The Journal of Wildlife Management 82(2):266–274; 2018; DOI: 10.1002/jwmg.21404

Special Section: Celebrating Waterfowl Conservation

Integrated Population Models Facilitate Ecological Understanding and Improved Management Decisions

TODD W. ARNOLD,[1] *Department of Fisheries, Wildlife and Conservation Biology, University of Minnesota, St. Paul, MN 55108, USA*
ROBERT G. CLARK, *Wildlife Research Division, Environment and Climate Change Canada, 115 Perimeter Road, Saskatoon, SK S7N 0X4, Canada*
DAVID N. KOONS,[2] *Department of Wildland Resources and the Ecology Center, Utah State University, Logan, UT 84322, USA*
MICHAEL SCHAUB, *Swiss Ornithological Institute, 6204 Sempach, Switzerland*

ABSTRACT Integrated population models (IPMs) represent a formal statistical methodology for combining multiple data sets such as population counts, band recoveries, and fecundity estimates into a single unified analysis with dual objectives: better estimating population size, trajectory, and vital rates; and formally describing the ecological processes that generated these patterns. Although IPMs have been used in population ecology and fisheries management, their use in wildlife management has been limited. Data sets available for North American waterfowl are unprecedented in terms of time span (>60 years) and geographic coverage, and are especially well-suited for development of IPMs that could improve the understanding of population ecology and help guide future harvest and habitat management decisions. In this overview, we illustrate 3 potential benefits of IPMs: integration of multiple data sources (i.e., population counts, mark-recapture data, and fecundity estimates), increased precision of parameter estimates, and ability to estimate missing demographic parameters by reanalyzing results from a historical study of canvasbacks (*Aythya valisineria*). Drawing from our own published and unpublished work, we demonstrate how IPMs could be used to identify the critical vital rates that have had the greatest influence on population change in lesser scaup (*Aythya affinis*), evaluate potential mechanisms of harvest compensation for American black ducks (*Anas rubripes*), or prioritize the most appropriate places to conduct habitat management to benefit northern pintails (*Anas acuta*). Integrated population models provide a powerful platform for evaluating alternative hypotheses about population regulation and they have potential to advance the understanding of wildlife ecology and help managers make ecologically based decisions. © 2017 The Wildlife Society.

KEY WORDS band recovery, fecundity, harvest surveys, integrated population models, survival, waterfowl management.

The North American waterfowl management community has used quantitative models for monitoring and decision making (Martin et al. 1978, Nichols 1991). These efforts began early in the twentieth century with the initiation of survey and banding programs to assess population size and distribution, which later developed into rigorous annual monitoring programs (Martin et al. 1978, Anderson et al. 2018). Early analyses to estimate annual survival and assess the effect of harvest on mallards (*Anas platyrhynchos*) and other waterfowl were instrumental in the development of modern multinomial models for analyzing band-recovery data (Anderson 1975, Brownie et al. 1985). Researchers at Northern Prairie Wildlife Research Center spearheaded efforts to better understand mallard population dynamics through the development of individual-based models to assess the effects of habitat composition and management activities on annual recruitment (Cowardin and Johnson 1979). In 1995, the United States Fish and Wildlife Service (USFWS) implemented adaptive harvest management models for midcontinent mallards to better understand the role of harvest in affecting population dynamics and to help guide annual decision making (Johnson et al. 1997, Nichols et al. 2007). Integrated population models (IPMs; Besbeas et al. 2002, Schaub and Abadi 2011) have potential to further advance the understanding of population regulation and help guide management decisions in the coming decades. Our objective in this review is to help introduce IPMs to a larger audience and provide simple examples of how IPMs could be used in future studies. Although our examples are focused on waterfowl, we believe these ideas are useful for all wildlife taxa (Zipkin and Saunders 2018).

Received: 3 March 2017; Accepted: 7 November 2017

---

[1] *E-mail: arnol065@umn.edu*
[2] *Present address: Department of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, CO 80523, USA.*

THE WATERFOWL COMMUNITY HAS ACCESS TO EXTENSIVE DATA

The strength of IPMs rests in their integration of parameter estimates from multiple data sets, including annual estimates of population size, survival, and fecundity (Besbeas et al. 2002). Fortunately, the North American waterfowl community has access to long-term, spatially replicated data for many of these population parameters (Martin et al. 1978, Nichols 1991, Anderson et al. 2018). Using mallards from midcontinent North America as an example, waterfowl researchers have access to long-term data on sightability-adjusted counts of breeding pairs and flooded ponds beginning in 1955 (USFWS 2015), banding and recovery data since 1950 (Anderson 1975), and measures of species, sex, and age composition from the harvest since the 1960s (Gendron and Smith 2012, Raftovich et al. 2015). These operational surveys were explicitly designed to inform harvest management decisions (Nichols et al. 2007) and have undergone periodic assessments and improvements (Anderson 1975, Smith 1995, Padding and Royle 2012, Pearse et al. 2014).

The annual survey of breeding duck populations within midcontinent North America may be the largest-scale and longest-running survey of any continental animal population and these data have been widely used for management purposes (Nichols et al. 2007) and to address ecological questions about population regulation (Jamieson and Brooks 2004, Ross et al. 2015). Similar surveys were initiated in eastern Canada beginning in 1990 to assess populations of breeding ducks, with special emphasis on American black ducks (*Anas rubripes*; Zimmerman et al. 2012). In addition, a variety of regional breeding and wintering surveys, including the Breeding Bird Survey, provide estimates of population size or trajectory that could be used to develop IPMs (USFWS 2015, Zimmerman et al. 2017).

North American waterfowl represent some of the most intensively banded bird populations in the world, with large numbers of band encounters obtained through hunting (Fig. 1). Banding usually occurs in August and September immediately before the hunting season (i.e., preseason bandings). When combined with estimates of band reporting rates ($\hat{\rho}$) and under the assumption of no natural mortality prior to hunting season (Nichols et al. 1982), direct recovery rates ($\hat{f}$) during the first hunting season after banding provide estimates of harvest rates ($\hat{h} = \hat{f}/\hat{p}$), or if band reporting rates are unknown but relatively constant, direct recovery rates can still provide indices of annual harvest rates ($\hat{h}_t \propto \hat{f}_t$). Direct recovery rates also enable estimation of population sex- and age-ratios based on proportions of males versus females or juveniles versus adults in the harvest (Zimmerman et al. 2010). Recoveries during subsequent years can be used to estimate annual survival (S_t) and assess the relationship between harvest rate and survival (Burnham and Anderson 1984, Arnold et al. 2016). Large-scale banding operations also occur for some species after hunting seasons have finished (i.e., postseason bandings). Although determining harvest rates from postseason bandings is problematic (Nichols and Hines 1987), they can provide useful data for estimating annual adult survival and can also be combined with preseason bandings to estimate seasonal survival between banding occasions provided both banding samples have similar recovery probabilities (Brownie et al. 1985, Pollock et al.

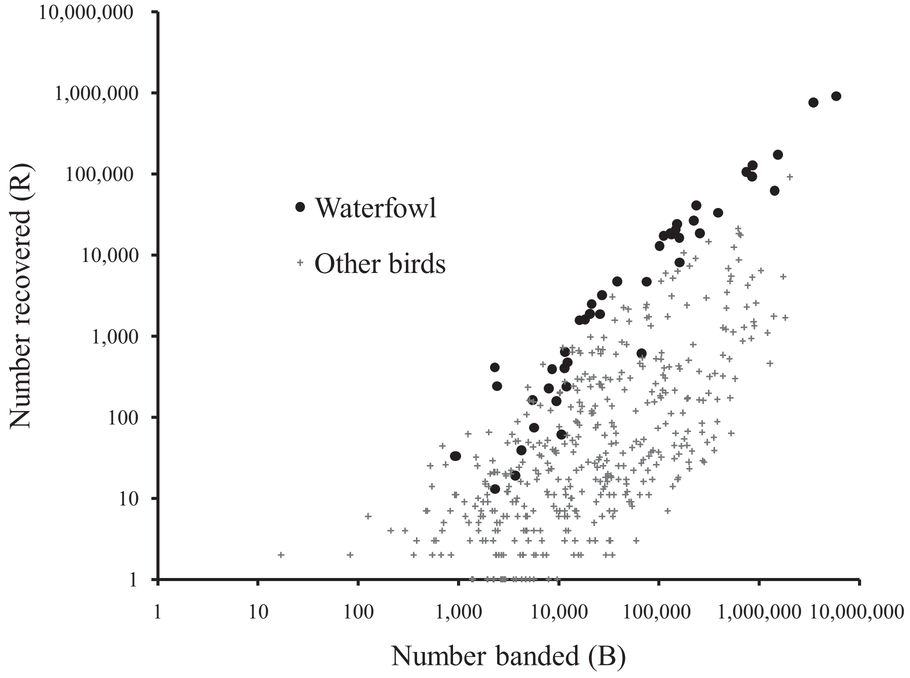

Figure 1. Cumulative bandings (B) and recoveries (R; 1950–2010) for 473 species of North American birds. Cumulative recovery rates (R/B) averaged 8.5% for waterfowl and 0.8% for non-waterfowl (data from U.S. Geological Survey Bird Banding Lab).

1995). Many waterfowl populations have been the subjects of long-term mark-recapture studies, where live-encounter data based on field-readable collars, bands, or nasal-markers provide additional means of estimating annual apparent survival (Anderson et al. 1997, Cleasby et al. 2017), age-specific breeding propensity (Gauthier et al. 2007), and temporary or permanent emigration (Lindberg et al. 2001).

Harvest surveys provide information about harvest of ducks and geese in Canada and the United States and data from the parts collection survey (duck wings, goose tails) allow the harvest to be partitioned by species, sex (ducks only), and age (Gendron and Smith 2012, Raftovich et al. 2015). After correcting for vulnerability to harvest using banding information, harvest data can be used to estimate population size and composition (Zimmerman et al. 2010, Alisauskas et al. 2014). Because of its continental nature, vulnerability-corrected harvest data probably provide the most useful metric of annual fecundity for waterfowl at large spatial scales (Péron et al. 2012, Osnas et al. 2016) and for species that breed in regions with no reliable count-based surveys, harvest-based Lincoln estimates often provide the only reliable estimates of annual population size (Alisauskas et al. 2009). Other important data sources that could be used in IPMs include productivity data from nesting studies (Gauthier et al. 2007), age structure from visual surveys where juveniles and adults can be discriminated (e.g., winter surveys of swans or geese; Weegman et al. 2016, Cleasby et al. 2017), band reporting rates from reward band studies that can help reduce bias in estimates of harvest rates (Boomer et al. 2013), and movement rates among geographic sub-populations (Fonnesbeck and Conroy 2004).

Because IPMs integrate data from ≥2 independent sources to make inference about the same population, geographic and temporal congruency among data sets is critical (i.e., all data sets should reference the same population). In practice, this is most easily achieved if all data come from the same well-studied population (Abadi et al. 2010*b*). Incongruence can occur if data on vital rates are available for only some years of the study (Davis et al. 2014) or from only a limited portion of the population's range (Gauthier et al. 2007). For waterfowl data, spatial incongruence can occur between survey and harvest data (e.g., population counts from the midcontinent traditional survey area vs. harvest data from all of Canada and the U.S.; Alisauskas et al. 2014), or when banding data are obtained from restricted geographic locations that might not be representative of the entire continental population (Arnold et al. 2016). Temporal incongruence can occur if investigators wish to use all available data for a midcontinent duck species (i.e., banding data begin in 1950, count data in 1955, and U.S. harvest data in 1961; Koons et al. 2017). Investigators must be clear when combining such data sets to indicate they are assuming that demographic rates during unmeasured years have the same mean and variance as during sampled years, or that demographic rates and observation error in geographically sampled areas are similar to those of unsampled areas.

HOW DO IPMS WORK?

Typically, IPMs are constructed using a combination of ≥2 data sets, including population surveys to estimate population size or trajectory, band-recovery or live-encounter data to estimate stage-specific survival or apparent survival, and nesting or harvest composition data to provide estimates of annual fecundity (Besbeas et al. 2002, Schaub and Abadi 2011, Péron et al. 2012). A common feature of all IPMs is that they include ≥1 data set that is informative about population size or structure. Changes in population size or structure over time are governed by demographic rates, which provide the basis for integration of the different data sets. The first step in building an IPM is to identify an appropriate demographic model that is consistent with life history and available data. Relevant questions include whether to model a pre- or post-birth pulse population, how many life stages to recognize, and whether to include or exclude males. For pre-birth pulse data with an early-maturing dabbling duck exhibiting little evidence of sex-specific variation in survival, the demographic model could be as simple as $N_{t+1} = N_t(S_{at} + F_t S_{jt})$, where N_t represents breeding population size in year t, S_{at} is adult annual survival, F_t is annual fecundity (sexes combined), and S_{jt} is juvenile annual survival. For species with post-birth pulse surveys where there is interest in modeling size of the juvenile and adult populations (i.e., fall flight), investigators might use a 2 × 2 projection matrix with count, survival, and fecundity data restricted to juvenile (*jf*) and adult females (*af*):

$$\begin{bmatrix} N_{jf} \\ N_{af} \end{bmatrix}_{t+1} = \begin{bmatrix} S_{jf}0.5F & S_{af}0.5F \\ S_{jf} & S_{af} \end{bmatrix}_t \times \begin{bmatrix} N_{jf} \\ N_{af} \end{bmatrix}_t \tag{1}$$

For species that exhibit even greater age structure (e.g., sea ducks, geese, or swans), projection matrices could accommodate additional dimensionality; for example, Gauthier et al. (2007) recognized 4 age classes in their greater snow goose (*Anser caerulescens atlantica*) IPM to accommodate age-specific variation in breeding propensity. Males are often excluded from population models, especially for ducks where males contribute little parental care and sex ratios are strongly male-biased (Afton and Anderson 2001, Howerter et al. 2014). Nevertheless, investigators might consider including males in their projection model if demographic rates are likely to be correlated between sexes and data from males can help inform vital rate estimates for females (Koons et al. 2017). The following represents a female-limited projection matrix that would be appropriate for a pre-birth pulse survey of both sexes, where yearlings (1) and older adults (2+) have different survival or fecundity rates and sex ratio at fledging is assumed to be 0.5:0.5. If sex ratio at fledging is unequal, 0.5 could be replaced by π for females and (1−π) for males.

$$\begin{bmatrix} N_{1,f} \\ N_{2+,f} \\ N_{1,m} \\ N_{2+,m} \end{bmatrix}_{t+1} = \begin{bmatrix} 0.5F_1S_{j,f} & 0.5F_{2+}S_{j,f} & 0 & 0 \\ S_{1,f} & S_{2+,f} & 0 & 0 \\ 0.5F_1S_{j,m} & 0.5F_{2+}S_{j,m} & 0 & 0 \\ 0 & 0 & S_{1,m} & S_{2+,m} \end{bmatrix}_t \times \begin{bmatrix} N_{1,f} \\ N_{2+,f} \\ N_{1,m} \\ N_{2+,m} \end{bmatrix}_t \tag{2}$$

The second step in building an IPM is to identify appropriate likelihoods for each of the component data sets. For estimates of population size, this typically involves a state-space model (de Valpine and Hastings 2002) to separate true variation in population size (i.e., process variation) from observation error (i.e., noise; advanced models can also accommodate bias; Schmidt et al. 2015). State-space models have recently been adopted for analyzing waterfowl count data from the eastern survey area (Zimmerman et al. 2012) and have been used in other applications (Sauer and Link 2011). For banding data, either Seber or Brownie likelihoods can be used if information comes from dead recoveries (Seber 1970, Brownie et al. 1985), Cormack-Jolly-Seber likelihoods if data originate from live encounters (Lebreton et al. 1992), and joint recovery likelihoods for combinations of live and dead encounters (Barker 1997). Fecundity data might come from field studies of nest and brood survival (Koons et al. 2006, Howerter et al. 2014), vulnerability-adjusted age ratios from harvest data (Péron et al. 2012, Osnas et al. 2016), fall age-ratio surveys (Weegman et al. 2016, Cleasby et al. 2017), or estimates of age ratios during fall banding operations (Ross et al. 2017).

The final step in IPM construction is to combine the component data sets into a joint likelihood (Fig. 2). Provided that the data sets are independent, the joint likelihood is a product of the individual likelihoods (Besbeas et al. 2002, Brooks et al. 2004), but simulations suggest that IPMs are robust to violations of the independence assumption (Abadi et al. 2010*a*; M. D. Weegman, University of Missouri, personal communication). An important consideration during this final step is to correct for any differences in survey timing; for example, if breeding pair surveys occur during May and preseason bandings occur during August, then annual survival should be partitioned into 2 components ($\text{Aug}_t - \text{May}_{t+1}$, $\text{May}_{t+1} - \text{Aug}_{t+1}$) to allow survival estimates to match up with census dates (Péron et al. 2012, Koons et al. 2017). Juvenile survival in this formulation will be measured over a 9-month interval (Péron et al. 2012), so it is important that these estimates not be confused with annual survival. Investigators should also make certain that there are no missing vital rates in their formulation of the population life-cycle; for example, if fecundity is measured based on number of ducklings surviving to 30 days of age (Howerter et al. 2014), but juvenile survival is measured from August banding until May census, then juvenile mortality between 30 days of age and August banding will have been omitted from the model. In such cases, investigators can specify the missing parameter as a latent variable and estimate it within the IPM framework, or use published estimates from a closely related population. For mallards, investigators often use the estimate from Hestbeck et al. (1989) for post-fledging survival (Howerter et al. 2014), and in a Bayesian analysis investigators could use point estimates and formal measures of parameter uncertainty. Breeding propensity is a particularly difficult parameter to estimate if nonbreeding individuals use different habitats (Sedinger et al. 2001), but in situations where there are no data to inform a missing parameter, it can be estimated in an IPM framework provided there are no other missing parameters. Robinson et al. (2014) provide an example of using a parameter to account for unmeasured variation in post-fledging survival of common British birds, while also acknowledging that this correction factor includes any other unmodeled vital rates (e.g., breeding propensity) plus any other unaccounted for biases.

$$L_{IPM}\left(y,m,w\,|\,\tau,\mathbf{N},F,\mathbf{S},\mathbf{r},\theta_0\right) = L_{SS}\times L_{CR}\times L_W$$

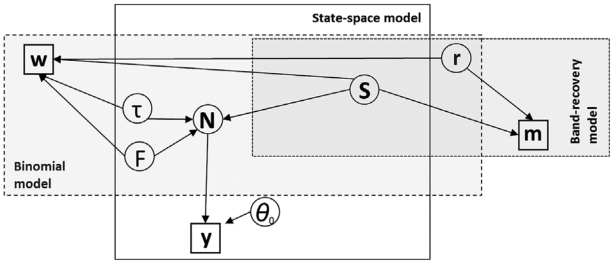

Figure 2. Diagrammatic model for the individual and joint likelihoods (L) of an integrated population model (IPM) for waterfowl. Data sources in small squares include annual population counts (y), m-arrays (m) of band-recovery data, and age-sex composition of wing-receipt data (w) from the Parts Collection Survey. Estimated parameters are in circles and include annual survival (*S*), Seber reporting rate (*r*), fecundity (*F*), population structure (τ; i.e., proportion of juvenile and adult males and females), population size (*N*), and survey precision (θ_0). The large rectangles represent the individual likelihoods for the state-space model (L_{SS}; count data), Seber recovery model (L_{CR}; band recovery data), and multinomial model (L_W; parts collection survey). In regions where these rectangles overlap, multiple data sets contribute to parameter estimation. The joint likelihood of the IPM (L_{IPM}) represents the product of all 3 data sources, given the estimated parameters, and is obtained as the joint product of the 3 individual likelihoods.

Once the joint likelihood has been constructed, inference can be obtained using Kalman filters within the frequentist framework (Besbeas et al. 2002) or Markov chain Monte Carlo (MCMC) simulation within the Bayesian framework (Brooks et al. 2004, Kéry and Schaub 2012:chapter 11). We prefer the Bayesian framework, which offers greater flexibility in modeling, and is readily accessible to wildlife ecologists through the simple clarity of the BUGS programming language as implemented in WinBUGS, OpenBUGS, or JAGS (Lunn et al. 2000, Plummer 2003, Kéry and Schaub 2012).

A SIMPLE IPM: REANALYZING HISTORICAL CANVASBACK DATA

We use a historical data set on canvasback (*Aythya valisineria*) population dynamics (Anderson et al. 1997) to develop a simple model that demonstrates 3 key benefits of IPMs: ability to reconcile spatiotemporal variation in population vital rates with spatiotemporal variation in estimates of population size, more precise estimates of population size and vital rates, and ability to estimate an unmeasured component of population change (e.g., net immigration; Abadi et al. 2010*b*, Schaub and Fletcher 2015). Although IPMs are typically constructed using summarized data (e.g., m-array summaries of band-recovery data), they can also be developed using parameter estimates and variances from independent analyses of component data sets (Besbeas et al. 2002, Davis et al. 2014), which we demonstrate here.

Anderson et al. (1997) tested whether population growth rate in a canvasback population in Manitoba, Canada was limited by recruitment. They monitored canvasback populations from 1983 to 1990 on 2 15.8-km^2 study sites: an unmanipulated control site and an experimental site where nest fences and clutch augmentations were used to increase nest success and hatched brood size (Anderson et al. 1997: tables 1, 2). Survey and nest monitoring data included annual counts of breeding pairs (BP), total hatched nests (HN), total hatched ducklings (HD), total fledged ducklings (FD), and hatched ducklings per successful nest (HDN). Juvenile and adult females were individually marked using nasal markers, and juvenile and adult annual apparent survival (φ_{jt} and φ_{at}, which include permanent emigration) and annual resighting probability (p_t) were estimated using Cormack-Jolly-Seber models in Program JOLLYAGE (Pollock et al. 1990). Anderson et al. (1997) reported that their experimental population grew to become almost twice as large as the control population by 1988, but both populations crashed in 1989 during a severe drought. Population projections based on measured vital rates were inconsistent with observed population counts (Anderson et al. 1997:fig. 7) and the authors speculated that unmeasured immigration might be responsible for some of this disparity.

We developed a single-stage, female only, pre-birth-pulse projection model to describe the population dynamics of each study population:

$$N_{t+1} = \text{Binomial}(\varphi_{at}, N_t) + \text{Poisson}(0.5 \times HS_t \times HDN_t \times DS_t \times \varphi_{jt} \times N_t) \tag{3}$$

where our measure of annual fecundity was half (i.e., female only) the product of *per capita* hatching success (HS = HN/BP, the probability a breeding female hatches a nest in ≥1 nesting attempts), HDN, and duckling survival (DS = FD/HD; Anderson et al. 1997:tables 1, 2). We modeled HS, DS, φ_{jt}, and φ_{at} as binomials with vague priors (~uniform[0,1]), converted them to logit scale, and treated site-years as random effects with vague prior distributions ($\sigma \sim$ uniform[0,4], logit scale). We considered treatment effects as uniform offsets for HS (−4 to 4, logit scale) and HDN (−2 to 2, real scale) and considered them to be significant if 95% credible intervals excluded zero. Our observational data included estimated numbers of breeding pairs, hatched nests, fledged ducklings, ducklings per hatched nest ($\bar{x}$, SE), and maximum likelihood estimates of φ_{jt} and φ_{at} ($\bar{x}$, SE; Anderson et al. 1997:tables 1, 2, 4). We used 3 MCMC chains of 60,000 iterations each, with the first 10,000 iterations discarded as burn-in, and retained every fifth remaining iteration for the posterior distribution (see Appendix S1, available online in Supporting Information, for additional modeling details).

Our simple IPM converged rapidly (<1 min) for all parameters ($\hat{R} < 1.001$). Estimates of annual population size for each study area represented a compromise between survey data and population projections based on vital rates, with 95% credible intervals that usually included both alternative estimates (Fig. 3). Our analysis confirmed a positive effect of treatment on hatched brood size (+1.04 ducklings/nest, $P[X < 0] = 0.004$), but results were ambivalent for hatching success and suggested a negative overall effect (−1.51 on logit scale, $P[X < 0] = 0.94$). Apparent adult survival (φ_{at}), averaged over both sites and all years, was 0.679 (SD = 0.102, $\bar{x}$ SE = 0.061) based on maximum likelihood estimates in Anderson et al. (1997:table 4) and 0.686 ($\hat{\sigma} = 0.072$, $\bar{x}$ SD = 0.049) based on our IPM, which represents a 50% reduction in annual process variation and an average 35% reduction in total variance for each site year. Our IPM analysis confirmed that hatching success and adult female survival were the 2 most important vital rates affecting variation in annual population growth.

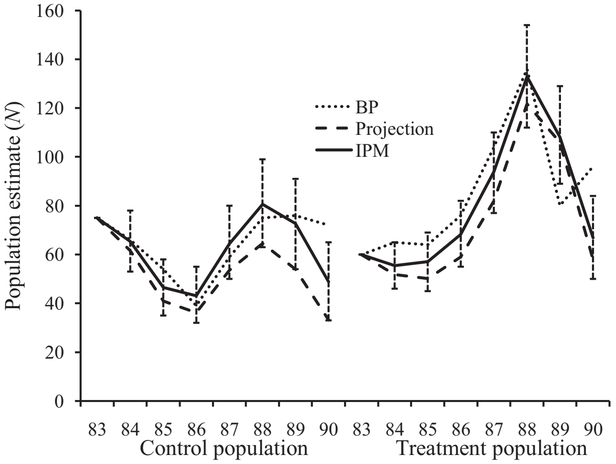

Figure 3. Population estimates for 2 study populations of canvasbacks from Minnedosa, Manitoba, Canada, 1983–1990 (years indicated on the *x*-axis by the last 2 digits). The dotted lines indicate results from annual breeding pair (BP) surveys and the dashed lines represent population projections from measured vital rates (Anderson et al. 1997). The solid lines (with 95% credible intervals) are from our integrated population model (IPM) that combines information from both data streams.

Anderson et al. (1997) considered immigration as a potential confounding factor but were unable to measure potential rates of immigration. In an IPM, immigration can be estimated as the missing parameter in a balance equation, assuming that fecundity, survival, and permanent emigration (E) are all measured without bias. Our Cormack-Jolly-Seber analysis of canvasback apparent survival measured the product of *S* and [1–E], not the separate components, but we note that by including data from dead recoveries each of these components could be uniquely estimated (Lindberg et al. 2001). We therefore altered our balance equation (Eq. 4) to include annual numbers of immigrants (I_t), which we modeled as a Poisson distribution with a vague uniform prior for the mean (Uniform[0,20]) and a treatment effect to account for different immigration rates to treatment versus control sites (Uniform[−10,10]):

$$N_{t+1} = \text{Binomial}(\varphi_{at}, N_t) + \text{Poisson}(0.5 \times HS_t \times HDN_t \times DS_t \times \varphi_{jt} \times N_t) + \text{Poisson}(I_t) \tag{4}$$

This model also converged rapidly (<1 min) for all parameters ($\hat{R} < 1.002$). Estimates of annual adult female immigrants averaged 3.2 (SD = 0.3) on the treatment block and 5.0 (SD = 0.3) on the control block, suggesting that higher immigration to the control block may have dampened the treatment effect. However, we caution that our estimate of immigration could also include any systematic biases in measured vital rates (e.g., marker loss leading to underestimates of apparent survival, missed nests or broods leading to underestimates of hatching success or duckling survival) and estimated immigration might therefore be best interpreted as immigration plus systemic bias (Schaub and Fletcher 2015).

USING IPMS TO IDENTIFY KEY PARAMETERS INFLUENCING LESSER SCAUP POPULATION DECLINES

Even simple IPMs provide a powerful platform for identifying demographic parameters that are most important in affecting population change, which can help direct future management and research efforts to focus on these parameters. Traditional approaches for identifying the most influential demographic parameters have either been *ad hoc* or have focused on long-term, asymptotic population growth rates. However, asymptotic growth rates (i.e., the first eigenvector of a projection matrix) can be very different from realized growth rates (N_{t+1}/N_t) that populations experience in the near-term or in non-stationary environments induced by anthropogenic changes (Nichols et al. 2011). Transient life table response experiments (LTREs) have been developed for measuring retrospective contributions of vital rates and stage or age structure to 1) temporal variation in N_{t+1}/N_t, 2) changes in N_{t+1}/N_t between successive time steps, and 3) differences in the geometric means of realized growth rates between 2 time periods (i.e., a change in population trajectory; Koons et al. 2016). A caveat for applying transient LTREs is that vital rates and stage or age structure need to be estimated over time. However, IPMs are ideally suited for estimating latent stage or age structure and thereby provide all the necessary information for applying transient LTREs. We recently applied this methodology to the continental population of lesser scaup (*Aythya affinis*; Koons et al. 2017).

Using a process model like Equation (2), there are several novel aspects of our lesser scaup IPM that we mention here because of their applicability to other studies. First, we sought a flexible modeling approach for estimating temporal change in each vital rate. This included the estimation of non-stationary trends coupled with temporal random effects (ε_t) to capture environmental stochasticity about the trend of each vital rate (Nichols et al. 2011). We defined 3 *a priori* time periods: an initial interval from 1957 to 1983 when scaup populations fluctuated substantially, an intermediary interval from 1983 to 2006 when populations exhibited a long-term decline, and a final interval from 2006 to 2016 when populations recovered. The most notable trend in our analysis was a pronounced population decline from 1983 to 2006 and our analysis identified declining fecundity as the key vital rate that drove this decline, whereas population recovery during the last decade was influenced by improved survival of adult females (Koons et al. 2017). For the ε_t we used correlated random effects, which naturally accommodated similarity or dissimilarity of temporal deviations among demographic parameters (Schaub et al. 2013). This allowed for more efficient estimation of potentially correlated parameters (e.g., survival was highly correlated between males and females for both juveniles and adults) and this approach can also allow for assessment of intra-annual tradeoffs such as lower survival of adult females associated with years of greater fecundity (Link and Barker 2005).

Second, we used harvest composition data to inform several parameters, including annual fecundity ($F_{a,t}$; the number of offspring fledged per adult female of a given age class), but also survival (S), Seber recovery rates (r), and stage-specific population sizes (n) for hatch-year (HY) males (m) and females (f), and after-hatch-year (AHY) females. Although it would have been straightforward to include AHY males in this likelihood, goodness-of-fit tests indicated that these were the one source of data that did not fit the IPM, and thus adult males were excluded from the final analyses (Koons et al. 2017:supplemental materials). We hypothesize that adult male wings may be over reported in the Parts Collection Survey, which raises another important caveat about data quality. If any data sets are biased, IPMs will reconcile this bias by shrinking other parameter estimates in the direction of the bias (Schaub and Fletcher 2015). Another potential solution would be to include data from adult males but assign them lower weight (Maunder et al. 2017).

We modeled the annual probability of attaining a juvenile female wing ($W_{f,HY,t}$) from the Parts Collection Survey as follows:

$$W_{f,HY,t} = \frac{(F_{1,t} \cdot n_{f,1,t} + F_{2+,t} \cdot n_{f,2+,t}) \cdot 0.5 \cdot (1 - S^7_{f,HY,monthly,t}) \cdot r_{f,HY,t}}{\begin{bmatrix} (F_{1,t} \cdot n_{f,1,t} + F_{2+,t} \cdot n_{f,2+,t}) \cdot \cdot 0.5 \cdot (1 - S^7_{f,HY,monthly,t}) \cdot r_{f,HY,t} + \\ (F_{1,t} \cdot n_{f,1,t} + F_{2+,t} \cdot n_{f,2+,t}) \cdot 0.5 \cdot (1 - S^7_{m,HY,monthly,t}) \cdot r_{m,HY,t} + \\ (n_{f,1,t} + n_{f,2+,t}) \cdot S^3_{f,AHY,monthly,t-1} \cdot (1 - S^7_{f,AHY,monthly,t}) \cdot r_{f,HY,t} \end{bmatrix}} \quad (5)$$

The numerator of this equation, $(F_{1,t} \cdot n_{f,1,t} + F_{2+,t} \cdot n_{f,2+,t})$ is fecundity of all yearling and older females, respectively, 0.5 is the presumed sex ratio of offspring, $(1 - S^7_{f,HY,monthly,t})$ is the probability that a juvenile female scaup died between fall and spring banding, and $r_{f,HY,t}$ is the probability that a dead juvenile female was recovered and reported to the bird banding office (note that $(1-S) \cdot r$ in the Seber likelihood is equivalent to f in the Brownie likelihood). Note also that we rescaled annual survival to monthly survival ($S_{annual} = S_{monthly}{}^{12}$) to facilitate our combined analysis of pre- and postseason bandings and to reconcile the timing of data collection between spring banding and population surveys (2 months), population surveys and fall banding (3 months), and fall versus spring banding (7 months). The denominator equation is of similar format to the numerator, summing over HY females, HY males, and AHY females (i.e., vulnerability adjusted proportions of each cohort in the preseason banding sample, with AHY females subject to 3 months of additional mortality because they must survive from the May survey to August banding). The probabilities of attaining HY male and AHY female wings from the Parts

Collection Survey were written in a similar manner by replacing the numerator in Equation (5) with the corresponding part of the denominator. These probabilities were then related to the harvest composition data using a standard multinomial likelihood, which represented our primary data source for estimating annual fecundity but also provided auxiliary data for estimating all other parameters in the likelihood. This was especially important for HY survival, given the paucity of preseason banding data (Arnold et al. 2016). Although all model parameters appear in the likelihood for the Parts Collection Survey, they only become estimable in the presence of additional data from population counts and band-recovery data.

Finally, a Bayesian implementation allowed for complete propagation of parameter uncertainty to derived parameters (Maunder and Punt 2013), including population growth rates (Koons et al. 2017) and adult sex ratio (Arnold et al. 2017:fig. 2). The transient LTRE identified juvenile female survival as having the greatest influence on historical variation in scaup population growth (Koons et al. 2017), with declining fecundity having the greatest effect during the prolonged 1983–2006 population decline. Changes in age structure had little effect on population growth, but growth was diminished during years following high recruitment because of a greater preponderance of yearling females with lower fecundity (Koons et al. 2017). Our next step will be to identify environmental and anthropogenic covariates that might be correlated with the most influential demographic parameters and assess these covariates in an updated version of our IPM.

OTHER POTENTIAL APPLICATIONS OF IPMS TO WATERFOWL MANAGEMENT

Seminal work on mallard survival in relation to harvest rate has had a tremendous impact on harvest management in waterfowl (Anderson 1975, Burnham and Anderson 1984, USFWS 2016). But despite years of formal investigation, uncertainty persists about whether duck mortality due to harvest is additive or compensated by density-dependent survival, density-dependent fecundity, or individual heterogeneity in survival (Cooch et al. 2014). The flexibility offered by IPMs could help resolve some of this uncertainty by treating these different compensation mechanisms as multiple working hypotheses. Using historical harvest and banding data from American black ducks during 1969–1988, a period with extensive preseason and postseason banding, we have developed an IPM that includes Lincoln estimates of population size at the beginning and end of the hunting season, as well as estimates of survival during the hunting versus non-hunting season. This framework allows us to test for a negative process correlation between harvest rate and hunting season survival (Otis and White 2004, Arnold et al. 2016), negative density dependence in non-hunting season survival or fecundity (Abadi et al. 2012), and individual heterogeneity in hunting and non-hunting season survival (Pledger and Schwarz 2002). Currently, annual parameter updates from another integrated population model are used to inform the international black duck adaptive harvest management decision framework (Conroy 2010 *in* USFWS 2016). In addition, an integrated population model is also being considered as the estimation framework for the revision of the model set that supports the mid-continent mallard adaptive harvest management decision framework (G. S. Boomer, USFWS, personal communication).

Mattsson et al. (2012) developed a heuristic metapopulation framework for northern pintails (*Anas acuta*) that recognized 3 major breeding areas (Alaska, Prairie Potholes, and a northern unsurveyed region) and 2 major wintering areas (California and Gulf Coast). Their model included stage-specific population sizes, seasonal survival rates, harvest rates, wintering-to-breeding and breeding-to-wintering transition probabilities, and fecundity (fall age ratios). Mattsson et al. (2012:156) recognized that efforts to formally develop their model would require Bayesian implementation in an IPM framework. To date, follow-up efforts have formally addressed cross-seasonal effects of winter habitat conditions on future fecundity (Osnas et al. 2016) and continental estimates of population size, survival, and fecundity (E. E. Osnas, USFWS, personal communication), but additional modeling effort is required to estimate transition probabilities and fecundity for each subpopulation. These efforts have been coordinated under the auspices of the Pintail Action Group, part of the North American Waterfowl Management Plan, and findings from these efforts will be used to allocate resources for future research and conservation.

MANAGEMENT IMPLICATIONS

Integrated population models (IPMs) have enormous potential to help biologists identify the most important limiting factors affecting wildlife populations and to help managers make informed decisions about population management. A main advantage of using IPMs for population projection is proper error propagation and population projections can be conducted with the same model used to analyze historical data. Harvest and habitat manipulations have been conducted via Adaptive Harvest Management and North American Waterfowl Management Plan Joint Ventures for more than 2 decades (Osnas et al. 2014) and IPMs provide a powerful tool to formally test predictions arising from these manipulations. Given extensive available demographic data, IPMs have enormous potential to meld waterfowl ecology, monitoring, and management efforts in the coming century.

ACKNOWLEDGMENTS

We thank the organizers of the Seventh North American Duck Symposium, especially C. K. Williams and S. E. Richman, for inviting us to develop a plenary session and special symposium on integrated population models. We thank our other symposium presenters, E. E. Osnas, T. V. Riecke, and M. D. Weegman for helping to make our symposium a success. We thank M. S. Lindberg and an anonymous reviewer for constructive comments on the manuscript. Our work on integrated population models in waterfowl has been supported by the Black Duck Joint Venture, Ducks Unlimited Canada, and Environment and Climate Change Canada.

LITERATURE CITED

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

Abadi, F., O. Gimenez, H. Jakober, W. Stauber, R. Arlettaz, and M. Schaub. 2012. Estimating the strength of density dependence in the presence of observation errors using integrated population models. Ecological Modelling 242:1–9.

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

Afton, A. D., and M. G. Anderson. 2001. Declining scaup populations: a retrospective analysis of long-term population and harvest survey data. Journal of Wildlife Management 65:781–796.

Alisauskas, R. T., T. W. Arnold, J. O. Leafloor, D. L. Otis, and J. S. Sedinger. 2014. Lincoln estimates of mallard (*Anas platyrhynchos*) abundance in North America. Ecology and Evolution 4:132–143.

Alisauskas, R. T., K. L. Drake, and J. D. Nichols. 2009. Filling a void: abundance estimation of North American populations of Arctic geese using hunter recoveries. Environmental and Ecological Statistics 3:463–489.

Anderson, D. R. 1975. Population ecology of the mallard: V. Temporal and geographic estimates of survival, recovery, and harvest rates. U.S. Fish and Wildlife Service, Resource Publication No. 125, Washington, D.C., USA.

Anderson, M. G., R. T. Alisauskas, B. D. J. Batt, R. J. Blohm, K. F. Higgins, M. C. Perry, J. K. Ringelman, J. S. Sedinger, J. R. Serie, D. E. Sharp, D. L. Trauger, and C. K. Williams. 2018. The Migratory Bird Treaty and a century of waterfowl conservation. Journal of Wildlife Management 82: this issue.

Anderson, M. G., R. B. Emery, and T. W. Arnold. 1997. Reproductive success and female survival affect local population density of canvasbacks. Journal of Wildlife Management 61:1174–1191.

Arnold, T. W., A. D. Afton, M. J. Anteau, D. N. Koons, and C. A. Nicolai. 2016. Temporal variation in survival and recovery rates of lesser scaup. Journal of Wildlife Management 80:850–861.

Arnold, T. W., A. D. Afton, M. J. Anteau, D. N. Koons, and C. A. Nicolai. 2017. Temporal variation in survival and recovery rates of lesser scaup: a response. Journal of Wildlife Management 81:1142–1148.

Barker, R. J. 1997. Joint modeling of live-recapture, tag-resight, and tag-recovery data. Biometrics 53:666–677.

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.

Boomer, G. S., G. S. Zimmerman, N. L. Zimpfer, P. R. Garrettson, M. D. Koneff, T. A. Sanders, K. D. Magruder, and J. A. Royle. 2013. Band reporting probabilities for mallards recovered in the United States and Canada. Journal of Wildlife Management 77:1059–1066.

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

Brownie, C., D. R. Anderson, K. P. Burnham, and D. S. Robson. 1985. Statistical inference from band recovery data: a handbook. Second edition. U.S. Fish and Wildlife Service Resource Publication 156, Washington, D.C., USA.

Burnham, K. P., and D. R. Anderson. 1984. Tests of compensatory *vs.* additive hypotheses of mortality in mallards. Ecology 65:105–112.

Cleasby, I. R., T. W. Bodey, F. Vigfusdottir, J. L. McDonald, G. McElwaine, K. Mackie, K. Colhoun, and S. Bearhop. 2017. Climatic conditions produce contrasting influences on demographic traits in a long-distance Arctic migrant. Journal of Animal Ecology 86:285–295.

Cooch, E. G., M. Guillemain, G. S. Boomer, J.-D. Lebreton, and J. D. Nichols. 2014. The effects of harvest on waterfowl populations. Wildfowl Special Issue 4:220–276.

Cowardin, L. M., and D. H. Johnson. 1979. Mathematics and mallard management. Journal of Wildlife Management 43:18–35.

Davis, A. J., M. B. Hooten, M. L. Phillips, and P. F. Doherty Jr. 2014. An integrated modeling approach to estimating Gunnison sage-grouse population dynamics: combining index and demographic data. Ecology and Evolution 4:4247–4257.

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

Fonnesbeck, C. J., and M. J. Conroy. 2004. Application of integrated Bayesian modeling and Markov chain Monte Carlo methods to the conservation of a harvested species. Animal Biodiversity and Conservation 27:267–281.

Gauthier, G., P. Besbeas, J.-D. Lebreton, and B. J. T. Morgan. 2007. Population growth in snow geese: a modeling approach integrating demographic and survey information. Ecology 86:1420–1429.

Gendron, M. H., and A. C. Smith. 2012. National Harvest Survey web site. Bird Populations Monitoring, National Wildlife Research Centre, Canadian Wildlife Service, Ottawa, Ontario, Canada. <https://www.ec.gc.ca/reom-mbs/default.asp?lang=En&n=453CF2F4-1>. Accessed 10 Nov 2017.

Hestbeck, J. B., A. Dzubin, J. B. Gollop, and J. D. Nichols. 1989. Mallard survival from local to immature stage in southwestern Saskatchewan. Journal of Wildlife Management 53:428–431.

Howerter, D. W., M. G. Anderson, J. H. Devries, B. L. Joynt, L. M. Armstrong, R. B. Emery, and T. W. Arnold. 2014. Variation in mallard vital rates in Canadian Aspen Parklands: The Prairie Habitat Joint Venture Assessment. Wildlife Monographs 188:1–37.

Jamieson, L. E., and S. P. Brooks. 2004. Density dependence in North American ducks. Animal Biodiversity and Conservation 27:113–128.

Johnson, F. A., C. T. Moore, W. L. Kendall, J. A. Dubovsky, D. F. Caithamer, J. R. Kelley, and B. K. Williams. 1997. Uncertaintly and the management of mallard harvests. Journal of Wildlife Management 61:202–216.

Kéry, M., and M. Schaub. 2012. Bayesian population analysis using WinBUGS: a hierarchical perspective. Academic Press, Amsterdam, The Netherlands.

Koons, D. N., T. W. Arnold, and M. Schaub. 2017. Understanding the demographic drivers of realized population growth rates. Ecological Applications 27:2102–2115.

Koons, D. N., D. T. Iles, M. Schaub, and H. Caswell. 2016. A life-history perspective on the demographic drivers of structured population dynamics in changing environments. Ecology Letters 19:1023–1031.

Koons, D. N., J. J. Rotella, D. W. Willey, M. Taper, R. G. Clark, S. Slattery, R. W. Brook, R. M. Corcoran, and J. R. Lovvorn. 2006. Lesser scaup population dynamics: what can be learned from available data? Avian Conservation and Ecology 1(3):6.

Lebreton, J.-D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypothesis using marked animals: a unified approach with case studies. Ecological Monographs 62:67–118.

Lindberg, M. S., W. L. Kendall, J. E. Hines, and M. G. Anderson. 2001. Combining band recovery data and Pollock's robust design to model temporary and permanent emigration. Biometrics 57:273–281.

Link, W. A., and R. J. Barker. 2005. Modeling association among demographic parameters in analysis of open population capture-recapture data. Biometrics 61:46–54.

Lunn, D. J., A. Thomas, N. Best, and D. Spiegelhalter. 2000. WinBUGS - A Bayesian modelling framework: concepts, structure, and extensibility. Statistics and Computing 10:325–337.

Martin, F. W., R. D. Pospahala, and J. D. Nichols. 1978. Assessment and population management of North American migratory birds. Pages 187–239 *in* J. Cairns, G. P. Patil, and W. E. Waters, editors. Environmental biomonitoring, assessment, prediction, and management —Certain case studies and related quantitative issues. International Cooperative Publishing House, Fairland, Maryland, USA.

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.

Maunder, M. N., P. R. Crone, A. E. Punt, J. L. Valero, and B. X. Semmens. 2017. Data conflict and weighting, likelihood functions and process error. Fisheries Research 192:1–4.

Maunder, M. N., and A. E. Punt. 2013. A review of integrated analysis in fisheries stock assessment. Fisheries Research 142:61–74.

Nichols, J. D. 1991. Extensive monitoring programs viewed as long-term population studies: the case of North American waterfowl. Ibis 133(Supplement):89–98.

Nichols, J. D., and J. E. Hines. 1987. Population ecology of the mallard VIII: Winter distribution patterns and survival rates of winter-banded mallards. U.S. Fish and Wildlife Service Resource Publication 162, Washington, D.C., USA.

Nichols, J. D., M. D. Koneff, P. J. Heglund, M. G. Knutson, M. E. Seamans, J. E. Lyons, J. M. Morton, M. T. Jones, G. S. Boomer, and B. K. Williams. 2011. Climate change, uncertainty, and natural resource management. Journal of Wildlife Management 75:6–18.

Nichols, J. D., M. C. Runge, F. A. Johnson, and B. K. Williams. 2007. Adaptive harvest management of North American waterfowl populations: a brief history and future prospects. Journal of Ornithology 148(Suppl. 2): S343–S349.

Nichols, J. D., S. L. Stokes, J. E. Hines, and M. J. Conroy. 1982. Additional comments on the assumption of homogeneous survival rates in modern bird banding estimation models. Journal of Wildlife Management 46:953–962.

Osnas, E. E., M. C. Runge, B. J. Mattsson, J. Austin, G. S. Boomer, R. G. Clark, J. Austin, P. Devers, J. M. Eadie, E. V. Lonsdorf, and B. G. Tavernia. 2014. Managing harvest and habitat as integrated components. Wildfowl Special Issue 4:305–328.

Osnas, E. E., Q. Zhao, M. C. Runge, and G. S. Boomer. 2016. Cross-seasonal effects on waterfowl productivity: implications under climate change. Journal of Wildlife Management 80:1227–1241.

Otis, D. L., and G. C. White. 2004. Evaluation of ultrastructure and random effects band recovery models for estimating relationships between survival and harvest rates in exploited populations. Animal Biodiversity and Conservation 27:157–173.

Padding, P. I., and J. A. Royle. 2012. Assessment of bias in US waterfowl harvest estimates. Wildlife Research 39:336–342.

Pearse, A. T, D. H. Johnson, K. D. Richkus, F. C. Rohwer, R. R. Cox Jr., and P. I. Padding. 2014. Accuracy of aging ducks in the U.S. Fish and Wildlife Service Waterfowl Parts Collection Survey. Wildlife Society Bulletin 38:26–32.

Péron, G., C. A. Nicolai, and D. N. Koons. 2012. Demographic response to perturbations: the role of compensatory density dependence in a North American duck under variable harvest regulations and changing habitat. Journal of Animal Ecology 81:960–969.

Pledger, S., and C. J. Schwarz. 2002. Modelling heterogeneity of survival in band-recovery data using mixtures. Journal of Applied Statistics 29:315–327.

Plummer, M. 2003. JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. Proceedings of the 3rd International Workshop on Distributed Statistical Computing (DSC 2003), Vienna, Austria.

Pollock, K. H., M. J. Conroy, and W. S. Hearn. 1995. Separation of hunting and natural mortality using ring-return models: an overview. Journal of Applied Statistics 22:557–566.

Pollock, K. H., J. D. Nichols, C. Brownie, and J. E. Hines. 1990. Statistical inference for capture-recapture experiments. Wildlife Monograph 107:1–97.

Raftovich, R. V., S. C. Chandler, and K. A. Wilkins. 2015. Migratory bird hunting activity and harvest during the 2013-14 and 2014-15 hunting seasons. U.S. Fish and Wildlife Service, Laurel, Maryland, USA.

Robinson, R. A., C. A. Morrison, and S. R. Baillie. 2014. Integrating demographic data: towards a framework for monitoring wildlife populations at large spatial scales. Methods in Ecology and Evolution 5:1361–1372.

Ross, B. E., M. B. Hooten, J. M. DeVink, and D. N. Koons. 2015. Combined effects of climate, predation, and density dependence on greater and lesser scaup population dynamics. Ecological Applications 25:1606–1617.

Ross, M. V., R. T. Alisauskas, D. C. Douglas, and D. K. Kellett. 2017. Decadal declines in avian herbivore reproduction: density-dependent nutrition and phenological mismatch in the Arctic. Ecology 98:1869–1883.

Sauer, J. R., and W. A. Link. 2011. Analysis of the North American Breeding Bird Survey using hierarchical models. Auk 128:87–98.

Schaub, M., and F. Abadi. 2011. Integrated population models: a novel analysis framework for deeper insights into population dynamics. Journal of Ornithology 152:227–237.

Schaub, M., and D. Fletcher. 2015. Estimating immigration using a Bayesian integrated population model: choice of paratemerization and priors. Environmental and Ecological Statistics 22:535–549.

Schaub, M., H. Jakober, and W. Stauber. 2013. Strong contribution of immigration to local population regulation: evidence from a migratory passerine. Ecology 94:1828–1838.

Schmidt, J. H., D. S. Johnson, M. S. Lindberg, and L. G. Adams. 2015. Estimating demographic parameters using a combination of known-fate and open N-mixture models. Ecology 96:2583–2589.

Seber, G. A. F. 1970. Estimating time-specific survival and reporting rates for adult birds from band returns. Biometrika 57:313–318.

Sedinger, J. S., M. S. Lindberg, and N. D. Chelgren. 2001. Age-specific breeding probability in black brant: effects of population density. Journal of Animal Ecology 70:798–807.

Smith, G. W. 1995. A critical review of the aerial and ground surveys of breeding waterfowl in North America. U.S. Department of the Interior, National Biological Service. Biological Science Report 5, Washington, D.C., USA.

U.S. Fish and Wildlife Service. 2015. Waterfowl population status, 2015. U.S. Department of the Interior, Washington, D.C. USA.

U.S. Fish and Wildlife Service. 2016. Adaptive Harvest Management: 2017 Hunting Season. U.S. Department of the Interior, Washington, D.C. USA.

Weegman, M. D., S. Bearhop, A. D. Fox, G. M. Hilton, A. J. Walsh, J. L. McDonald, and D. J. Hodgson. 2016. Integrated population modelling reveals a perceived source to be a cryptic sink. Journal of Animal Ecology 85:467–475

Zimmerman, G. S., W. A. Link, M. J. Conroy, J. R. Sauer, K. D. Richkus, and G. S. Boomer. 2010. Estimating migratory game-bird productivity by integrating age ratio and banding data. Wildlife Research 37:612–622.

Zimmerman, G. S., J. R. Sauer, K. Fleming, G. S. Boomer, P. K. Devers, and P. R. Garrettson. 2017. Integrating Breeding Bird Survey and demographic data to estimate wood duck population size in the Atlantic Flyway. Condor 119:616–628.

Zimmerman, G. S., J. R. Sauer, W. A. Link, and M. Otto. 2012. Composite analysis of black duck breeding population surveys in Eastern North America. Journal of Wildlife Management 76:1165–1176.

Zipkin, E. F., and S. P. Saunders. 2018. Synthesizing multiple data types for biological conservation using integrated population models. Biological Conservation 217:240–250.

Associate Editor: Christopher Williams.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website.