BioOne COMPLETE

Full-annual-cycle population models for migratory birds

Authors: Hostetler, Jeffrey A., Sillett, T. Scott, and Marra, Peter P.

Source: The Auk, 132(2) : 433-449

Published By: American Ornithological Society

URL: https://doi.org/10.1642/AUK-14-211.1

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://bioone.org/journals/The-Auk on 29 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

The Auk
Ornithological Advances
www.aou.org

Volume 132, 2015, pp. 433–449
DOI: 10.1642/AUK-14-211.1

RESEARCH ARTICLE

Full-annual-cycle population models for migratory birds

Jeffrey A. Hostetler,[a]* T. Scott Sillett, and Peter P. Marra

Migratory Bird Center, Smithsonian Conservation Biology Institute, National Zoological Park, Washington, D.C., USA
[a] Current address: Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute, St. Petersburg, FL, USA
* Corresponding author: Jeffrey.Hostetler@myfwc.com

Submitted September 16, 2014; Accepted December 21, 2014; Published March 4, 2015

ABSTRACT

Full-annual-cycle (FAC) models integrate seasonal demographic and environmental processes to elucidate the factors that limit and regulate animal populations. Unlike traditional, breeding-season-focused models of migratory populations, FAC population models include the effects on population dynamics of events in both the breeding and the nonbreeding season (i.e. winter and migration). Given that migratory birds can spend most of the year away from the breeding grounds and face seasonally specific threats and limitation, FAC models can provide critical and unique insights about their population dynamics. We review existing FAC population model types, including demographic network models, seasonal matrix models, and individual-based models, with examples of each type. We also suggest some approaches new to FAC population modeling—integrated population models and integral projection models—and make recommendations for the development and implementation of these models. Incorporating model components such as density dependence, migratory connectivity (the demographic linkages between breeding and nonbreeding areas), and seasonal interactions can be critical for model realism but can also increase model complexity and development time. Much of the development of FAC population models has been more theoretical than applied. The main limitation to the application of the developed models is availability of empirical data for all annual stages, particularly knowledge of migratory connectivity and density-dependent seasonal survival. As these data become more available, the models outlined here should find additional uses.

Keywords: density dependence, full life-cycle, migratory connectivity, nonbreeding, population dynamics, population limitation, seasonal, vital rates

Modelos poblacionales de ciclo anual completo para aves migratorias

RESUMEN

Los modelos de ciclo anual completo (CAC) integran los procesos ambientales y demográficos estacionales para dilucidar los factores que limitan y regulan las poblaciones animales. A diferencia de los modelos tradicionales enfocados en la estación reproductiva de las poblaciones migrantes, los modelos poblacionales CAC incluyen los efectos de los eventos tanto de la estación reproductiva como no reproductiva (i.e. invierno y migración) en las dinámicas poblacionales. Dado que las aves migratorias pueden pasar la mayoría del año alejadas de las áreas reproductivas y enfrentar amenazas estacionales específicas y limitantes, los modelos CAC pueden aportar una visión crítica y única sobre sus dinámicas poblacionales. En este trabajo revisamos los tipos de modelos poblacionales CAC existentes, incluyendo modelos de redes demográficas, modelos matriciales estacionales y modelos basados en individuos, con ejemplos de cada tipo. También sugerimos algunos enfoques nuevos para el modelado poblacional CAC, para modelos poblacionales integrados y para modelos de proyección integral, y brindamos recomendaciones para el desarrollo y la implementación de estos modelos. La incorporación de componentes al modelo como la denso-dependiente, la conectividad migratoria (los vínculos demográficos entre las áreas reproductivas y no reproductivas) y las interacciones estacionales puede ser fundamental para el realismo de los modelos, pero también aumenta la complejidad de los modelos y su tiempo de desarrollo. Gran parte del desarrollo de los modelos poblacionales CAC ha sido más teórico que aplicado. La limitante principal para la aplicación de los modelos desarrollados es la disponibilidad de datos empíricos para todas las etapas anuales, particularmente del conocimiento de la conectividad migratoria y la supervivencia estacional denso-dependiente. A medida que estos datos se tornan más disponibles, los modelos delineados aquí deberían tener usos adicionales.

Palabras clave: ciclo de vida completo, conectividad migratoria, denso-dependencia, dinámica poblacional, estacional, limitación poblacional, no reproductiva, tasas vitales

© 2015 American Ornithologists' Union. ISSN 0004-8038, electronic ISSN 1938-4254
Direct all requests to reproduce journal content to the Central Ornithology Publication Office at aoucospubs@gmail.com

Downloaded From: https://bioone.org/journals/The-Auk on 29 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

INTRODUCTION

Many avian and other animal populations are migratory, making regular, seasonal movements, and therefore encounter different conditions and threats across seasons (Marra et al. 2011). For example, the Semipalmated Sandpiper (*Calidris pusilla*), a small shorebird, breeds in Arctic North America and spends its stationary nonbreeding season (hereafter "winter"; see Table 1) mostly in northern South America. This species may be declining as a result of winter hunting, declines in food availability during migration, and climate change on the breeding grounds, among other factors (Hitchcock and Gratto-Trevor 1997, Morrison et al. 2012). For logistical reasons, models used to understand the population dynamics of migratory birds or to make recommendations for their conservation have traditionally included data from only 1 season (generally the breeding season). However, demographic events in one season can affect population dynamics in subsequent seasons in ways impossible to predict from traditional 1-season population models, through carryover effects, density dependence, environmental change, and other factors in the other seasons (Sillett et al. 2000, Webster and Marra 2005, Calvert et al. 2009). Most population models have not included the full annual cycle because information about migratory connectivity (defined in Table 1; Webster et al. 2002) and published studies outside the breeding season (P. P. Marra personal observation) are lacking. As these data become more available, a review of the approaches available for full-annual-cycle (FAC) population modeling seems appropriate.

A population model is a mathematical model that is applied to the study of population dynamics, or how and why population abundances change over time and space (Table 1; Turchin 2003). We include models that only make inferences about population growth, but we exclude those that simply model occupancy dynamics (e.g., Taylor and Hall 2012) or only estimate individual demographic components of population growth, such as survival (e.g., Sillett and Holmes 2002, Gullett et al. 2014). We define an "FAC population model" as a model that includes the effects of events in both the breeding and the nonbreeding season (i.e. winter and migration) on the population dynamics of migratory animals. FAC population models can divide the annual cycle in different ways; for example, most but not all FAC population models separate migration and winter seasons, but only a few models of migratory birds explicitly model molting season. FAC population models are also sometimes referred to as "full-life-cycle" (FLC) population models. However, "FLC" more generally designates modeling all stages from birth to death for any organism, and we consider "FAC" a clearer term.

FAC population models can be used for both theoretical and applied questions. In general, population models are built for several reasons, including (1) to estimate population trends, (2) to estimate overall levels of population viability, (3) to estimate vulnerability to specific threats, (4) to understand the dynamics of biological invasions, (5) to determine what limits population growth, and (6) to recommend management actions (Morris and Doak 2002, Williams et al. 2002). FAC population models represent a way to express and test hypotheses on how events that occur at multiple stages of the annual cycle affect the dynamics of migratory populations. An FAC approach to both studying and conserving migratory birds is critical, but questions remain about the development of FAC population models.

There are many types of FAC population model, with different advantages, drawbacks, and data requirements. Despite their importance, there has never been a comprehensive review of the models available to ecologists. The purpose of the present review is to describe existing and potential modeling approaches for FAC inference, organized roughly in order of increasing model detail and/or complexity. For each model type, we discuss data requirements, response variables, examples when available, and assumptions, strengths, and limitations. This review is not meant to be exhaustive, but rather to highlight models of different types. The majority of the examples we present are from avian studies; however, we suggest that these models are critical for migratory animals of all taxa. We make modeling recommendations for different modeling and conservation goals and discuss the way forward.

MODEL TYPES

Single-season Count Models

Single-season count models examine the effects of the breeding and nonbreeding environments on changes in relative abundance in 1 of the 2 seasons. The data required are simply counts from 1 season (such as the North American Breeding Bird Survey), environmental data from >1 season, and migratory connectivity estimates (Figure 1A). Migratory connectivity estimates, which are generally the most difficult type of data to acquire, might not be needed if the environmental data being modeled apply to the whole range in the noncount season. However, applying environmental data from the entire noncount-season range (as opposed to data from where each counted population is actually going in the noncount season) will reduce the power of the analysis to detect the environmental effect in the noncount season.

Kölzsch et al. (2007) examined how density dependence in the breeding season and environmental factors in the breeding and nonbreeding seasons affected the population dynamics of a population of Great Snipes (*Gallinago media*) in central Norway using a raw-count (Figure 1B) stochastic Ricker-logistic population model. They found

Downloaded From: https://bioone.org/journals/The-Auk on 29 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

TABLE 1. Glossary.

Term	Definition
Carryover effects	Nonlethal events occurring in one season that influence individual performance in a subsequent season
Demographic stochasticity	Variation in population dynamics due to the sequence of birth and death of individuals
Density dependence	Change in vital rates with change in abundance or density
Environmental stochasticity	Change in vital rates over time due to random variation in the environment or other species
Full-annual-cycle (FAC) population model	Model that includes the effects of events in both breeding and nonbreeding seasons on population dynamics for migratory animals
Full-life-cycle (FLC) population model	Population model that includes all stages from birth to death
Individual-based model (IBM)	Population model that tracks individual organisms, not just numbers in categories or distributions of traits
Individual heterogeneity	Inherent, persistent differences between individuals of the same population and sex
Integral projection model	Generalization of matrix population models that allow 1 or more of the ways in which individuals are characterized to be continuous instead of categorical
Integrated population model	Single, unified analysis of population count data and demographic data that can be used for both estimating parameters and projecting populations
Link and Sauer model	A spatially hierarchical model for count data that estimates population trends and allows for observer effects and other nuisance variables
Matrix population model	A population model that projects numbers within a population in different ages, stages, or other categories through time, implemented with a matrix (a rectangular array of mathematical elements)
Migratory	Animal species or population that makes regular, directed seasonal movements
Migratory connectivity	The movement and mixing of individuals between summer and winter populations and stopover areas
Optimal annual routine (OAR) model	Optimality-based IBM that allow individual behavior to be predicted over the full annual cycle
Population	A group of organisms of the same species that live in the same region
Population dynamics	The study of how and why population abundances change over time and space
Population model	A mathematical model that is applied to the study of population dynamics
Season	A section of the year relevant to the population ecology of the migratory taxa in question (e.g., breeding, fall migration, winter, and spring migration)
Seasonal interactions	Any events occurring in one season that influence individual performance or density dependence in a subsequent season
Seasonal matrix population model	A matrix population model that projects populations within and between years through a series of seasonal matrices
State-space model	A hierarchical model with separate components for process (e.g., change in population abundance through time) and observation (conditional on process component)
Transient population dynamics	Short-term population dynamics, which can differ from long-term or asymptotic population dynamics due to environmental change or perturbations from stable population structure
Winter	The nonbreeding, nonmigratory season for the species in question

evidence of breeding-season density dependence and environmental effects on population dynamics, but no evidence of winter-season environmental effects. However, they did not include potential observation error in their model, although they provided some evidence that it was low and unlikely to have caused a spurious detection of density dependence. They also lacked direct information on where in Africa their breeding population wintered, which may be why they could not find evidence of winter-weather effects on the population.

Wilson et al. (2011) examined the effects of breeding season and winter weather on population trends in American Redstart (*Setophaga ruticilla*) using the Link and Sauer model (Table 1 and Figure 1D; Link and Sauer 2002). They used breeding-season count data, migratory connectivity estimates, and wintering and breeding weather data. They found winter-weather effects from the Caribbean on population trends of eastern breeding birds, but little evidence of breeding-weather effects or winter-weather effects in the west. The Link and Sauer model accounts for observation error in counts and for differences between observers.

Pasinelli et al. (2011) used stochastic Gompertz-logistic models in a state-space framework (Table 1 and Figure 1C; de Valpine and Hastings 2002) to examine the effects of breeding-population density dependence and of breeding,

Downloaded From: https://bioone.org/journals/The-Auk on 29 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

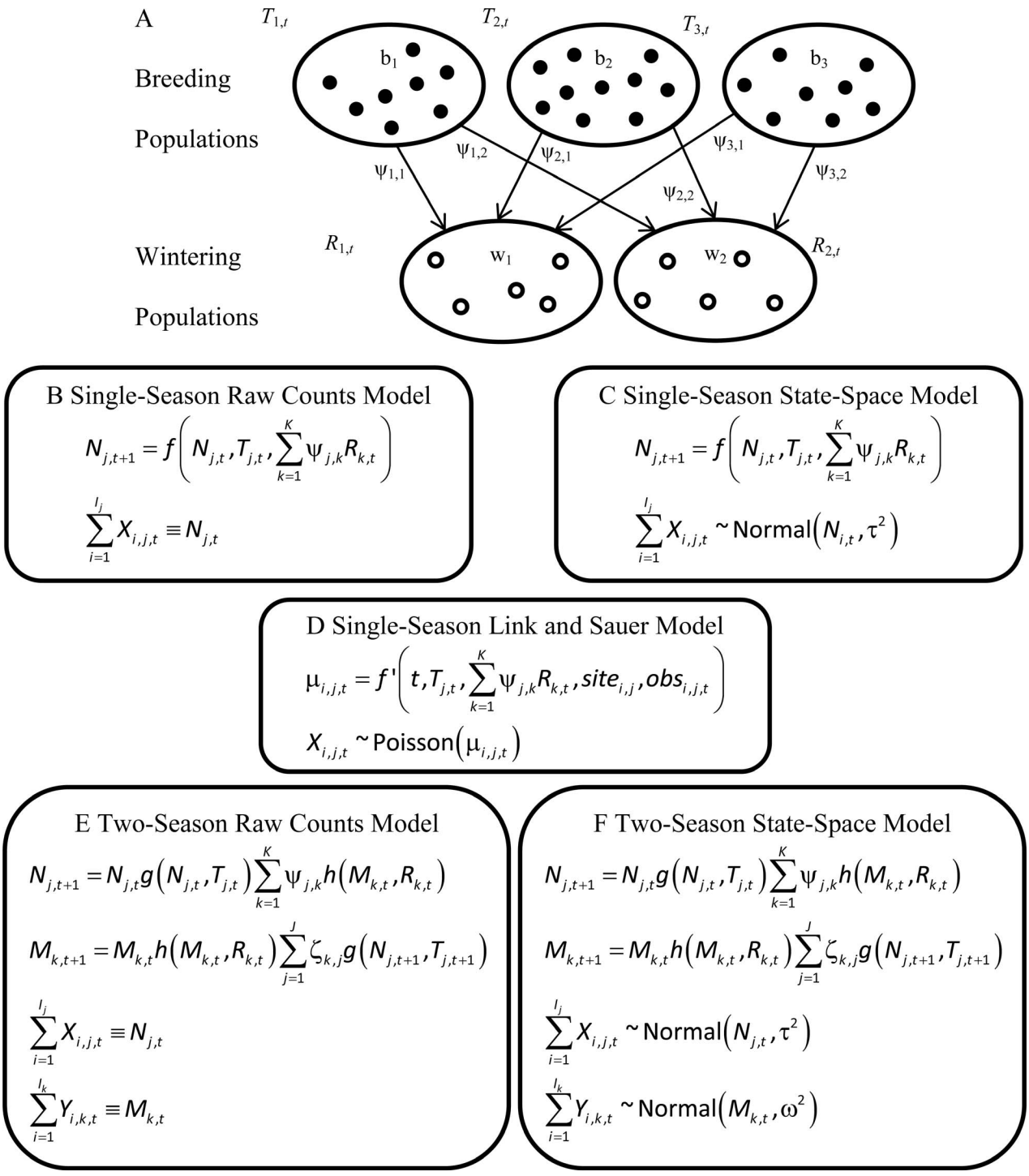


FIGURE 1. Map and equations for single-season and 2-season count models. (**A**) Example map of data collection and populations. In this example, there are 3 breeding populations (b_1, b_2, and b_3) and 2 wintering populations (w_1 and w_2) connected by migratory connectivity (i.e. $\psi_{j,k}$ is the proportion of birds from breeding population j that migrate to wintering population k). The population growth of birds from year t to year $t+1$ can be affected by the breeding-region temperature of that year ($T_{j,t}$) and the wintering region's rainfall of that year ($R_{k,t}$). Solid dots represent the beginning of the breeding-season count sites, and open circles represent the beginning of the winter-season count sites (used only in 2-season count models). (**B**) Equations for a single-season raw-count model, where the abundance of birds in breeding population j in year $t+1$, $N_{j,t+1}$, is a stochastic density-independent or -dependent function (f) of abundance in the previous year, breeding-season temperature, and winter-season rainfalls scaled by migratory connectivity. $X_{i,j,t}$ is the count of birds in site i within population j and year t (the total count from a breeding population is assumed

Downloaded From: https://bioone.org/journals/The-Auk on 29 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

wintering, and migratory staging-area environmental conditions on 6 populations of Red-backed Shrikes (*Lanius collurio*) breeding in Central Europe. They did not have data on migratory connectivity and, therefore, based fall, winter, and spring environmental conditions on the entire species range during those seasons. They found evidence of density dependence in all populations and evidence of fall or winter rainfall effects in 4 of the populations. State-space models also account for observation error.

The above 3 examples show that single-season count models can be formulated with raw counts (Kölzsch et al. 2007), Link and Sauer models (Wilson et al. 2011), or state-space models (Pasinelli et al. 2011). These methods differ in how they account for potential observer error. Models based on raw counts do not account for observation error and should generally be avoided with field data, especially because this biases estimates of density dependence and stochasticity (Staples et al. 2004, Freckleton et al. 2006). Both Link and Sauer models and state-space models account for observation error, but state-space models separate observation and population processes, allowing covariates to affect just one or the other. Traditional state-space models and Link and Sauer models provide estimates of an index of abundance, not true estimates of abundance, because they assume that false positive errors (overcounting) are about as likely as false negative errors (undercounting; Hostetler and Chandler 2015). Newer state-space models (Dail and Madsen 2011, Hostetler and Chandler 2015) overcome this problem by using a binomial model for detection probability. State-space models and raw-count models can include density dependence, but Link and Sauer models currently lack this process. However, Link and Sauer models provide a more developed, spatially hierarchical model of population trends than other models generally do.

Single-season count models generally cannot test hypotheses about the demographic mechanisms responsible for population dynamics, but they can be used to generate hypotheses. In addition, without individual-based data the models are perhaps more likely to get spurious effects. However, these models, especially in the state-space formulation, would be useful in a population viability analysis (PVA) framework to create a quantitative FAC climate vulnerability assessment, based on a priori hypotheses about how weather affects population dynamics (Small-Lorenz et al. 2013).

Two-season Count Models

If one has counts from 2 seasons, the models described above can be extended to allow for further insights. Link and Sauer (2007) described an extension of their hierarchical count model (Link and Sauer 2002) to account for 2 seasons of count data collected with different protocols. Although they applied this model to a nonmigratory species (and so used counts from the same locations), with good migratory connectivity estimates and counts from both breeding and wintering ranges, this model could be applied to examine seasonal changes in numbers in a migratory species. Betini et al. (2013, 2014) set up an experimental laboratory system of "migratory" populations with fruit flies (*Drosophila melanogaster*) and found evidence of density dependence in both breeding and nonbreeding seasons and carryover effects in both directions. Using a series of Ricker-logistic population models, they found that density dependence in both seasons and carryover effects both help stabilize population dynamics. Their laboratory setup enabled them to use raw counts without correcting for observation error (Figure 1E). Their model could be extended in a state-space framework to account for observation error in 2-season counts in natural migratory populations (Figure 1F).

Single-population Density-dependent Models

Single-population density-dependent models predict the equilibrium abundance of a migratory population in 2 seasons in response to habitat changes on both the breeding and wintering grounds (Sutherland 1996, 1998, Norris 2005, Sheehy et al. 2010). This class of FAC model requires estimates of density-dependent summer recruitment and winter mortality as well as habitat-change scenarios; optional inputs include effects of habitat quality on the density-independent component of summer

←

to be the abundance of that population in this model). (**C**) Equations for a single-season state-space model, which is identical to the single-season raw-count model, except that it accounts for variance in breeding-population counts around abundance (τ^2). (**D**) Equations for a single-season Link and Sauer model, where $\mu_{i,j,t}$ is the expected count in site i within population j and year t and is a stochastic density-independent function (f') of the weather covariates, year, the random effect of site ($site_{i,j}$), and the random effect of the count observer ($obs_{i,j,t}$). (**E**) Equations for a 2-season raw-count model, where g and h are functions for stochastic population growth rate over half the year (beginning of summer to beginning of winter and the reverse, respectively), $M_{k,t}$ is the abundance of wintering population k at the beginning of winter, $\zeta_{k,j}$ is the proportion of birds from wintering population k that migrate to breeding population j, and $Y_{i,k,t}$ is the count of birds in site i within wintering population k and year t. (**F**) Equations for a 2-season state-space model, which is identical to the 2-season raw-count model, except that it accounts for variance in breeding and wintering population counts around abundances (τ^2 and ω^2, respectively).

Downloaded From: https://bioone.org/journals/The-Auk on 29 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

recruitment and winter mortality, proportions and costs of habitats of different quality, and estimates of carryover effects between seasons. The original model (Sutherland 1996) can be used to predict the effects of breeding and wintering habitat loss on equilibrium abundance. Subsequent model extensions can account for carryover effects (Norris 2005, Norris and Taylor 2006, Sheehy et al. 2010) and habitats of different quality (Sutherland 1998, Norris 2005, Norris and Taylor 2006, Sheehy et al. 2010) and cost (Sheehy et al. 2010) for optimal conservation planning.

Sheehy et al. (2010) applied a single-population density-dependent model to the issue of where to purchase habitat for most effective conservation of the Hooded Warbler (*S. citrina*). Their model was parameterized with estimates of habitat quality and density dependence from the Hooded Warbler and the closely related Black-throated Blue Warbler (*S. caerulescens*) and of the costs of habitat in Belize and Ontario. When they incorporated habitats of different quality, the optimal strategy was to purchase only high-quality habitat from both seasons. A 4-season version of the model has also been developed (Sheehy et al. 2011).

Single-population density-dependent models are relatively simple to build, but with a key limitation: the assumption of a single population of animals. When applied to multiple breeding populations that winter in multiple areas, the implicit assumptions are that either migratory connectivity is weak and breeding dispersal is strong or that these processes do not have a strong effect on equilibrium abundance. Existing models in this category all assume that fecundity and winter mortality are both density dependent and that (adult) mortality is limited to the winter season. As presented in the literature, these models also do not account for stochasticity or transient dynamics. Transient dynamics (Table 1; Caswell 2007) could be relevant to the goal of evaluating the effects of changes in the amount and quality of habitat if habitat quantity and quality are continually changing (Dolman and Sutherland 1995). In this case, the migratory population might never reach an equilibrium abundance, because equilibrium abundance keeps changing.

Demographic Migratory Network Models

Demographic migratory network models generalize single-population density-dependent models to allow for multiple breeding and wintering populations (Sutherland and Dolman 1994, Dolman and Sutherland 1995, Taylor and Norris 2010). Breeding and wintering populations are linked through migratory connectivity, but connectivity is generally an output that arises from competition and migration costs rather than an input. Required inputs include estimates of density-dependent fecundity and winter survival parameters; optional inputs include distances between locations, migration mortality rates or food requirements, habitat quality of locations, carrying capacity of populations, how distances affect competitive ability, and habitat-loss scenarios. These models predict equilibrium abundance and migratory connectivity and the effects of habitat loss on the migratory connectivity, abundance, and population dynamics of multiple linked migratory populations.

Sutherland and Dolman (1994, Dolman and Sutherland 1995) developed models that allow for density dependence in multiple breeding and wintering populations for migratory vertebrates, and predicted patterns of migratory connectivity using evolutionarily stable strategies. They used their models to examine the effects of habitat loss on population size and migratory connectivity. They examined both equilibrium and dynamic properties of their models.

Taylor and Norris (2010) built on Sutherland and Dolman's framework using the terminology of graph theory, a branch of mathematics that concerns the pairwise interactions between objects. Each network contains breeding and wintering populations (or nodes) and migratory routes (or edges). The model incorporates migration mortality (distance dependent), breeding success (depends on node quality, density, and wintering population competitive ability), and winter mortality (depends on node quality, density, and the breeding population's competitive ability). It can be used to explore how changes in the number and arrangement of nodes affect total equilibrium population size and migratory connectivity, and how changes in the amount or quality of habitat in different nodes affect the same. James and Abbott (2014) used this model to explore how changes in migratory distance and breeding-season length would affect populations of migratory birds.

The Taylor and Norris (2010) model has been applied to migratory bat species (Wiederholt et al. 2013, Erickson et al. 2014). Wiederholt et al. (2013) applied the model to the Mexican free-tailed bat (*Tadarida brasiliensis mexicana*), which shows partial migration from the wintering grounds that varies by sex. Therefore, Wiederholt et al. extended the model to include 2 sexes and their differing effects on carrying capacity in winter and summer. They used their model to identify the most important breeding roosts and migratory roosts. Erickson et al. (2014) modeled the dynamics of bats in a theoretical landscape based on 2 species: the Indiana bat (*Myotis sodalis*) and the little brown bat (*M. lucifugus*). They extended the model to include age structure and relaxed the assumption that order of arrival affects competitive ability, because this seemed unlikely for colonially breeding bats. They found that after populations are disturbed from equilibria (because of factors such as disease or increased migration mortality), they may either be slow to return or move to alternative equilibria in ways that are difficult to predict.

Downloaded From: https://bioone.org/journals/The-Auk on 29 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Existing models in this category all assume that fecundity and winter mortality are both density dependent and that there is no adult mortality during the breeding season. Taylor and Norris (2010) assumed different density-dependent functions for fecundity and winter survival than Sutherland and Dolman (1994) did, and it could be informative to investigate how the choice of density-dependent function affects predictions by these models. In general, this is a powerful class of model, with many potential combinations with other classes of models, such as matrix and integrated population models.

The models of Martin et al. (2007) and Iwamura et al. (2013) could also be considered FAC network population models, and their goals are similar to those of the models in this section (determining optimal habitat preservation in the wintering range of American Redstarts and the effects of sea-level rise on stopover habitat for 10 Australasian shorebirds, respectively). However, they make very different assumptions: Migratory connectivity is fixed, and the size of a breeding population is controlled by habitat availability in the nonbreeding habitats it is connected to. Because there is no attempt to model density-dependent breeding success or winter survival, a model similar to these may be easier to parameterize than the demographic migratory-network models.

Annual Time-step Matrix Models

Animals within a population are not all identical demographically; at minimum, categorical factors such as age, stage, and sex can affect reproductive rates and survival probabilities. Matrix population models can incorporate the effects of these sources of demographic variation on population dynamics (Caswell 2001). Figure 2A shows a simple, 2-age-class life-cycle diagram and matrix model. The basic equation of matrix population projection is

$$\mathbf{N}_{t+1} = \mathbf{A}\mathbf{N}_t$$

where $\mathbf{A}$ is the population projection matrix and $\mathbf{N}_t$ is the vector of the number of animals in each stage or category at time t. These population projection models can equivalently be expressed as a set of difference equations instead of as a matrix equation; the key point is that they project age- or stage-structured populations forward from one year to the next.

Required inputs for an FAC annual time-step matrix population model are age- or stage-specific estimates of fecundity, annual survival probabilities, the effects of seasonal events on 1 or more of those vital rates, and starting population size. Estimates of migratory connectivity, density-dependent vital rates, and environmental stochasticity may also be incorporated. Matrix models could be used to estimate overall levels of vulnerability or viability; to estimate vulnerability to specific threats in breeding, wintering, or migratory seasons; to determine what limits populations; and to recommend management actions. They can be examined in either equilibrium or dynamic contexts.

Matrix models have been applied to a declining subspecies of Red Knot (*Calidris canutus rufa*) that feeds primarily on horseshoe crab (*Limulus polyphemus*) eggs during a critical spring migratory stopover in Delaware Bay (McGowan et al. 2011). Baker et al. (2004) hypothesized that the Red Knot decline is largely due to commercial harvest of horseshoe crabs in the mid-Atlantic. Early population models for Red Knots showed a declining population but did not explicitly tie this decline to horseshoe crab harvest (Baker et al. 2004). McGowan et al. (2011) developed matrix population models with annual time-steps for horseshoe crabs and Red Knots in Delaware Bay that link harvest type and limits to horseshoe crab abundance, horseshoe crab abundance to density of eggs available for Red Knot consumption, egg density to stopover weight gain by Red Knots, and Red Knot weight gain to annual adult survival and fecundity. They found that the trajectory of the Red Knot population and the effects of different harvest regimes were very sensitive to the choice of model for the effect of weight gain on annual survival, but that the model that most accurately predicted recent Red Knot population trajectories also predicted a large effect of horseshoe crab harvest on this population.

This example shows that annual time-step matrix models can account for carryover effects (Table 1) on fecundity explicitly; carryover effects on seasonal survival would be included implicitly, because only annual survival is included. The assumptions of annual time-step matrix models include no differences between animals in a category, and limitations include the difficulty of parameterization and not partitioning effects of survival by season. However, for density-independent models, the second limitation may not be important. Annual survival probability is simply the product of seasonal survival rates, and the elasticity, or proportional sensitivity, of the terms of a product are all identical. Therefore, in density-independent models, proportional changes in seasonal survival rates will all have the same effect. The next 4 model types are extensions of this model type that loosen these assumptions and limitations.

Seasonal Matrix Models

Most matrix models of wildlife populations have an annual time-step. However, seasonal or periodic matrix population models, which can be used to project population numbers and structure both within and between years (Figure 2B), have long been used in a variety of contexts (Skellam 1967, Caswell 2001). Such a model can be applied

Downloaded From: https://bioone.org/journals/The-Auk on 29 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

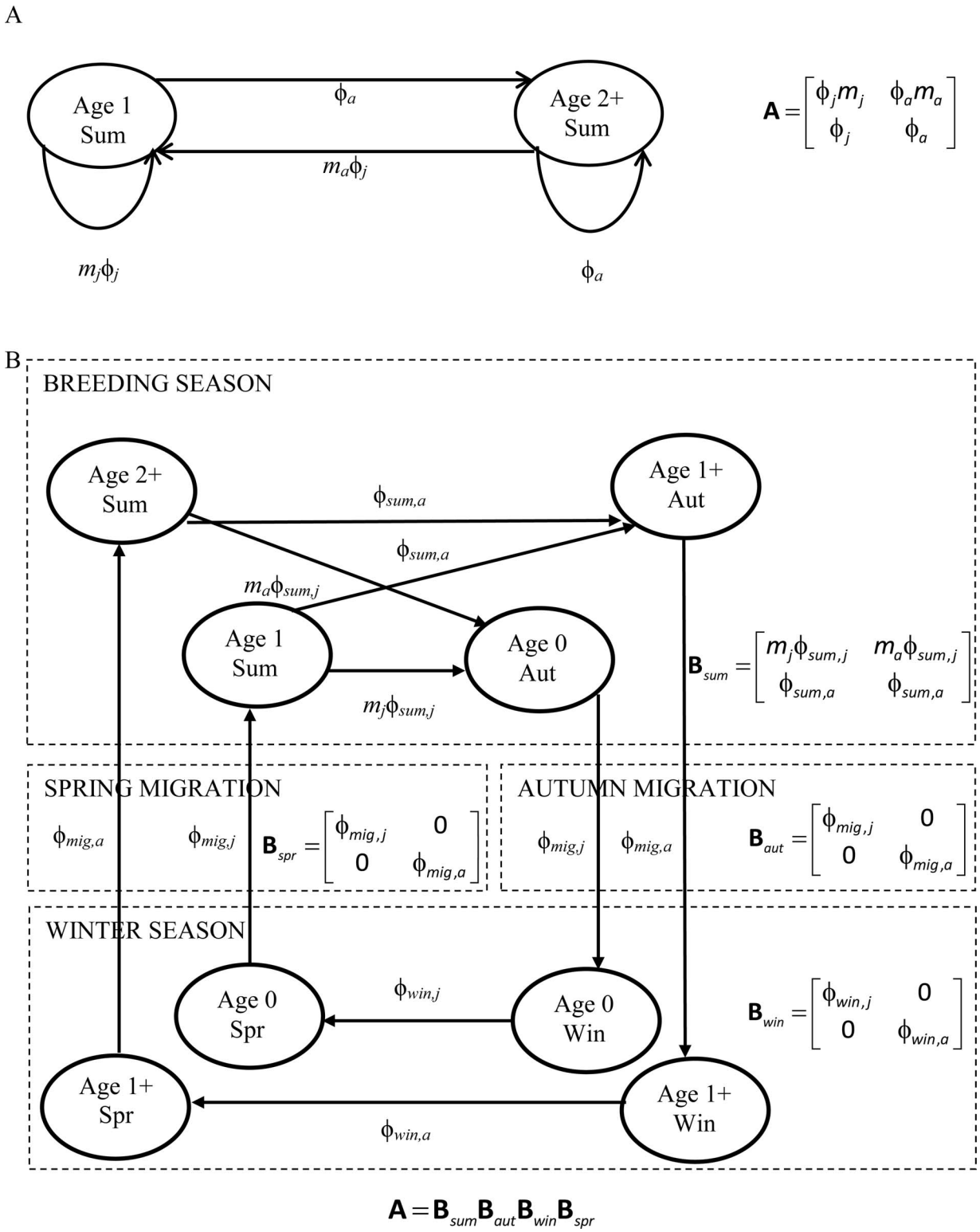


FIGURE 2. Life-cycle diagrams and equations for 2-stage, 1-sex (female) population-projection matrix models. (**A**) Annual time-step matrix model, with a prebreeding (beginning of summer) census. Age 1 females produce, on average, m_j female offspring, which survive to become age 1 females the next summer with probability ϕ_j. Age 2+ females produce, on average, m_a female offspring, which also survive to become age 1 females the next summer with probability ϕ_j. Age 1 and age 2+ females both survive to become or stay age 2+ the next summer with probability ϕ_a. **A** is the annual population projection matrix. To make this model full-annual-cycle, 1 or more of the vital rates should be affected by nonbreeding-season events. (**B**) Seasonal matrix model.

Downloaded From: https://bioone.org/journals/The-Auk on 29 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

to a migratory species, either in a relatively simple fashion (single breeding population, 1 sex, 2 age classes, density independent, and deterministic) or generalized to allow for more complexity using other well-established matrix-modeling approaches.

Required inputs for seasonal matrix population models are age- or stage-specific estimates of fecundity, seasonal survival probabilities, and starting population size. Depending on the model complexity, estimates of migratory connectivity, density-dependent vital rates, and deterministic or stochastic environmental effects on vital rates may also be required. Seasonal matrix models can be used in the same ways as annual time-step matrix models but can also break down the effects of survival on population growth by season. Seasonal matrix models also permit the modeling of migratory populations in which animals survive <1 yr and of density dependence in both the breeding and nonbreeding seasons. Seasonal matrix population models can be more difficult to parameterize than any of the previously discussed models.

Runge and Marra (2005) developed a seasonal matrix model to examine the effects of habitat limitation, sexual habitat segregation, and carryover effects (Table 1) in breeding and nonbreeding seasons on the equilibrium population sizes and sex ratios of a migratory bird species. Their exploration was mostly theoretical but was patterned and somewhat parameterized from data on American Redstarts. Instead of structuring the population by age or stage, they structured it on the basis of sex and habitat quality (poor and good habitats in the winter season; source and sink habitats in the breeding season). They found that habitat availability on both the breeding grounds and the wintering grounds, carryover effects, and sex ratio all strongly affect equilibrium population abundance.

Mattsson et al. (2012) developed a 2-sex, age-class-structured, density-dependent seasonal metapopulation model to determine the optimal habitat management to maximize sustainable harvest for the Northern Pintail (*Anas acuta*). They incorporated estimates and educated guesses of current abundances; migratory connectivity; survival dependent on sex, age class, and season; harvest rates; recruitment dependent on density and habitat conditions; and density-dependent emigration rates. They found that increasing the habitat quality for the Prairie Pothole breeding population increased carrying capacity and sustainable harvest rate more than the same habitat-quality increase for the Gulf Coast wintering population.

Flockhart et al. (2015) developed a stochastic, density-dependent seasonal matrix model to examine the drivers of monarch butterfly (*Danaus plexippus*) declines and model the population viability over the next 100 yr. They modeled 5 life stages, 3 breeding regions, and 1 winter region (Mexico) with a 1-mo time step. They used estimates from many sources on migratory connectivity, fecundity, adult breeding survival, overwinter survival, density-dependent larval survival, and pupal survival, as well as an expert-opinion survey for migratory survival; they allowed most vital rates to be stochastic. They tested the effects of 3 potential threats to monarch population viability: habitat loss in the breeding regions, habitat loss in the winter region, and extreme weather events in the winter region. Using simulations and transient elasticities of abundance (Caswell 2007), they found that habitat (milkweed) declines on the breeding grounds were the largest driver of declines and of the probability of quasi-extinction. Habitat loss and extreme weather events both increase the probability of mass mortality events during the winter; however, their model predicts that climate change will eventually remove the chance of the mass-mortality events.

The limitations and assumptions of seasonal matrix models are similar to those of annual time-step matrix models, except that they are generally more difficult to parameterize. The strengths of these models include that they can partition effects of survival by season. They can also explicitly account for carryover effects, although not mechanistically (e.g., through body condition; see below). We provide example R code for a seasonal matrix model in Supplemental Material Appendix S1.

Integrated Population Models

Integrated population models, an extension to matrix population models, can be easier to parameterize than those models (Besbeas et al. 2002, Brooks et al. 2004, Schaub and Abadi 2011). Integrated population modeling is a tool used for both estimating parameters and projecting populations. It is a unified analysis of population count data and demographic data, and an extension to state-space models (Table 1), which contain a model for the biological process and models for detection (e.g., counts). Integrated population models can be fit in either

←

Age 1 and age 2+ females both survive the summer with probability $\phi_{sum,a}$. Age 1 and age 2+ females produce m_j and m_a female offspring, respectively, which survive to become age 0 females at the beginning of autumn with probability $\phi_{sum,j}$. These individuals survive autumn migration with probability $\phi_{mig,j}$ to be age 0 at the beginning of winter; survive the winter with probability $\phi_{win,j}$ to be age 0 at the beginning of spring; then survive spring migration with probability $\phi_{mig,j}$ to be age 1 at the beginning of summer. Age 1+ females at the beginning of autumn similarly survive autumn migration with probability $\phi_{mig,a}$; survive the winter with probability $\phi_{win,a}$; then survive spring migration with probability $\phi_{mig,a}$ to be age 2+ at the beginning of summer. The annual population projection matrix **A** is the product of the seasonal matrices $\mathbf{B}_{sum}$, $\mathbf{B}_{aut}$, $\mathbf{B}_{win}$, and $\mathbf{B}_{spr}$.

Downloaded From: https://bioone.org/journals/The-Auk on 29 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

the classical (Besbeas et al. 2002) or the Bayesian statistical framework (Brooks et al. 2004), though the Bayesian framework is generally more flexible. These models are useful for including multiple sources of data, especially when individual sources of data considered alone would provide imprecise parameter estimates. In fact, when there are no data for a demographic parameter (e.g., immigration), but data for other parameters are of good quality, these models can be used to estimate the missing parameter (Abadi et al. 2010b). To our knowledge, however, no seasonal or FAC integrated population models have been published.

Like matrix models, integrated population models can be used to estimate overall levels of vulnerability or viability; to estimate vulnerability to specific threats in breeding, wintering, or migratory seasons; and to determine what limits populations and recommend management actions; and they can be examined in either equilibrium or dynamic contexts. Generally, an integrated population model requires both count data and individual-based demographic data, such as capture–mark–recapture and reproductive success, although a recently developed integrated population model requires only spatial capture–mark–recapture data (Chandler and Clark 2014). Ideally, for an FAC integrated population model, data would be available from multiple seasons. Potential weaknesses include time required for model design and programming, time and computer resources required to run models, and lack of adequate data. We provide example R and JAGS code for an integrated population model in Supplemental Material Appendix S2.

Integral Projection Models

Several of the model types described above can be used to model carryover effects on population dynamics (Runge and Marra 2005, Norris and Taylor 2006, Betini et al. 2013). Generally, they do this by keeping track of a previous season's habitat type or quality, and letting that have an effect on performance in the current season. However, a more mechanistic approach to modeling nonlethal carryover effects would keep track of a continuous variable such as body condition, mass, or arrival date (Harrison et al. 2011). This could be affected by factors such as habitat quality, population density, and environmental stochasticity and could change between seasons, depending on the costs of migration and other factors. This approach could be implemented either as an individual-based model (see next section) or as an integral projection model.

Integral projection models are a generalization of matrix population models that allow one or more of the ways in which individuals are characterized to be continuous instead of categorical (Easterling et al. 2000, Ozgul et al. 2010, Coulson 2012). Inputs for an FAC integral projection model based on body condition would be similar to those for an FAC matrix model but would also include estimates of the starting distribution of body conditions, the distribution of body conditions at birth, how body condition changes over the seasons (and in response to environmental conditions), and how body condition affects survival and reproduction. We know of no FAC integral projection models to date, although between-year carryover effects have been modeled with standard integral projection models (Kuss et al. 2008). An FAC implementation of the integral projection model has the potential to be very powerful but would be challenging to design, program, and parameterize.

Integral projection models, under the name "integro-difference models," were originally developed to treat space as continuous, rather than internal state or size (Kot et al. 1996, Neubert and Caswell 2000). Thus, they can be viewed as a generalization of metapopulation or network models, which divide space into discrete patches. These models allow dispersal and other vital rates to depend on position in space and have mostly been used to model the spread of invasive organisms. We know of no application of continuous-space integral projection models to migratory organisms, but they could be very useful where it is difficult to divide the breeding and winter ranges into discrete patches or populations.

Individual-based Models

Individual-based models (IBMs) track individual animals within a population, instead of tracking populations as numbers of animals within stages or simply as a distribution of a covariate. Survival, reproduction, and behavior can be functions of individual traits, time within the simulation, and (in spatially explicit models) location of the individual. Behavioral rules can either be empirically derived or based on optimality, although some authors restrict the term "IBM" to the former (Grimm and Railsback 2005). IBMs with optimality-based behavioral rules are often called "behavior-based models" (BBMs).

Piou and Prévost (2012) built an empirically derived IBM for the dynamics and evolution of an Atlantic salmon population (*Salmo salar*). Their model has 2 seasons, but with a daily time-step for many processes, such as survival. The model has 2 locations (a river and the Atlantic Ocean), allows for variable life-history strategies seen in this species, models both sexes, includes demographic and environmental stochasticity, and incorporates size- and age-dependent survival, migration, and reproduction. The authors subsequently used their model to examine the FAC climate vulnerability of this species (Piou and Prévost 2013). They tried different levels of 3 potential effects of climate change: river temperature increase, river flow increase, and reduced salmon growth in the ocean. They found that the latter 2 processes were likely to increase the

Downloaded From: https://bioone.org/journals/The-Auk on 29 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

probability of population extinction within the next 30 yr, but this was partially countervailed by the benefits of increased river temperature.

Pettifor et al. (2000) developed FAC BBMs for 2 migratory species: Barnacle Goose (*Branta leucopsis*) and Brant (*B. bernicla*). Their model is spatially explicit and game-theoretic (an optimization model that accounts for conflict and cooperation with other individuals), which allows the geese to compete for resources in the winter and on spring stopovers. The model also incorporates carry-over effects (winter–spring to breeding) based on energetic reserves, although in somewhat limited ways. For Barnacle Geese, an unspecified threshold of energy is required to breed, but that is the only effect of energy on breeding. For Brant, breeding productivity in successful years is a function of female body mass but at the population, not the individual, level. However, their spatially explicit, FAC approach allowed them to examine the relative population effects of habitat loss in different configurations and in winter habitat versus spring.

Optimal annual routine (OAR) models provide another way to set up an FAC BBM (Table 1; McNamara et al. 1998, Feró et al. 2008, McNamara and Houston 2008). They are especially effective for addressing issues of optimal timing of actions (such as migration and molt) within the annual cycle. They can be analyzed either to find the optimal strategy for an individual (assuming no feedback with other individuals of the population) or to find an evolutionarily stable strategy for a population (McNamara and Houston 2008). Although OAR models are generally used to address theoretical questions, Feró et al. (2008) showed that these models can be applied to conservation issues. They examined how theoretical example birds with different food peaks (and therefore different molt strategies) reacted to declines in food availability on their stopover locations.

The strength of IBMs is that their flexibility allows the modeler to address any subset of the goals of FAC population modeling. The weaknesses are that they are generally computationally intensive, very difficult to parameterize, and require time and expertise for model development. As a class of models, they include few if any inherent assumptions, although individual IBMs will include many assumptions.

POTENTIAL MODEL COMPONENTS

Model assumptions must be carefully considered (both within and between model categories) and should be guided primarily by which components (primarily model structure and processes) are of greatest importance or interest. To some extent, model components and assumptions are each other's opposites; for example, when density-dependent components are not included, the assumption is that the population behaves in a density-independent fashion. We do not mean to imply, from the following list of components, that complex FAC models are preferable to simple ones. Simple models are generally easier to parameterize, analyze, and present and can even outperform complex models in prediction (Ward et al. 2014). There is a tradeoff that must be considered for each modeling program between these issues and the greater realism of complex models.

Within-Population Processes

Density dependence. Density dependence represents the change in a per capita vital rate with a change in population density (Williams et al. 2002). Population models with density dependence typically reach a stable equilibrium abundance or carrying capacity (e.g., Sillett and Holmes 2005), although cycles, chaotic dynamics, and a stationary distribution of population densities (when stochasticity is also included) are also possible (Williams et al. 2002, Turchin 2003). Many population models are density-independent, because of the difficulty of estimating density-dependent vital rates or feedback and the ease of analyzing density-independent models. However, density dependence is likely ubiquitous and is key to population regulation and dynamics. Furthermore, one of the main purposes of developing FAC population models is to explore when and where migratory populations are limited, and this is not possible without including density dependence. Some of the model types discussed here (single-population, 2-season, and demographic network) are intrinsically density-dependent, and others can be so. However, empirical information on density can be lacking for 1 or more seasons, especially for species with a tendency toward within-season movement.

Vital rates decreasing with higher population densities are just one type of density dependence, sometimes known as "negative density dependence." Allee effects occur either when total individual fitness decreases as population abundances or densities decrease (demographic Allee effect) or when some aspect of fitness (such as probability of breeding) does so (component Allee effects; Courchamp et al. 1999, Stephens and Sutherland 1999, Stephens et al. 1999). Population processes that can cause Allee effects include difficulty finding mates at low densities, cooperative breeding or antipredator behavior, predator dilution, inbreeding depression, increased exploitation risk, and social thermoregulation, among others (Stephens et al. 1999, Berec et al. 2007). Allee effects can affect the spread of invasive species (Taylor and Hastings 2005) and, along with demographic stochasticity (see next section) and other factors, contribute to the "extinction vortex," whereby positive feedback pulls small populations closer and closer to extinction (Gilpin and Soulé 1986, Morris and Doak 2002, Fagan and Holmes 2006). We know of no

Downloaded From: https://bioone.org/journals/The-Auk on 29 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

FAC population models that have incorporated Allee effects, but, given their importance for extinction risk, we recommend their inclusion in FAC PVAs whenever there is good reason to believe they are present.

Stochasticity. Populations fluctuate in numbers over time for reasons that cannot be fully understood or predicted. Deterministic population models are easier to parameterize and analyze (Williams et al. 2002), but they ignore this uncertainty and do not estimate risk for populations, such as probability of extinction (Lande et al. 2003). Environmental stochasticity is change in vital rates (and therefore in population dynamics) over time due to random variation in the environment or other species. This refers to random fluctuations between years for a given season, not the more predictable differences between seasons within a year, and should not be modeled in the same manner (e.g., using periodic matrices; Caswell 2001). Morris and Doak (2002) recommended a minimum of 4–10 yr of field data to estimate environmental stochasticity and build a PVA based on it. Demographic stochasticity is variation in population dynamics due to the sequence of births and deaths of individuals and is most relevant at small population sizes (sometimes specified as either <20 individuals or <20 individuals stage^{-1}; Morris and Doak 2002). Fluctuation in sex ratio is also generally considered a type of demographic stochasticity; because it affects individual fitness, fluctuation in sex ratio can also be considered an Allee effect (Stephens et al. 1999). Demographic and environmental stochasticity and density dependence can be important determinants of population dynamics and viability (Hostetler et al. 2012). Some of the model types described here (single-population density-dependent and demographic migratory network models) have been explored only in a deterministic framework, but stochastic versions are possible.

Within-Population Structure

Age and stage. Individuals within a population of different ages or stages will generally have different vital rates. These differences can often affect population dynamics and may be of inherent interest to researchers and conservationists. Many avian population models have only 1 or 2 age classes (e.g., Bonnot et al. 2011, Rolland et al. 2011, Schaub et al. 2012), because of difficulties in precisely aging adult birds or as a result of minimal variation in demographic rates with age after the first year. There are other ways to classify individuals into stages other than age classes, such as body size and developmental stage.

Sex. Most population models either ignore the sex of individuals or model only 1 sex. This is generally appropriate when the abundance of the other sex does not limit the population, when external factors affect the sexes similarly, and when the sexes are not expected to compete for space or resources. Modeling reproduction can become far more complex in 2-sex models, depending on how the number of males affects the per female probability of reproduction (Caswell 2001:17). However, FAC population models of territorial species that show sexual habitat selection in the nonbreeding season should probably model both sexes (Runge and Marra 2005). There is empirical evidence that sexual segregation in some migratory birds can influence survival and lead to carryover effects (Marra et al. 1998, Marra and Holmes 2001).

Individual heterogeneity. Inherent, persistent differences between individuals of the same population and sex can be due to genetic, maternal, and/or spatiotemporal effects (Vindenes et al. 2008). This variation has been shown to be important for population dynamics (Conner and White 1999, Vindenes et al. 2008), although most population models ignore it. Among the FAC models reviewed here, only integral projection models and IBMs can incorporate individual heterogeneity. One of the reasons individual heterogeneity is seldom incorporated in population models is that its estimation requires long-term longitudinal data for many individuals. These data are more challenging to get in an FAC context for migratory animals because of the large distances involved.

Spatial configuration of habitat. The arrangement of habitat within a region can also be important for both population dynamics and management decisions (Pettifor et al. 2000). To examine this, spatially explicit models are required. We have discussed 2 types of models that can be spatially explicit in this sense: IBMs and integral projection models (with space as the continuous variable). Others exist (e.g., RAMAS GIS; Akçakaya and Root 2002), but not yet in an FAC context. Because of the additional complexity of spatially explicit IBMs, we recommend incorporating this component only when there is strong evidence that the configuration of habitat within a region affects demography.

Migratory and Interseasonal Processes

Migratory connectivity. Demographic linkages between breeding and nonbreeding areas can affect population size and dynamics (Webster et al. 2002, Webster and Marra 2005, Martin et al. 2007). Some model types, such as single-population 2-season models, do not incorporate migratory connectivity. For others, such as some of the matrix models, migratory connectivity estimates are an input (Iwamura et al. 2013, Flockhart et al. 2015). For demographic migratory network models, equilibrium migratory connectivity is an output of the model and is affected by the arrangement, size, and quality of nodes (Dolman and Sutherland 1995, Taylor and Norris 2010). Migratory connectivity should be included in FAC models of multiple populations whenever reasonable. In some

Downloaded From: https://bioone.org/journals/The-Auk on 29 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

cases, this is very simple. Species that are panmictic (weak connectivity) can be modeled as a single population; conversely, species that exhibit very strong geographic structure (strong connectivity) can have each population modeled separately.

Seasonal interactions and carryover effects. Carryover effects and other seasonal interactions (Table 1; Norris and Marra 2007, Harrison et al. 2011) appear to be pervasive for migratory populations (e.g., Marra et al. 1998, Inger et al. 2010; but see Senner et al. 2014). Carryover effects can have large effects on population dynamics (Runge and Marra 2005, Norris and Taylor 2006), although they can sometimes be safely ignored. For example, whether winter habitat quality affects either winter survival directly or spring migration survival probably does not matter if one is looking at the number of animals the next summer, because annual survival probability is the product of seasonal survival probabilities. However, when survival is estimated by season, ignoring carryover effects can lead to incorrect inference about the importance of seasonal environmental factors and density dependence. Several of the models described here incorporate 1 or more forms of carryover effect, but integral projection models and IBMs have the greatest potential for mechanistic modeling of these interseasonal processes.

Variable timing of events and behaviors. The timing of many biological events and behaviors can affect population dynamics. Spring arrival time is perhaps the best-studied phenological variable for migratory birds and has been shown to be an important predictor of reproductive success, especially for males (e.g., Møller 1994, Lozano et al. 1996). The models described here are mostly discrete-time models, although many of them have time-steps smaller than a year. Modeling within-season timing effects when the smallest time-step is a season becomes difficult. With integral projection models, one could treat departure and arrival dates as state variables. However, a more natural approach is probably to use an IBM with a daily or weekly time-step. OAR models look promising for these types of questions, especially in an evolutionary context, although the complexity of these models exceeds available data for most species.

Movement models. Some FAC population models explicitly model drivers of migratory movements (Feró et al. 2008, Taylor and Norris 2010). The outputs of these models can include the timing of migration (McNamara et al. 1998), where birds migrate (migratory connectivity; Sutherland and Dolman 1994), and even whether birds migrate (Taylor and Norris 2007). Most models of migratory movements implicitly assume either that migratory patterns will not change with changes in the environment or that they will rapidly change to the newly optimal pattern. In this, the model of Dolman and Sutherland (1995) stands out: They used a simple genetic model to explore the potential lag between habitat change and changes in migratory connectivity. Although their model is probably oversimplistic, we consider it a good starting point for developing more realistic models of how migratory behavior might change over time.

DISCUSSION

We have shown how several different types of population models have been used to explore FAC population dynamics. These models have only begun to explore the potential of FAC analyses. Several of the models that have been explored only in an equilibrium context, such as the single-population 2-season model, have an underlying dynamic model and could be extended to explore transient dynamics. There are also possibilities for combinations of model types. For example, Schaub and Abadi (2011) discussed the possibility of combining integrated population modeling with integral projection modeling. In the FAC context, such a model could be called an "integrated integral population projection and migration model," or $(IPM)^2$, and could allow using multiple data sources to help determine the effects of continuous variables such as mass on population dynamics throughout the annual cycle. Erickson et al. (2014) recently developed a model that combines demographic migratory network models with elements of seasonal matrix models.

Choosing which model type to use for an FAC population model should depend on (1) which components of the real-world system are of greatest importance or interest in producing the FAC population dynamics; (2) the scientific and management goals; and (3) what data and/or estimates are available. We discussed the first criterion in the previous section. For the second criterion, for example, if project goals include determining the demographic mechanisms of population change or limitation, then most count-based models would not be appropriate.

Parameterization is a key challenge in building an FAC population model, especially when the goals of the model include prediction or making management recommendations. When several sources of data are available, integrated population models often make the most efficient use of the data and produce more accurate estimates and predictions (Abadi et al. 2010a). However, when data are sparse, a more theoretical approach using a simpler model may be more appropriate; conversely, when good estimates are available for all relevant parameters of the species, the integrated approach might be overkill, because improvements would be slight from the extra effort involved in developing the integrated model.

Despite the challenges involved in using FAC population models, they offer the opportunity to determine what factors in which seasons and locations limit migratory populations (Flockhart et al. 2015). This, in turn, allows

Downloaded From: https://bioone.org/journals/The-Auk on 29 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

conservation managers to consider the full annual cycle when making decisions. Failure to do so can lead to wasted conservation resources and reduced population viability (Martin et al. 2007). These models are also well suited to examining where and how migratory populations might be vulnerable to climate change.

Population models for migratory species that consider only 1 season may provide skewed estimates of climate vulnerability (Small-Lorenz et al. 2013) because climate change may affect breeding, migratory, and wintering habitats differently. Even for short-distance migratory birds, an FAC vulnerability assessment may be preferable. For example, Jenouvrier et al. (2009) originally developed a stochastic matrix population model to examine how past and future changes in breeding-season (Antarctic winter) sea-ice extent affect the population dynamics and viability of a migratory Emperor Penguin (*Aptenodytes forsteri*) population. The authors later built an FAC population model that extended their original model to account for seasonal and spatial variation in sea ice and its effects on penguin vital rates, behavior, and vulnerability differences between the sexes (Jenouvrier et al. 2010, 2012). Although the projected abundance by 2100 was similar between model types, the stochastic population growth rate changed from an almost linear relationship with the frequency of warm events (extreme lower annual sea-ice extent) to a bell-shaped relationship with annual mean sea-ice concentrations, with a complex response to increasing variance of annual sea ice. In addition, the results showed that the growth rate declined with increasing seasonal differences in sea-ice extent, which would have been impossible to see from the original model. Therefore, the FAC model provided additional insight on how climate change might affect this population.

FAC population modeling has already made important theoretical advances and presented novel hypotheses about where and how migratory populations are limited. These hypotheses include that the effects of habitat loss in breeding and winter seasons on population decline depend on the relative strengths of density dependence in the 2 seasons (Sutherland 1996); that food reduction at various locations will have different effects on the abundance of birds with summer and winter molt (Feró et al. 2008); and that the position of a node within a migratory network affects both its equilibrium abundance and the effects of habitat loss (Taylor and Norris 2010). Further applications and tests of these hypotheses are likely to follow as our ability to track migratory animals throughout the year continues to improve.

ACKNOWLEDGMENTS

We thank R. Dettmers and T. Will for recommending this review and E. Cohen, V. Ruiz-Gutierrez, B. Brost, F. Buderman, M. Hooten, and P. Williams for manuscript suggestions. E. Cohen, V. Ruiz-Gutierrez, A. Ozgul, C. Rushing, S. Jenouvrier, and the participants of the Partners in Flight symposium on this subject provided useful discussions.

Funding statement: Funding support was provided by the U.S. Fish and Wildlife Service. None of the funders had any input into the content of the manuscript. None of the funders required their approval of the manuscript before submission or publication.

Ethics statement: The work described here did not involve any human or animal use.

LITERATURE CITED

Abadi, F., O. Gimenez, R. Arlettaz, and M. Schaub (2010a). An assessment of integrated population models: Bias, accuracy, and violation of the assumption of independence. Ecology 91:7–14.

Abadi, F., O. Gimenez, B. Ullrich, R. Arlettaz, and M. Schaub (2010b). Estimation of immigration rate using integrated population models. Journal of Applied Ecology 47:393–400.

Akçakaya, H. R., and W. Root (2002). RAMAS GIS: Linking Spatial Data with Population Viability Analysis, version 4.0. Applied Biomathematics, Setauket, NY, USA.

Baker, A. J., P. M. Gonzalez, T. Piersma, L. J. Niles, I. de Lima Serrano do Nascimento, P. W. Atkinson, N. A. Clark, C. D. Minton, M. K. Peck, and G. Aarts (2004). Rapid population decline in Red Knots: Fitness consequences of decreased refuelling rates and late arrival in Delaware Bay. Proceedings of the Royal Society of London, Series B 271:875–882.

Berec, L., E. Angulo, and F. Courchamp (2007). Multiple Allee effects and population management. Trends in Ecology & Evolution 22:185–191.

Besbeas, P., S. N. Freeman, B. J. T. Morgan, and E. A. Catchpole (2002). Integrating mark–recapture–recovery and census data to estimate animal abundance and demographic parameters. Biometrics 58:540–547.

Betini, G. S., C. K. Griswold, and D. R. Norris (2013). Carry-over effects, sequential density dependence and the dynamics of populations in a seasonal environment. Proceedings of the Royal Society of London, Series B 280:20130110.

Betini, G. S., C. K. Griswold, L. Prodan, and D. R. Norris (2014). Body size, carry-over effects and survival in a seasonal environment: Consequences for population dynamics. Journal of Animal Ecology 83:1313–1321.

Bonnot, T. W., F. R. Thompson III, and J. J. Millspaugh (2011). Extension of landscape-based population viability models to ecoregional scales for conservation planning. Biological Conservation 144:2041–2053.

Brooks, S. P., R. King, and B. J. T. Morgan (2004). A Bayesian approach to combining animal abundance and demographic data. Animal Biodiversity and Conservation 27:515–529.

Calvert, A. M., S. J. Walde, and P. D. Taylor (2009). Nonbreeding-season drivers of population dynamics in seasonal migrants: Conservation parallels across taxa. Avian Conservation & Ecology 4:5.

Caswell, H. (2001). Matrix Population Models: Construction, Analysis, and Interpretation, second edition. Sinauer Associates, Sunderland, MA, USA.

Downloaded From: https://bioone.org/journals/The-Auk on 29 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Caswell, H. (2007). Sensitivity analysis of transient population dynamics. Ecology Letters 10:1–15.

Chandler, R. B., and J. D. Clark (2014). Spatially explicit integrated population models. Methods in Ecology and Evolution 5: 1351–1360.

Conner, M. M., and G. C. White (1999). Effects of individual heterogeneity in estimating the persistence of small populations. Natural Resource Modeling 12:109–127.

Coulson, T. (2012). Integral projections models, their construction and use in posing hypotheses in ecology. Oikos 121: 1337–1350.

Courchamp, F., T. Clutton-Brock, and B. Grenfell (1999). Inverse density dependence and the Allee effect. Trends in Ecology & Evolution 14:405–410.

Dail, D., and L. Madsen (2011). Models for estimating abundance from repeated counts of an open metapopulation. Biometrics 67:577–587.

de Valpine, P., and A. Hastings (2002). Fitting population models incorporating process noise and observation error. Ecological Monographs 72:57–76.

Dolman, P. M., and W. J. Sutherland (1995). The response of bird populations to habitat loss. Ibis 137:S38–S46.

Easterling, M. R., S. P. Ellner, and P. M. Dixon (2000). Size-specific sensitivity: Applying a new structured population model. Ecology 81:694–708.

Erickson, R. A., W. E. Thogmartin, R. E. Russell, J. E. Diffendorfer, and J. A. Szymanski (2014). A stage-structured, spatially explicit migration model for *Myotis* bats: Mortality location affects system dynamics. Letters in Biomathematics 1:157–172.

Fagan, W. F., and E. E. Holmes (2006). Quantifying the extinction vortex. Ecology Letters 9:51–60.

Feró, O., P. A. Stephens, Z. Barta, J. M. McNamara, and A. I. Houston (2008). Optimal annual routines: New tools for conservation biology? Ecological Applications 18:1563–1577.

Flockhart, D. T. T., J.-B. Pichancourt, D. R. Norris, and T. G. Martin (2015). Unravelling the annual cycle in a migratory animal: Breeding-season habitat loss drives population declines of monarch butterflies. Journal of Animal Ecology 84:155–165.

Freckleton, R. P., A. R. Watkinson, R. E. Green, and W. J. Sutherland (2006). Census error and the detection of density dependence. Journal of Animal Ecology 75:837–851.

Gilpin, M. E., and M. E. Soulé (1986). Minimum viable populations: Processes of species extinction. In Conservation Biology: The Science of Scarcity and Diversity (M. E. Soulé, Editor). Sinauer Associates, Sunderland, MA, USA. pp. 19–34.

Grimm, V., and S. F. Railsback (2005). Individual-Based Modeling and Ecology. Princeton University Press, Princeton, NJ, USA.

Gullett, P., K. L. Evans, R. A. Robinson, and B. J. Hatchwell (2014). Climate change and annual survival in a temperate passerine: Partitioning seasonal effects and predicting future patterns. Oikos 123:389–400.

Harrison, X. A., J. D. Blount, R. Inger, D. R. Norris, and S. Bearhop (2011). Carry-over effects as drivers of fitness differences in animals. Journal of Animal Ecology 80:4–18.

Hitchcock, C. L., and C. Gratto-Trevor (1997). Diagnosing a shorebird local population decline with a stage-structured population model. Ecology 78:522–534.

Hostetler, J. A., and R. B. Chandler (2015). Improved state-space models for inference about spatial and temporal variation in abundance from count data. Ecology 96. In press.

Hostetler, J. A., E. Kneip, D. H. Van Vuren, and M. K. Oli (2012). Stochastic population dynamics of a montane ground-dwelling squirrel. PLOS One 7:e34379.

Inger, R., X. A. Harrison, G. D. Ruxton, J. Newton, K. Colhoun, G. A. Gudmundsson, G. McElwaine, M. Pickford, D. Hodgson, and S. Bearhop (2010). Carry-over effects reveal reproductive costs in a long-distance migrant. Journal of Animal Ecology 79: 974–982.

Iwamura, T., H. P. Possingham, I. Chadès, C. Minton, N. J. Murray, D. I. Rogers, E. A. Treml, and R. A. Fuller (2013). Migratory connectivity magnifies the consequences of habitat loss from sea-level rise for shorebird populations. Proceedings of the Royal Society of London, Series B 280:20130325.

James, A. R., and K. C. Abbott (2014). Phenological and geographical shifts have interactive effects on migratory bird populations. The American Naturalist 183:40–53.

Jenouvrier, S., H. Caswell, C. Barbraud, M. Holland, J. Stroeve, and H. Weimerskirch (2009). Demographic models and IPCC climate projections predict the decline of an Emperor Penguin population. Proceedings of the National Academy of Sciences USA 106:1844–1847.

Jenouvrier, S., H. Caswell, C. Barbraud, and H. Weimerskirch (2010). Mating behavior, population growth, and the operational sex ratio: A periodic two-sex model approach. The American Naturalist 175:739–752.

Jenouvrier, S., M. Holland, J. Stroeve, C. Barbraud, H. Weimerskirch, M. Serreze, and H. Caswell (2012). Effects of climate change on an Emperor Penguin population: Analysis of coupled demographic and climate models. Global Change Biology 18:2756–2770.

Kölzsch, A., S. A. Sæther, H. Gustafsson, P. Fiske, J. Höglund, and J. A. Kålås (2007). Population fluctuations and regulation in Great Snipe: A time-series analysis. Journal of Animal Ecology 76:740–749.

Kot, M., M. A. Lewis, and P. van den Driessche (1996). Dispersal data and the spread of invading organisms. Ecology 77:2027–2042.

Kuss, P., M. Rees, H. H. Ægisdóttir, S. P. Ellner, and J. Stöcklin (2008). Evolutionary demography of long-lived monocarpic perennials: A time-lagged integral projection model. Journal of Ecology 96:821–832.

Lande, R., S. Engen, and B.-E. Sæther (2003). Stochastic Population Dynamics in Ecology and Conservation. Oxford University Press, New York, NY, USA.

Link, W. A., and J. R. Sauer (2002). A hierarchical analysis of population change with application to Cerulean Warblers. Ecology 83:2832–2840.

Link, W. A., and J. R. Sauer (2007). Seasonal components of avian population change: Joint analysis of two large-scale monitoring programs. Ecology 88:49–55.

Lozano, G. A., S. Perreault, and R. E. Lemon (1996). Age, arrival date and reproductive success of male American Redstarts *Setophaga ruticilla*. Journal of Avian Biology 27:164–170.

Marra, P. P., K. A. Hobson, and R. T. Holmes (1998). Linking winter and summer events in a migratory bird by using stable-carbon isotopes. Science 282:1884–1886.

Downloaded From: https://bioone.org/journals/The-Auk on 29 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Marra, P. P., and R. T. Holmes (2001). Consequences of dominance-mediated habitat segregation in American Redstarts during the nonbreeding season. The Auk 118:92–104.

Marra, P. P., D. Hunter, and A. M. Perrault (2011). Migratory connectivity and the conservation of migratory animals. Environmental Law 41:317–354.

Martin, T. G., I. Chadès, P. Arcese, P. P. Marra, H. P. Possingham, and D. R. Norris (2007). Optimal conservation of migratory species. PLOS One 2:e751.

Mattsson, B. J., M. C. Runge, J. H. Devries, G. S. Boomer, J. M. Eadie, D. A. Haukos, J. P. Fleskes, D. N. Koons, W. E. Thogmartin, and R. G. Clark (2012). A modeling framework for integrated harvest and habitat management of North American waterfowl: Case-study of Northern Pintail metapopulation dynamics. Ecological Modelling 225:146–158.

McGowan, C. P., D. R. Smith, J. A. Sweka, J. Martin, J. D. Nichols, R. Wong, J. E. Lyons, L. J. Niles, K. Kalasz, J. Brust, M. Klopfer, and B. Spear (2011). Multispecies modeling for adaptive management of horseshoe crabs and Red Knots in the Delaware Bay. Natural Resource Modeling 24:117–156.

McNamara, J. M., and A. I. Houston (2008). Optimal annual routines: Behaviour in the context of physiology and ecology. Philosophical Transactions of the Royal Society of London, Series B 363:301–319.

McNamara, J. M., R. K. Welham, and A. I. Houston (1998). The timing of migration within the context of an annual routine. Journal of Avian Biology 29:416–423.

Møller, A. P. (1994). Phenotype-dependent arrival time and its consequences in a migratory bird. Behavioral Ecology and Sociobiology 35:115–122.

Morris, W. F., and D. F. Doak (2002). Quantitative Conservation Biology: Theory and Practice of Population Viability Analysis. Sinauer Associates, Sunderland, MA, USA.

Morrison, R. I. G., D. S. Mizrahi, R. K. Ross, O. H. Ottema, N. de Pracontal, and A. Narine (2012). Dramatic declines of Semipalmated Sandpipers on their major wintering areas in the Guianas, northern South America. Waterbirds 35:120–134.

Neubert, M. G., and H. Caswell (2000). Demography and dispersal: Calculation and sensitivity analysis of invasion speed for structured populations. Ecology 81:1613–1628.

Norris, D. R. (2005). Carry-over effects and habitat quality in migratory populations. Oikos 109:178–186.

Norris, D. R., and P. P. Marra (2007). Seasonal interactions, habitat quality, and population dynamics in migratory birds. The Condor 109:535–547.

Norris, D. R., and C. M. Taylor (2006). Predicting the consequences of carry-over effects for migratory populations. Biology Letters 2:148–151.

Ozgul, A., D. Z. Childs, M. K. Oli, K. B. Armitage, D. T. Blumstein, L. E. Olson, S. Tuljapurkar, and T. Coulson (2010). Coupled dynamics of body mass and population growth in response to environmental change. Nature 466:482–485.

Pasinelli, G., M. Schaub, G. Häfliger, M. Frey, H. Jakober, M. Müller, W. Stauber, P. Tryjanowski, J.-L. Zollinger, and L. Jenni (2011). Impact of density and environmental factors on population fluctuations in a migratory passerine. Journal of Animal Ecology 80:225–234.

Pettifor, R. A., R. W. G. Caldow, J. M. Rowcliffe, J. D. Goss-Custard, J. M. Black, K. H. Hodder, A. I. Houston, A. Lang, and J. Webb (2000). Spatially explicit, individual-based, behavioural models of the annual cycle of two migratory goose populations. Journal of Applied Ecology 37 (Supplement):103–135.

Piou, C., and E. Prévost (2012). A demo-genetic individual-based model for Atlantic salmon populations: Model structure, parameterization and sensitivity. Ecological Modelling 231: 37–52.

Piou, C., and E. Prévost (2013). Contrasting effects of climate change in continental vs. oceanic environments on population persistence and microevolution of Atlantic salmon. Global Change Biology 19:711–723.

Rolland, V., J. A. Hostetler, T. C. Hines, F. A. Johnson, H. F. Percival, and M. K. Oli (2011). Effects of harvest and climate on population dynamics of Northern Bobwhites in south Florida. Wildlife Research 38:396–407.

Runge, M. C., and P. P. Marra (2005). Modeling seasonal interactions in the population dynamics of migratory birds. In Birds of Two Worlds: The Ecology and Evolution of Migration (R. Greenberg and P. P. Marra, Editors). Johns Hopkins University Press, Baltimore, MD, USA. pp. 375–389.

Schaub, M., and F. Abadi (2011). Integrated population models: A novel analysis framework for deeper insights into population dynamics. Journal of Ornithology 152: S227–S237.

Schaub, M., T. S. Reichlin, F. Abadi, M. Kéry, L. Jenni, and R. Arlettaz (2012). The demographic drivers of local population dynamics in two rare migratory birds. Oecologia 168: 97–108.

Senner, N. R., W. M. Hochachka, J. W. Fox, and V. Afanasyev (2014). An exception to the rule: Carry-over effects do not accumulate in a long-distance migratory bird. PLOS One 9: e86588.

Sheehy, J., C. M. Taylor, K. S. McCann, and D. R. Norris (2010). Optimal conservation planning for migratory animals: Integrating demographic information across seasons. Conservation Letters 3:192–202.

Sheehy, J., C. M. Taylor, and D. R. Norris (2011). The importance of stopover habitat for developing effective conservation strategies for migratory animals. Journal of Ornithology 152: 161–168.

Sillett, T. S., and R. T. Holmes (2002). Variation in survivorship of a migratory songbird throughout its annual cycle. Journal of Animal Ecology 71:296–308.

Sillett, T. S., and R. T. Holmes (2005). Long-term demographic trends, limiting factors, and the strength of density dependence in a breeding population of a migratory songbird. In Birds of Two Worlds: The Ecology and Evolution of Migration (R. Greenberg and P. P. Marra, Editors). Johns Hopkins University Press, Baltimore, MD, USA. pp. 426–436.

Sillett, T. S., R. T. Holmes, and T. W. Sherry (2000). Impacts of a global climate cycle on population dynamics of a migratory songbird. Science 288:2040–2042.

Skellam, J. G. (1967). Seasonal periodicity in theoretical population ecology. In Proceedings of the Fifth Berkeley Symposium on Mathematical Statistics and Probability, vol. 4. University of California Press, Berkeley, CA, USA. pp. 179–205.

Small-Lorenz, S. L., L. A. Culp, T. B. Ryder, T. C. Will, and P. P. Marra (2013). A blind spot in climate change vulnerability assessments. Nature Climate Change 3:91–93.

Staples, D. F., M. L. Taper, and B. Dennis (2004). Estimating population trend and process variation for PVA in the presence of sampling error. Ecology 85:923–929.

Downloaded From: https://bioone.org/journals/The-Auk on 29 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Stephens, P. A., and W. J. Sutherland (1999). Consequences of the Allee effect for behaviour, ecology and conservation. Trends in Ecology & Evolution 14:401–405.

Stephens, P. A., W. J. Sutherland, and R. P. Freckleton (1999). What is the Allee effect? Oikos 87:185–190.

Sutherland, W. J. (1996). Predicting the consequences of habitat loss for migratory populations. Proceedings of the Royal Society of London, Series B 263:1325–1327.

Sutherland, W. J. (1998). The effect of local change in habitat quality on populations of migratory species. Journal of Applied Ecology 35:418–421.

Sutherland, W. J., and P. M. Dolman (1994). Combining behaviour and population dynamics with applications for predicting consequences of habitat loss. Proceedings of the Royal Society of London, Series B 255:133–138.

Taylor, C. M., and R. J. Hall (2012). Metapopulation models for seasonally migratory animals. Biology Letters 8:477–480.

Taylor, C. M., and A. Hastings (2005). Allee effects in biological invasions. Ecology Letters 8:895–908.

Taylor, C. M., and D. R. Norris (2007). Predicting conditions for migration: Effects of density dependence and habitat quality. Biology Letters 3:280–284.

Taylor, C. M., and D. R. Norris (2010). Population dynamics in migratory networks. Theoretical Ecology 3:65–73.

Turchin, P. (2003). Complex Population Dynamics: A Theoretical/Empirical Synthesis. Princeton University Press, Princeton, NJ, USA.

Vindenes, Y., S. Engen, and B.-E. Sæther (2008). Individual heterogeneity in vital parameters and demographic stochasticity. The American Naturalist 171:455–467.

Ward, E. J., E. E. Holmes, J. T. Thorson, and B. Collen (2014). Complexity is costly: A meta-analysis of parametric and non-parametric methods for short-term population forecasting. Oikos 123:652–661.

Webster, M. S., and P. P. Marra (2005). The importance of understanding migratory connectivity and seasonal interactions. In Birds of Two Worlds: The Ecology and Evolution of Migration (R. Greenberg and P. P. Marra, Editors). Johns Hopkins University Press, Baltimore, MD, USA. pp. 199–209.

Webster, M. S., P. P. Marra, S. M. Haig, S. Bensch, and R. T. Holmes (2002). Links between worlds: Unraveling migratory connectivity. Trends in Ecology & Evolution 17:76–83.

Wiederholt, R., L. López-Hoffman, J. Cline, R. A. Medellín, P. Cryan, A. Russell, G. McCracken, J. Diffendorfer, and D. Semmens (2013). Moving across the border: Modeling migratory bat populations. Ecosphere 4:art114.

Williams, B. K., J. D. Nichols, and M. J. Conroy (2002). Analysis and Management of Animal Populations: Modeling, Estimation, and Decision Making. Academic Press, San Diego, CA, USA.

Wilson, S., S. L. LaDeau, A. P. Tøttrup, and P. P. Marra (2011). Range-wide effects of breeding-and nonbreeding-season climate on the abundance of a Neotropical migrant songbird. Ecology 92:1789–1798.

Downloaded From: https://bioone.org/journals/The-Auk on 29 Mar 2024
Terms of Use: https://bioone.org/terms-of-use