population survey/census data as collected through transects,

987 point counts, or ground counts, (4) dead recovery/carcass data, (5) occupancy (detection-

988 nondetection) data, and (6) capture-mark-recapture data as collected by tagging, banding, or

989 other external marking techniques (top panel). The modeling process includes (1) identifying the

990 relevant population model with the aid of a life cycle diagram, (2) determining the likelihoods

991 for individual datasets relative to the demographic rates identified with the population model and

992 the sampling processes, and (3) using the joint likelihood to estimate parameter values (middle

993 panel). Joint analysis of multiple datasets allows for more precise estimates of population

994 abundance and demographic rates, such as stage-specific survival and recruitment. Two outputs

995 of particular interest within a conservation context are estimation of immigration rate and trends

996 in population abundance (bottom panel).

997

998 **Figure 3.** Examples of possible (a & b) retrospective and (c & d) prospective analyses using

999 results from an integrated population model incorporating three simulated 20-year datasets (i.e.,

1000 population counts, capture-recapture, productivity) from a hypothetical red-backed shrike

1001 (*Lanius collurio*) population (male shown in inset). Post-hoc correlations (*r*) between annual

1002 population growth rates and IPM-generated estimates of (a) immigration rate and (b) adult

1003 survival are plotted to demonstrate retrospective analyses that can elucidate the contribution of

1004 demographic rates to variation in population growth (adapted from Schaub *et al.* 2013, Tempel &

1005 Gutiérrez 2014). IPM-generated population abundance can be projected forward for prospective

1006 analyses to examine (c) the distribution of the time to extinction (of simulated populations that

1007 went extinct), as well as (d) cumulative extinction probabilities under different management

1008 strategies (e.g., increase productivity by 20%, reduce temporal variability in adult survival by

1009 50% shown; example and code taken from unpublished work by M. Schaub & M. Kéry).
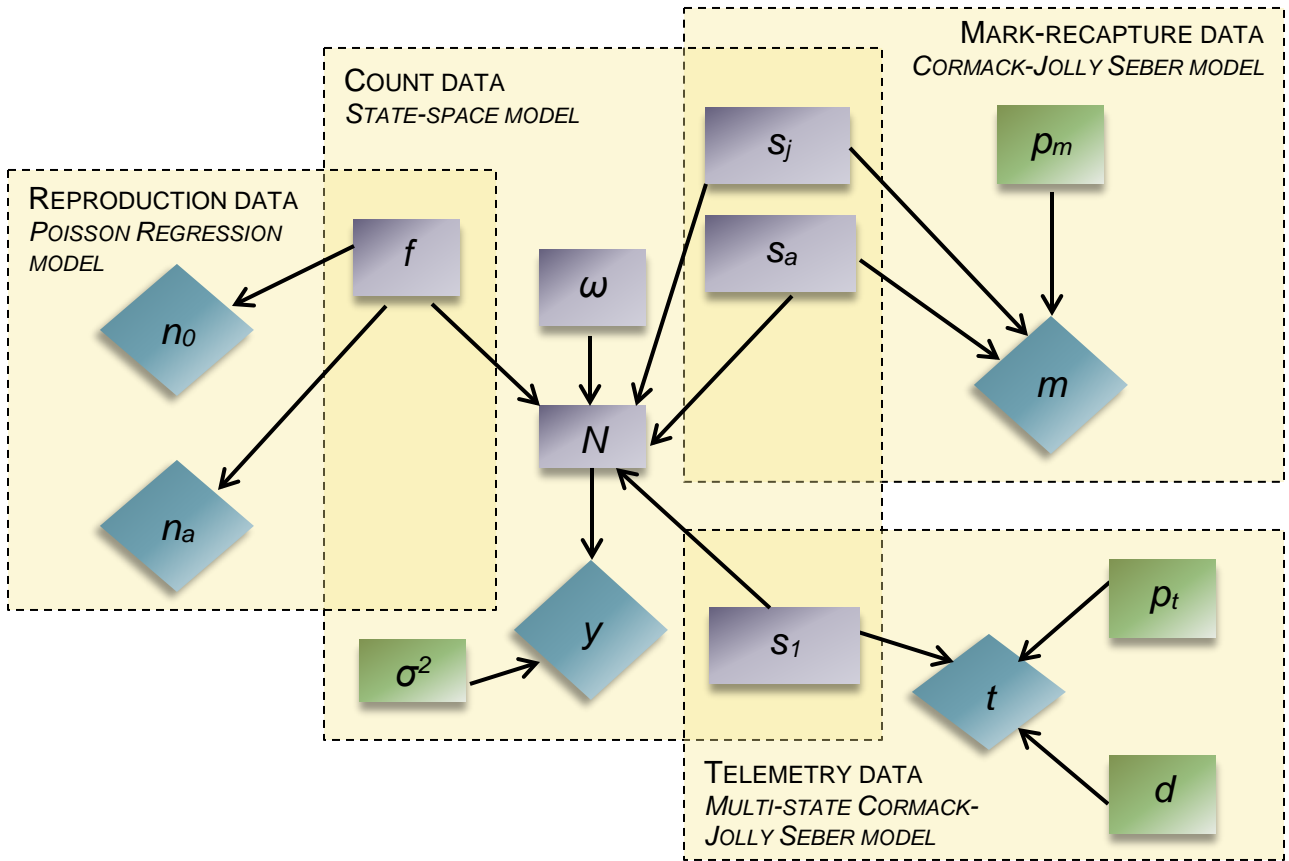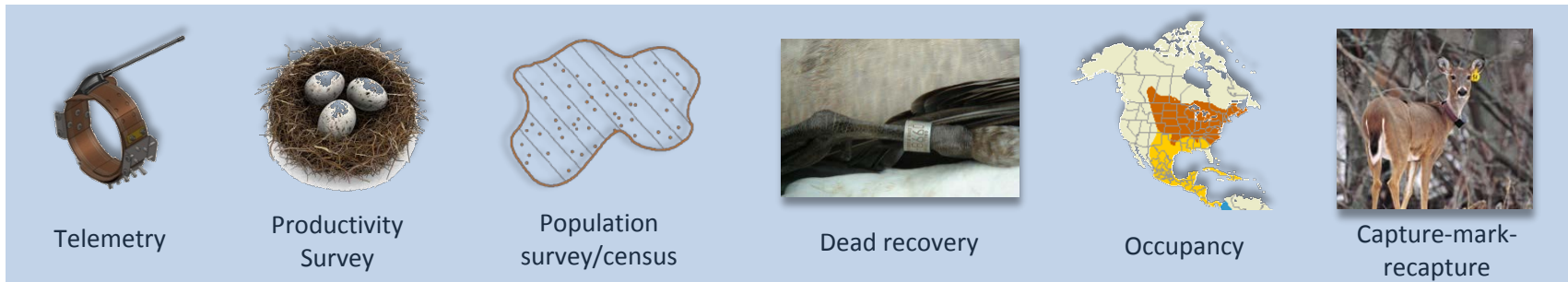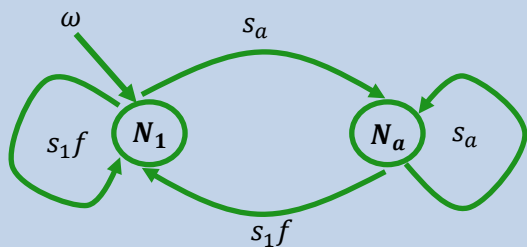
1010

Figure 1.

Figure 2.

Data input types:

| Telemetry | Productivity Survey | Population survey/census | Dead recovery | Occupancy | Capture-mark-recapture |

Steps in the modeling process:

Step 1: Specify the population model

ω s_a

$s_1 f$ N_1 N_a s_a

$s_1 f$

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

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

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

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

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

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

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

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:
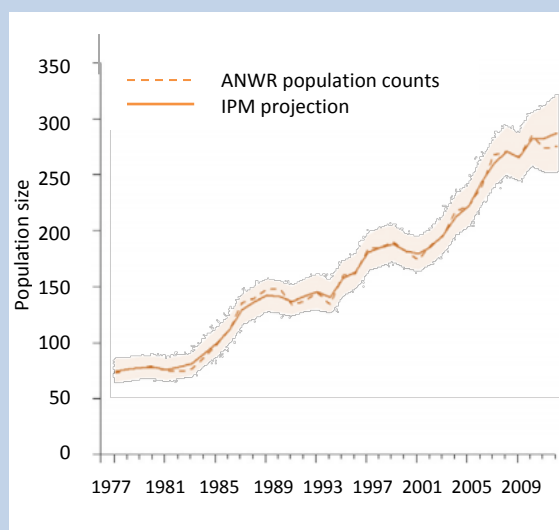
Two common IPM outputs sought for conservation: population size over time (left; figure based on whooping cranes from Wilson et al. 2016) and immigration rate (right; figure based on white-fronted geese from Weegman et al. 2016). Immigration is typically difficult to estimate and can rarely be inferred 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.
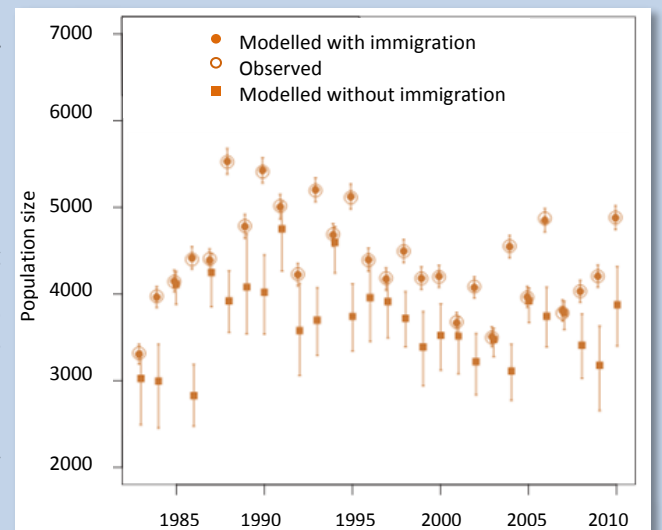
Left plot legend: ANWR population counts (dashed); IPM projection (solid). Y-axis: Population size (0–350). X-axis: 1977 1981 1985 1989 1993 1997 2001 2005 2009

Right plot legend: Modelled with immigration; Observed; Modelled without immigration. Y-axis: Population size (2000–7000). X-axis: 1985 1990 1995 2000 2005 2010

Figure 3.