Integrated Population Models Facilitate Ecological Understanding and Improved Management Decisions

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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 Drawing from our own published and unpublished work, we demonstrate how IPMs could be used to identify the critical vital rates that have had the greatest influence on population change in lesser scaup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.

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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).
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 ($\hat{p}$) 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 ($\hat{s}_t$) 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 (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 $N_{t+1} = N_t(S_{a} + F_{a} S_{j})$, where $N_t$ represents breeding population size in year $t$, $S_{a}$ is adult annual survival, $F_{a}$ is annual fecundity (sexes combined), and $S_{j}$ 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 $2 \times 2$ projection matrix with count, survival, and fecundity data restricted to juvenile ($j$) and adult females ($af$):

$$
[ N_{j} \ N_{af} ]_{t+1} = 
[ S_{j} 0.5F \ S_{af} 0.5F ] \times 
[ N_{j} \ N_{af} ]_{t},
$$

(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, Howerton 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 $\pi$ for females and $(1-\pi)$ for males.

$$
[ N_{1f} \ N_{2f} \ N_{1m} \ N_{2m} ]_{t+1} = 
[ 0.5F_{1} S_{1f} \ 0.5F_{2} S_{2f} \ 0 \ 0 ] \times 
[ N_{1f} \ N_{2f} \ N_{1m} \ N_{2m} ]_{t},
$$

(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, Howerton 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; 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 (Aug. – May, + 1, May, + 1 – Aug., + 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 (Howerton 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 (Howerton 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.

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. 2010b, 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

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**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 (θi). The large rectangles represent the individual likelihoods for the state-space model (LSS; count data), Seber recovery model (Lcr; band-recovery data), and multinomial model (Lw; parts collection survey). In regions where these rectangles overlap, multiple data sets contribute to parameter estimation. The joint likelihood of the IPM (LIPM) represents the product of all 3 data sources, given the estimated parameters, and is obtained as the joint product of the 3 individual likelihoods.
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-km² 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 (ψj and ψa, which include permanent emigration) and annual resighting probability (ρj) 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:

\[ N_{t+1} = \text{Binomial}(\phi, N_t) + \text{Poisson}(0.5 \times H_S \times HDN_t \times DS_t \times \psi_j \times N_t) \]

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, ψj, and ψa as binomials with vague priors (σ~uniform[0,1]), converted them to logit scale, and treated site-years as random effects with vague prior distributions (σ~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 (x̄, SE), and maximum likelihood estimates of ψj and ψa (x̄, 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 (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 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 (φa), averaged over both sites and all years, was 0.679 (SD = 0.102, x̄ SE = 0.061) based on maximum likelihood estimates in Anderson et al. (1997: table 4) and 0.686 (σ = 0.072, x̄ 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.

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 (L), 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]):

\[ N_{t+1} = \text{Binomial}(\phi, N_t) + \text{Poisson}(0.5 \times H_S \times HDN_t \times DS_t \times \psi_j \times N_t) + \text{Poisson}(L_t) \]

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.
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 \( e_t \) 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 \( e_t \) 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 trade-offs 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 \( F_{HY} \); the number of offspring fledged per adult female of a given age class), but also survival \( S \), Seber recovery rates \( \beta \), 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 \( W_{f,JFHY,t} \) from the Parts Collection Survey as follows:

\[
W_{f,JFHY,t} = \left( F_{HY} \cdot n_{f,HY,t} + F_{2+,f} \cdot n_{f,2+,t} \right) \cdot 0.5 \cdot (1 - S_{FHY,monthly,1}) \cdot r_{f,JFHY,t}
\]

The numerator of this equation, \( F_{HY} \cdot n_{f,HY,t} + F_{2+,f} \cdot n_{f,2+,t} \) is fecundity of all yearling and older females, respectively, 0.5 is the presumed sex ratio of offspring, \( (1 - S_{FHY,monthly,1}) \) is the probability that a juvenile female scaup died between fall and spring banding, and \( r_{f,JFHY,t} \) 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
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.

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LITERATURE CITED


