2-21-2023

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Received: 20 September 2022 | Revised: 30 January 2023 | Accepted: 21 February 2023

DOI: 10.1002/jwmg.22405

RESEARCH ARTICLE

THE JOURNAL OF WILDLIFE MANAGEMENT

THE WILDLIFE SOCIETY

Population dynamics and harvest management of eastern mallards

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Abstract

Managing sustainable harvest of wildlife populations requires regular collection of demographic data and robust estimates of demographic parameters. Estimates can then be used to develop a harvest strategy to guide decision-making. Mallards (*Anas platyrhynchos*) are an important species in the Atlantic Flyway for many users and they exhibited exponential growth in the eastern United States between the 1970s and 1990s. Since then, estimates of mallard abundance have declined 16%, prompting the Atlantic Flyway Council and United States Fish and Wildlife Service to implement more restrictive hunting regulations and develop a new harvest strategy predicated on an updated population model. Our primary objective was to develop an integrated population model (IPM) for use in an eastern mallard harvest management strategy. We developed an IPM using annual estimates of breeding abundance, 2-season banding and recovery data, and hunter-harvest data from 1998 to 2018. When developing the model, we used novel model selection methods to test various forms of a sub-model for survival including estimating the degree of harvest additivity and any age-specific trends. The top survival sub-model included a negative annual trend on juvenile survival. The IPM posterior estimates for population abundance tracked closely with the observed estimates and estimates of mean annual population growth rate ranged from 0.88 to 1.08. Our population model provided increased precision in abundance estimates compared to survey methods for use in an updated harvest strategy. The IPM posterior estimates of survival rates were relatively stable for adult cohorts, and annual growth rate was positively correlated with the female age ratio, a measure of reproduction. Either or both of those demographic parameters, juvenile survival or reproduction, could be a target for management efforts to address the population decline. The resulting demographic parameters provided information on the equilibrium population size and can be used in an adaptive harvest strategy for mallards in eastern North America.

KEYWORDS

Bayesian model selection, full annual cycle, integrated population model, survival

Managing sustainable harvest of wildlife populations typically requires robust estimates of population demographic parameters. There are multiple ways for managers to obtain demographic estimates, but all rely on some regular collection of data to obtain the parameters. The demographic estimates may then be used in a harvest strategy that guides decision making. Harvest strategies for waterfowl in North America are developed for species at the scale of 4 flyways: Atlantic, Mississippi, Central, and Pacific (Hawkins 1984, Nichols et al. 1995). In the United States, harvest regulations for multiple species are often based on the population dynamics of a single species such as mallards (*Anas platyrhynchos*; Johnson et al. 2015). Individual species that have restricted distributions or declining populations may have a species-specific harvest strategy in an attempt to react to those unique circumstances (Runge and Boomer 2005, Boomer and Johnson 2007). Each of the harvest strategies are based on an assessment of population dynamics in relation to harvest pressure, usually through a population model (U.S. Fish and Wildlife Service 2019*a*).

Waterfowl harvest strategies have increasingly relied on the use of integrated population models (IPMs), which link population count data and demographic parameters through a joint likelihood (Besbeas et al. 2002, Schaub et al. 2007, Arnold 2018). Harvest strategies for American black ducks (*Anas rubripes*; Conroy et al. 2002, USFWS 2019*a*), Atlantic brant (*Branta bernicula hrota*; Roberts et al. 2021), scaup (*Aythya* spp.; USFWS 2019*a*), and others rely on IPMs to obtain demographic estimates for use in making regulatory decisions. These models integrate multiple sources of data in a hierarchical model to use all data and the associated uncertainty with the result of more precise parameter estimates (Kéry and Royle 2020). There is often uncertainty about the appropriate functional form for a specific sub-model in the IPM. The Bayesian statistical framework allows for flexibility in model fit, but it can complicate model selection, and often formal model selection is omitted (Hooten and Hobbs 2015). Bayesian prediction information criterion (BPIC) and Watanabe-Akaike information criterion (WAIC; Watanabe 2010), an estimator of BPIC, provide robust, fully Bayesian model comparison based on out-of-sample predictive performance (Hooten and Hobbs 2015, Link and Sauer 2016). These tools, when combined with the robust and long-term datasets associated with North American waterfowl, provide an opportunity to improve our knowledge of relationships between demographic rates, ecological processes, and harvest effects but present computational challenges (Magnusson et al. 2019).

Full-annual-cycle models for birds are uncommon because of the lack of data from throughout the annual cycle for many species (Hostetler et al. 2015). North American waterfowl have been monitored for decades using multiple programs, which provide data to build a full-annual-cycle model, such as an IPM, that may be used in adaptive management decisions. For example, when combined with resource manager objectives, an IPM can be used to develop a defensible and robust harvest management decision-making tool. The implications of the equilibrium population dynamics estimated from more precise model parameters, using data from throughout the annual cycle, allow managers to set state-dependent regulations that can achieve the dual objectives of long-term population conservation and providing hunting opportunity.

The USFWS currently sets the general duck hunting season in the Atlantic Flyway using a multi-species adaptive framework that does not include mallards (Johnson et al. 2019). Mallards, however, are still an important species in the Atlantic Flyway for many users, comprise approximately 25% of the annual harvest, and are consistently in the top 2 species in the bag (Raftovich et al. 2022). Mallards exhibited exponential growth in the eastern United States between the 1970s and 1990s (Alisauskas et al. 2014) but have declined 16% since 2000 (USFWS 2019*b*). The population decline of eastern mallards, those breeding in the footprint of the Atlantic Flyway and eastern Canada, has not been linked to a decline in a specific demographic parameter, but there are several hypotheses that may explain the decline. Over the last century, the landscape configuration of eastern North America has undergone broad changes, from deforestation, urbanization, and subsequent forest succession that may influence survival or fecundity (Holmes and Sherry 2001). In addition, captive mallards have been released in large numbers in some parts of the Atlantic Flyway, potentially altering demographic rates (Lavretsky et al. 2020).

In response to declining abundance seen in a previous harvest strategy (Johnson et al. 2002), in 2018 the Atlantic Flyway Council (AFC) and the USFWS implemented restrictive regulations consisting of a 2-bird daily bag limit, based on harvest potential estimated using a prescribed take level framework (Runge et al. 2009). The AFC then initiated work to review mallard dynamics and the effect of harvest on those dynamics. Because of this review, the AFC and USFWS agreed to develop a new state-dependent eastern mallard harvest strategy. The fundamental objectives of the new strategy were to sustain an eastern mallard population that meets legal mandates (e.g., Migratory Bird Treaty Act) and provides consumptive and non-consumptive uses indefinitely. Relative to consumptive uses, the objectives were to manage harvest at 98% of maximum sustainable yield, minimize closed seasons, and minimize annual regulatory changes. These objectives were chosen to meet legal mandates and address concerns of stakeholders as represented by the AFC (Nichols et al. 1995).

Our primary objective was to develop an IPM for use in an eastern mallard harvest management strategy. The IPM needed to accurately describe the annual demographics, allow for potential additive or compensatory effects of harvest on annual survival and population growth, describe the effect of density dependence on annual population growth, and provide relatively precise estimates of demographic parameters for use in an optimization procedure to make annual regulatory decisions (Johnson et al. 1997, 2019). Our objectives included determining demographic rates linked to the population trend and equilibrium dynamics of the eastern mallard population.

STUDY AREA

Eastern mallards are defined as the population of mallards breeding in the United States Atlantic Flyway, and in Canada east of 86 degrees longitude (Figure 1), based on the distribution of band recoveries through time (Anderson and Henny 1972). Their range extends from upper James Bay south through Canada and the United States to northern Florida, an area nearly 3 million km^2. They generally migrate south out of Canada during winter and are year-round residents in the United States. Migration distance is often a function of available open water. The biology of eastern mallards appears to differ markedly in several important ways from mallards breeding farther west (mid-continent mallards; Johnson et al. 2002, Hoekman et al. 2010). Abundance of mid-continent mallards is much larger than eastern mallards and has not experienced a sustained decline in recent years (USFWS 2019*b*). Environmental conditions affecting each population are different between prairie breeding areas inhabited by mid-continent mallards versus the more forested landscapes occupied by eastern mallards (Heusmann 1991, Johnson et al. 2002). Mid-continent mallards rely on ephemeral wetlands for breeding, and their population naturally cycles with observed wetland conditions. In contrast, eastern mallards use more permanent waterbodies for breeding, and occupy areas of greater human densities. Accordingly, managers suspect there may be a significant difference between mid-continent and eastern mallards in sustainable rates of harvest. Managers collect data on mallard population dynamics throughout their annual cycle, from breeding season surveys in spring, to captures in summer, recoveries during fall, and captures again during winter.

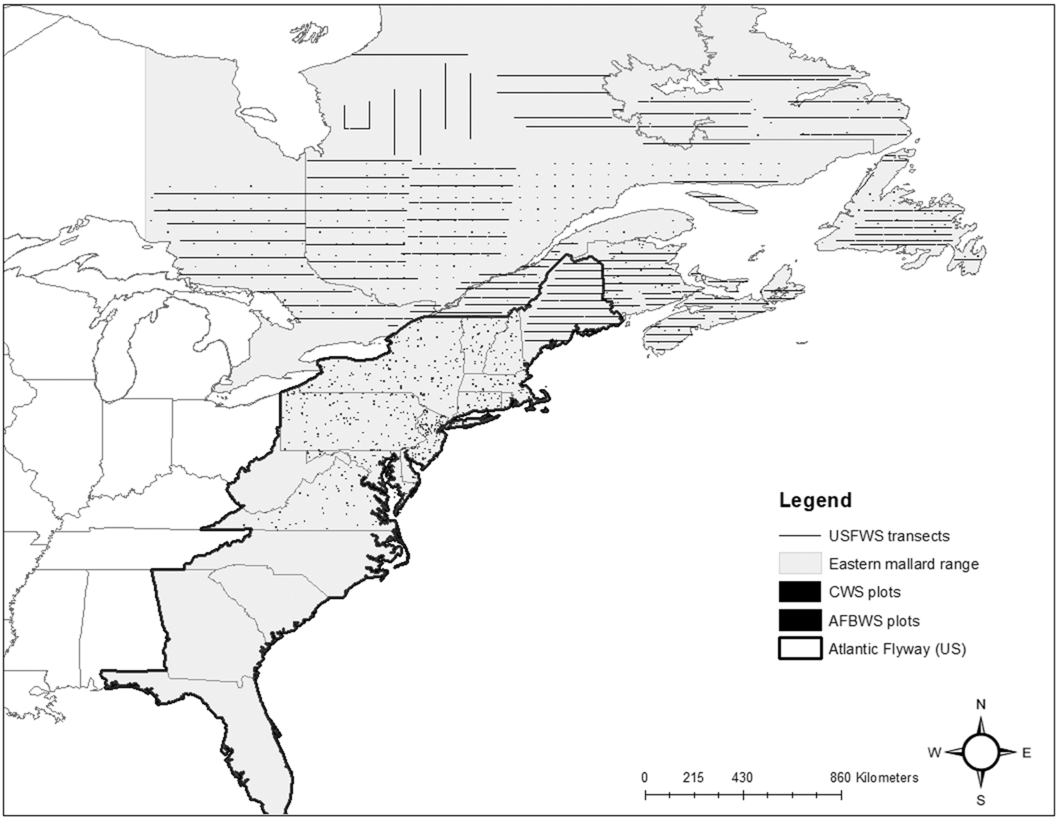

FIGURE 1 Eastern mallard range in the United States and Canada, and surveys used to estimate population abundance, 1998–2018. Plot surveys are conducted by the Canadian Wildlife Service (CWS) using helicopters, transect surveys conducted by the United States Fish and Wildlife Service (USFWS) using fixed-wing aircraft, and by states in the Atlantic Flyway Breeding Waterfowl Survey (AFBWS) using ground counts. Definition of eastern mallard range is based on management boundaries not true species range.

Eastern North America has a temperate climate with 4 seasons. Temperatures vary greatly from summer to winter with appreciable year-round precipitation. The Atlantic Ocean has a moderating effect on temperatures in coastal areas, warming in winter and cooling in summer. Average annual precipitation ranges from about 90–125 cm. Elevation goes from sea level to 1,900 m across the region with topography ranging from coastal plains to the Appalachian Mountains. Similarly, native vegetation communities vary greatly, though hardwood forests often dominate the northern portion of the study area, while softwoods are more common in the south. Land use varies as well, with agriculture and timber production dominating in most rural areas. The northeastern United States is the most densely populated region of the United States and there are large urban centers from southern Canada south through Florida.

METHODS

We developed an IPM using 3 sources of data: annual breeding abundance estimates, annual banding and recovery data, and annual hunter-harvested parts collection (i.e., wing) data. We used data from 1998–2018, as that was the start of the current eastern mallard abundance survey and some banding data (post-season) was sparse prior to 1998.

Abundance, survival, and age ratio data

Mallard breeding abundance in eastern North America is monitored using 2 surveys: the Eastern Breeding Waterfowl Population and Habitat Survey and the Atlantic Flyway Breeding Waterfowl Survey. The former consists of an aerial plot survey conducted by the Canadian Wildlife Survey (CWS) using helicopters (Bateman et al. 2017) and a transect survey conducted by the USFWS using fixed-wing aircraft (Smith 1995). A portion of the CWS plot surveys and USFWS transects overlap. These data are integrated using a hierarchical model to estimate total abundance in eastern Canada and Maine, USA, producing an eastern composite estimate (Zimmerman et al. 2012). In the Atlantic Flyway, a ground plot survey is used to estimate breeding waterfowl abundance from Virginia north to New Hampshire, USA (Heusmann and Sauer 1997, 2000). These data are analyzed in a Bayesian framework that accounts for time of day of the survey (Sauer et al. 2014). The totals from the eastern composite estimate and the Atlantic Flyway Breeding Waterfowl Survey are summed to obtain an estimate of mallard abundance in eastern North America.

We estimated annual survival and harvest rates using data from banded and hunter-recovered birds. Mallards were banded prior to the hunting season (i.e., pre-season; 1 July–30 September; calendar years 1998–2018) and directly following the hunting season (i.e., post-season; 15 January–31 March; calendar years 1999–2018) using standard protocols (Devers et al. 2021). We used all known-age and known-sex wild-caught birds that were not fitted with auxiliary markers (transmitters, nasal disks) and had no invasive procedures done (i.e., blood samples). Each bird was fitted with a standard United States Geological Survey leg band and the band number, sex, and age were recorded (Krapu et al. 1979, Carney 1992). During pre-season banding operations, birds were aged as hatch year (juvenile) or after hatch year (adult). During post-season banding operations, birds were aged as second year (juvenile) or after second year (adult). We removed all post-season banded birds aged as after hatch year from our data, as that indicates an ambiguous age. We used encounters of banded birds that were shot or found dead between September and January of each year (1998–2019).

We used data from the USFWS and CWS Parts Collection Surveys (PCS; Geissler 1990), in combination with mark-recovery data, to estimate adjusted fall age ratios and differential vulnerability to harvest (Paloheimo and Fraser 1981). The PCS survey provides information on the species, sex, and age composition of the annual harvest. We used all USFWS PCS records of mallards harvested in the Atlantic Flyway during the 1998–2018 hunting seasons. We used CWS PCS records from Ontario, Quebec, and Atlantic Canada (New Brunswick, Nova Scotia, Prince Edward Island, Newfoundland, and Labrador) from 1998–2018.

Integrated population model

We developed a full-annual-cycle IPM to describe eastern mallard population demographics (Besbeas et al. 2002, Schaub et al. 2007, Hostetler et al. 2015, Arnold 2018; Figure 2). The IPM was composed of 3 sub-models: a Brownie dead recovery model using pre- and post-season banding data to estimate age-specific harvest and seasonal survival rates (Brownie et al. 1985), a fecundity model integrating annual PCS and mark-recovery data, and a state-space model of the annual breeding abundance.

Survival sub-model and model selection

We linked cohort specific (*ch*, adult male, adult female, juvenile male, and juvenile female) annual ($S_{ch,t}$), hunting season ($S^{(h)}_{ch,t}$; August–January), and non-hunting season ($S^{(n)}_{ch,t}$; February–August) survival using the Brownie H_7 model (Brownie et al. 1985, Devers et al. 2021). We also estimated annual cohort-specific recovery ($f_{t,ch}$)

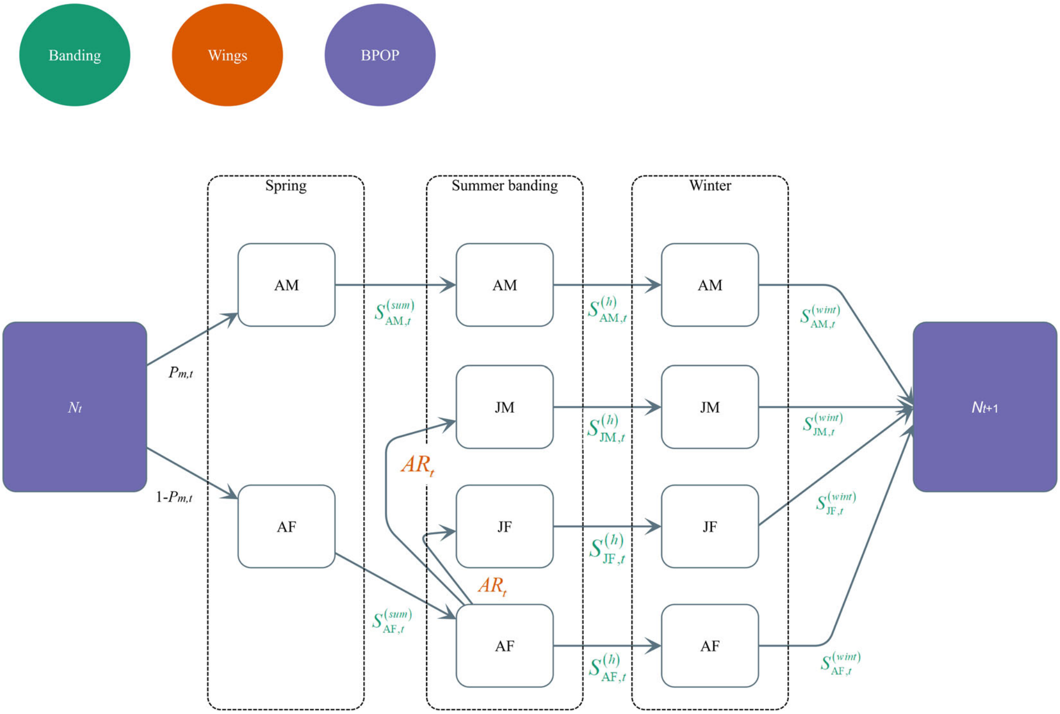

FIGURE 2 Annual life-cycle diagram of the integrated population model used for eastern mallards in the United States and Canada, 1998–2018. Time-step changes are cohort-specific abundance (adult male [AM], adult female [AF], juvenile male [JM], and juvenile female [JF]) and transition estimates based on data are color-coded to signify the data source (banding, hunter surveys [wings], and a state-space model of abundance [BPOP]). Population demographic estimates obtained from the model include annual (*t*) population abundance (*N*), proportion of the population that is male (*Pm*), and age ratio (*AR*). We also estimated survival (*S*) during summer (*sum*; May–July), the hunting season (*h*; August–January), and overwinter (*wint*; February–April).

probabilities from the Brownie H_7 model. We linked recovery to annual harvest rates ($h_{t,ch}$) using a prior probability distribution of beta (1,1) and reporting rates (r_t) by

$$f_{t,ch} = h_{t,ch} \times r_t.$$

We used year-specific values of mean reporting rates with associated standard deviations from work on the mid-continent population of mallards as prior information on r_t (G. S. Boomer, USFWS, personal communication), as those estimates are recent and previous work has suggested there are no differences in reporting rates among flyways (Arnold et al. 2020). We then estimated kill rates ($K_{t,ch,t}$) using an estimate of crippling loss (c; 0.2; Anderson and Burnham 1976) as

$$K_{t,ch} = h_{t,ch}/(1 - c).$$

We evaluated multiple structural forms of $S_{ch,t}$ as a function of $S^{(h)}_{ch,t}$, $S^{(n)}_{ch,t}$, and$K_{t,ch}$ (Table 1). We ran each survival sub-model form on the mark-recovery data alone and calculated WAIC (Watanabe 2010), a more reliable estimator of BPIC than the widely used deviance information criterion (DIC). Unlike true leave-one-out cross-validation, WAIC only requires running each model once (Gelman et al. 2014, Hooten and Hobbs 2015, Link and Sauer 2016). The WAIC estimate is computed on the likelihood of each data point, over the full posterior probability sample:

$$WAIC = -2\sum_{i=1}^{n} \log(\text{mean}^s(\Pr(y_i \mid \theta^s))) + 2\sum_{i=1}^{n} \text{var}^s(\log(\Pr(y_i \mid \theta^s))),$$

TABLE 1 Definition and results of statistical tests for functional form of the annual survival sub-model of eastern mallards in the United States and Canada. Testing was to determine the best model for use in an integrated population model using data from 1998–2018. We identified the appropriate model using Watanabe-Akaike information criteria (WAIC). Demographic variables are year (*t*) and cohort-specific (*ch*) annual survival ($S_{ch,t}$) and kill rate ($K_{ch,t}$). Beta values are an intercept term (a_0), a measure of the level of additivity in harvest (a_1), and a linear trend through time (a_3) by age (*A*), either adult or juvenile (*j*), and *I* is an indicator to set a_3 to 0 for adult cohorts in the juvenile-only trend models. In the model allowing for different slopes, the year where the slope changed is indicated by t_{th}.

Description	Annual survival	WAIC	Difference from top model
Partial compensation on annual survival	$S_{ch,j} = \min(a_{0,ch}(1 - a_{1,ch}K_{ch,j}), 1 - K_{ch,t})$	480,448.5	30.3
Common linear trend	$S_{ch,j} = \min(a_{0,ch}(1 - a_{1,ch}K_{ch,j}), 1 - K_{ch,t}) - a_3 t$	480,434.6	16.4
Age-based linear trend	$S_{ch,j} = \min(a_{0,ch}(1 - a_{1,ch}K_{ch,j}), 1 - K_{ch,t}) - a_{3,A} t$	480,419.6	1.4
Juvenile-only linear trend	$S_{ch,j} = \min(a_{0,ch}(1 - a_{1,ch}K_{ch,j}), 1 - K_{ch,t}) - I[A = j]a_3 t$	480,418.2	0.0
Juvenile-only trend, allowing for 2 different slopes	$S_{ch,j} = \min(a_{0,ch}(1 - a_{1,ch}K_{ch,j}), 1 - K_{ch,t}) - I[A = j]a_3 \min(t, t_{th})$	480,418.7	0.5

where *n* is the sample size, y_i is a single data point, and θ^s is posterior sample *s* of the model parameters. Therefore, the first term is the sum of the log of the likelihoods of each data point, averaged over the full posterior probability sample, and the second term is the sum of the variances (over the full posterior probability sample) of the log-likelihoods of each data point. In the case of mark-recovery data, the data points are the outcomes of each release of a marked animal (either recovered in year *t* or not). There were 2 potential issues with estimating WAIC: amount of data and accuracy. With over 300,000 releases and 60,000 samples from the posterior probability, our dataset precluded standard methods for estimating WAIC. Therefore, we relied on the multiple data points that all have the same outcome (for example, there were 216 adult females banded pre-season in 1998 and recovered the same year):

$$WAIC = -2\sum_{O=1}^{O} n_O \log(\text{mean}^s(\Pr(y_O \mid \theta^s))) + 2\sum_{O=1}^{O} n_O \text{var}^s(\log(\Pr(y_O \mid \theta^s))).$$

where *O* is the number of outcomes with ≥1 data point, n_O is the number of data points with outcome *o*, and y_O is an example data point with outcome *o*. In this way, computing WAIC became tractable.

Under some circumstances, such as unusually influential data points, WAIC can fail to estimate BPIC accurately (Vehtari et al. 2017, Link et al. 2020). The R package loo contains functions that not only calculate WAIC and Pareto smoothed importance-sampling leave-one-out cross validation (PSIS-LOOIC; functions waic and loo, respectively) but also provide diagnostics on the reliability of each estimator for a specific dataset and model (Vehtari et al. 2017). Because of the size of our dataset and posterior probability sample, we could not run these functions on the full set of data points; however, we determined that the results of the diagnostics for each data point with the same outcome would be the same. Therefore, we ran the waic and loo functions on the results of the model with a single data point standing in for each outcome with ≥1 data point. Both sets of diagnostics indicated no unusually influential data points, and WAIC and PSIS-LOOIC gave the same estimate of BPIC for the stand-in dataset. These results indicated that WAIC was a reliable model selection tool in this case.

We then used the sub-model with the lowest WAIC value in the full IPM. All forms of the survival sub-model included a relationship with K to estimate the strength of cohort-specific partially-additive harvest mortality on annual survival in the general form of:

$$S_t = a_{0,ch} \times (1 - a_{1,ch} \times K_{ch,t}),$$

where a_0 was an intercept and a_1 was a measure of the additivity relationship. The estimation of $S^{(h)}_{ch,t}$ was the same in all models, where:

$$S^{(h)}_{ch,t} = 1 - K_{ch,t}.$$

In addition, the estimation of $S^{(n)}_{ch,t}$ was the same in all models (Table 1), where:

$$S^{(n)}_{ch,t} = S_{ch,t} / S^{(h)}_{ch,t}.$$

In all cases, we assumed a_0 and the term for linear trend through time (a_3) to have a normal prior with mean 0 and a variance of 1,000. We gave the parameter a_1 a uniform prior constrained to 0–1. In this case 0 represents pure compensation and 1 pure additivity. In all models we estimated cohort-specific seasonal non-hunting season survival for 2 periods. We estimated survival from postseason banding to the spring population survey ($S^{(wint)}_{ch,t}$) and survival from the spring breeding survey to preseason banding ($S^{(sum)}_{ch,t}$) as:

$$S^{(wint)}_{ch,t} = S^{(n)\ 2/3}_{ch,t}$$
$$S^{(sum)}_{ch,t} = S^{(n)\ 1/3}_{ch,t}.$$

Recruitment sub-model

We estimated fall age ratios (juvenile female:adult female) using the ratio of juvenile female to total female wings in the PCS. We used females rather than males in our ratio because they represent the limited reproductive individuals, and using males may have biased our overall estimate high because sex ratios potentially skewed towards males (Johnson and Sargeant 1977, Ohde et al. 1983). We modeled the observed number of juvenile female wings as a binomial distribution from the total female wings. The proportion of juvenile female wings (j_t) was related to the true number of juveniles per adult in the harvest as:

$$j_t = AR^{(1)}_t / 1 + AR^{(1)}_t,$$

where $AR^{(1)}_t$ represented the age ratio uncorrected for differential vulnerability to harvest (DV). We corrected the age ratio for DV to get the corrected age ratio (AR_t) by:

$$AR^{(1)}_t = AR_t \times DV_t$$

We estimated the differential vulnerability of juvenile females (JF) and adult females (AF) as:

$$DV = \frac{\bar{f}_{\mathrm{JF},t}}{\bar{f}_{\mathrm{AF},t}}$$

thus linking mark-recovery data with PCS data. Finally, we modeled AR_t as a function of mallard population size and time:

$$AR_t = \max(\gamma_0 - \gamma_1 \times N_t - \gamma_2 \times t, 0),$$

where γ_0 was the age ratio intercept, γ_1 was the coefficient for population size, N is mallard abundance in year t, and γ_2 was the coefficient for year, allowing for a time trend. We assumed the prior for the age ratio intercept to be uniform from 0 to 2 to limit to realistic values and gave the other coefficients in the recruitment sub-model a normal prior (mean 0, variance 1,000). In addition, we truncated the γ_1 parameter at 0 to not allow positive density dependence.

State-space sub-model

We modeled the breeding abundance estimate from surveys as normal from the mean of latent spring abundance and the variance of the estimate. We split the spring population abundance between males and females and between adults and juveniles by multiplying by the proportion male and the proportion juvenile in the population, respectively. We gave the initial proportion of males in the population a uniform prior (0.5, 0.75), gave the initial proportion of juveniles in the population a uniform prior (0.1, 0.8), and calculated subsequent proportions from the annual sex- and age-specific estimates from the model.

We estimated latent cohort-specific (adult male, adult female, juvenile male, and juvenile female) population sizes through the annual cycle (breeding [spring], post-breeding [fall], and post-hunting season [winter]; Figure 2). We assumed that the juvenile sex ratio in the population at the time of harvest was 1:1 when using AR_t in the model. The life-cycle model transitions juveniles to adults after the breeding season, immediately before pre-season banding operations, to match with the annual juvenile survival estimate from pre-season banding. We estimated the finite annual population growth rate ($\lambda_t = N_{t+1}/N_t$) as the latent breeding season population change over one year.

Model implementation

We estimated posterior parameter distributions using Markov chain Monte Carlo methods in JAGS (Plummer 2003) with the jagsUI package (Kellner 2019) for Program R (R Core Team 2018; code and data are available at https://doi.org/10.5066/P9ZMPO0J [Roberts et al. 2023]). We considered the Gelman statistic $\hat{R}$ with values <1.1 as indicative of adequate model convergence (Gelman and Hill 2006). We calculated Bayesian *P*-values for each of the sub-models within the IPM (Conn et al. 2018, Kéry and Royle 2020). If Bayesian *P*-values are too close to 0 or 1, it indicates lack of fit or unreasonably good fit. Although Bayesian *P*-values can be biased towards 0.5, they are a widely used, generally accepted, and informative test of fit. We also calculated $\hat{c}$, another fit statistic that estimates the magnitude of lack of fit. When $\hat{c}$ is >1, the value suggests overdispersion of the data compared to the model, although values <4 can be corrected for. To quantify the strength of the contribution of temporal variation in demographic parameters to variation in λ_t, we calculated the correlation between model parameters and λ_t using all Markov chain Monte Carlo posterior estimates and function cor. We also calculated the probability that the correlation was greater than 0.

We used the resulting model estimates to quantify equilibrium dynamics of the harvested eastern mallard population. We used the estimate of annual survival from the final year and beta parameters from the IPM to derive the optimum harvest rate for each population size (i.e., the harvest rate that resulted in a stable population). For each harvest rate over a range (0–0.5 by 0.001), we used the optimize function in Program R to estimate the breeding population abundance that eastern mallards would equilibrate at by calculating the 1-year change in abundance that was closest to 0. We considered the harvest rate that resulted in the highest harvest to be the equilibrium harvest rate. The result pertains to the harvest rate on the spring breeding abundance, so we corrected the harvest rate to account for average reproductive rate to get the equilibrium harvest rate of the fall flight (breeding abundance plus reproduction minus mortality). We adjusted the harvest rate by c to get an equilibrium K.

RESULTS

Annual observed population estimates ranged from 1,421,000 in 1998 to 1,066,000 in 2018 (Table S1, available in Supporting Information; Figure 3). During 1998–2018, 91,148 adult and 196,908 juvenile mallards were marked during pre-season banding, with an average of nearly 14,000 mallards banded each year. Post-season banding from 1999–2018 yielded 8,613 adults and 9,471 juveniles, an average of just over 900 mallards/year. The female mallard wings submitted annually in the United States and Canada ranged from 3,743 in 2000 to 1,773 in 2015 (Table S1).

We tested 5 forms of the survival sub-model. The top model included a juvenile trend in annual survival, which we used in the IPM. The second ranked model included a trend in juvenile survival with an inflection point allowing for 2 different slopes over time, with a difference in WAIC from the top model of 0.5 (Table 1). The top 3 models all included a negative trend on juvenile survival.

The IPM posterior estimates for population abundance tracked closely with the observed estimates (Figure 3). Posterior median estimates ranged from 1,590,000 in 2000 to 1,130,000 in 2018. Abundance estimates from the IPM showed a less consistent year-to-year decline compared to the observed estimates. The IPM posterior median estimates of mean annual growth rate from 1998–2018 ranged from 0.88 in 2000 to 1.08 in 2001. Average population growth rate over the entire period (geometric mean) was 0.99 (95% credible interval = 0.98–1.00).

The IPM posterior median estimates of annual and seasonal survival rates were relatively stable for adult cohorts and declined through time for juvenile cohorts (Figure 4; Table S2, available in Supporting Information). The

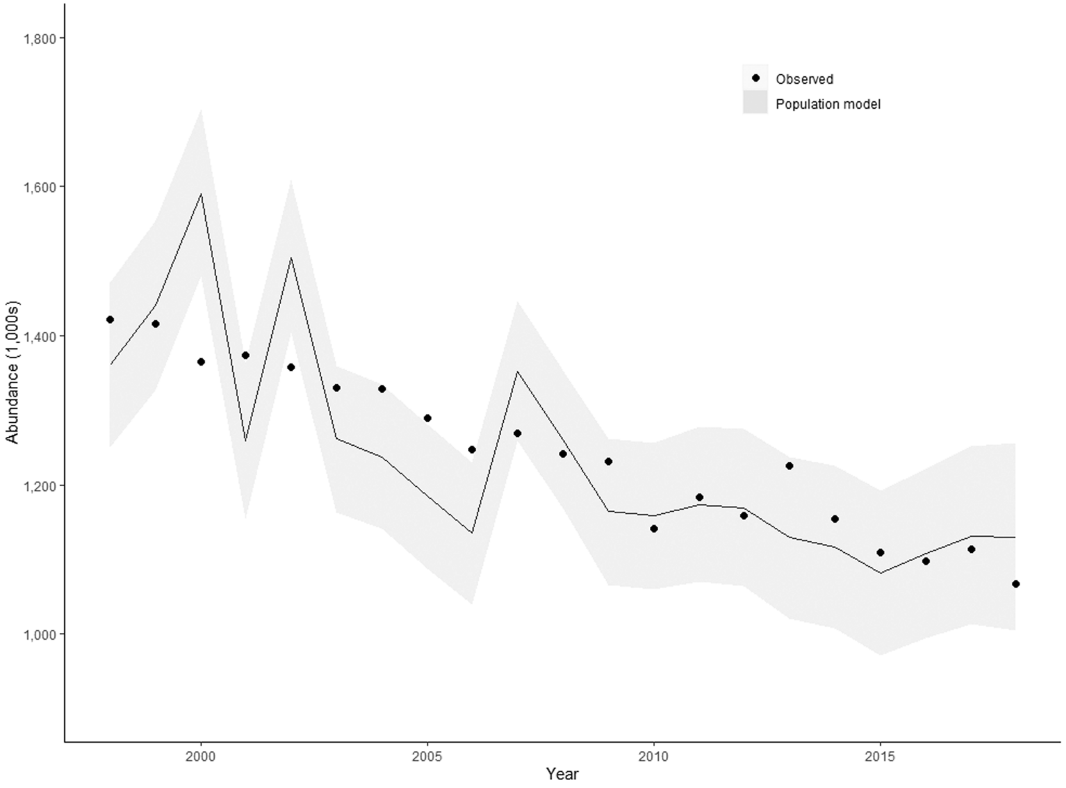

FIGURE 3 Population abundance of eastern mallards in the United States and Canada based on 2 methods, 1998–2018. The observed population is derived from multiple aerial surveys during the breeding season. The observed data is used in a full-annual-cycle integrated population model. We present posterior median estimates (line) and 95% credible intervals (shading) of population abundance from the model.

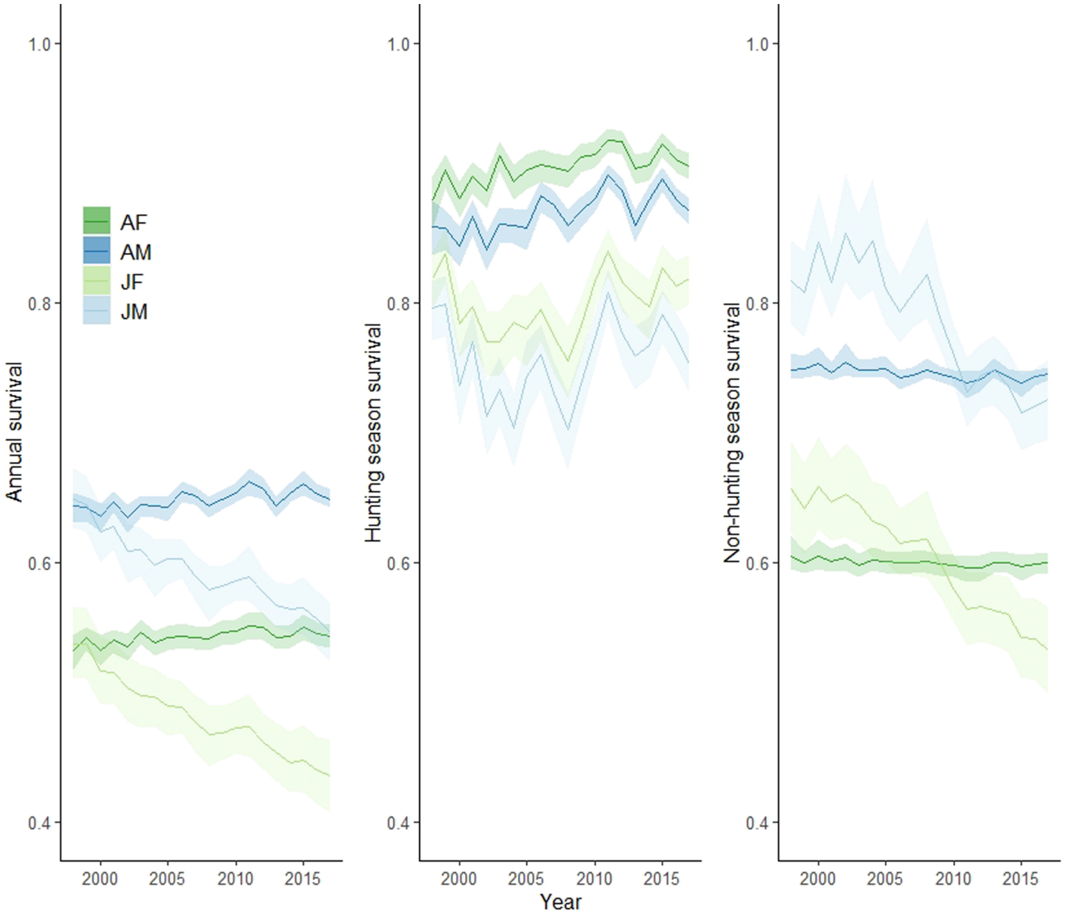

FIGURE 4 Plots of annual (August–August, left), hunting season (August–January, middle), and non-hunting season (February–August; right) survival of eastern mallards in the United States and Canada derived from an integrated population model, 1998–2018. Estimates are cohort-specific (adult male [AM], adult female [AF], juvenile male [JM], and juvenile female [JF]). Dark lines represent the posterior median estimate and the shading represents the 95% credible interval.

time trend on annual juvenile survival had a 95% credible interval of 0.014–0.032. Harvest rates were stable for all cohorts in the last 10 years, a period with consistent regulations (60-day season with a 4-bird bag limit) except the final year (2-bird bag limit). The additivity parameter had a wide credible interval for all cohorts and was similar between adult cohorts (95% credible intervals for male = 0.24–0.96 and female = 0.14–0.99) and between juvenile cohorts (male = 0.02–0.75, female = 0.04–0.97). Posterior median estimates of annual age ratios ranged from 0.74 juvenile females per adult female in 2000 to 1.06 in 2006 (Table S2). The age ratio density-dependent effect (γ_1) was 0.001–0.003, and the reproduction time trend (γ_2) was 0.019–0.064.

Annual growth rate was positively correlated with the female age ratio (r = 0.58–0.80; Figure 5). Estimated correlations between finite population growth rate and adult female survival or harvest rates or with juvenile female survival or harvest rates all overlapped zero. Fit statistics suggested lack of fit for the full IPM using the top survival sub-model (Table 2). Evidence for lack of fit was near zero in pre- and post-season juvenile banding data. The results of the equilibrium analysis suggested a population abundance (during spring breeding) at maximum sustainable yield of 792,000 with a carrying capacity of 1,347,000. The equilibrium population abundance would be reached at an

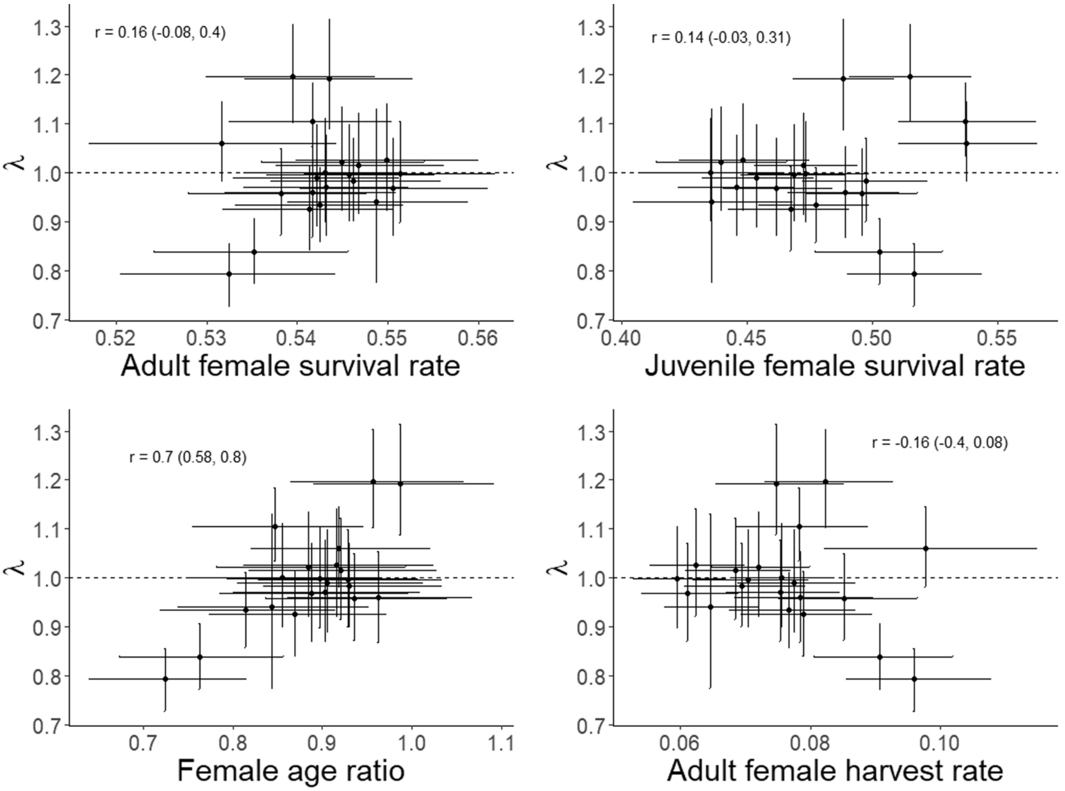

FIGURE 5 Estimated correlation (r) between finite population growth rate (λ) of eastern mallards and adult female (top left) and juvenile female (top right) annual survival, female fall age ratio (juveniles:adults; bottom left), and adult female harvest rate (bottom right). Results are from an integrated population model using data from 1998–2018 in the eastern United States and Canada.

equilibrium kill rate (pooled across cohorts) on the fall flight of 0.19. Observed average estimated kill rate over the time series was 0.17.

DISCUSSION

Our population model provided increased precision in abundance estimates compared to the eastern composite estimates and offered insight into demographic parameters that may be contributing to the population trajectory since 2000. Relative to mallards in the mid-continent of North America, mallards in eastern North America are understudied, and recent declines in population abundance have been attributed to habitat loss or maladaptive genetics (Lavretsky et al. 2020). Our model estimated a declining trend in juvenile survival, and a strong correlation between annual growth rate and reproduction, a result similar to other mallard populations (Zhao et al. 2019). Those demographic parameters, alone or in combination, could be targets for managers to address to reduce the population decline (Horn et al. 2005).

Declining reproduction or juvenile survival may be explained by a couple of primary hypotheses. Forest coverage has increased in the northeastern United States because land previously in agriculture has reverted to forested areas or human development (Brooks 2003, Adams et al. 2019). Mallard breeding density is generally higher in areas with more open vegetation communities (Pospahala et al. 1974), so an increase in forested

TABLE 2 Fit statistics for the various sub-models of an eastern mallard integrated population model. Sub-models included pre-season (1 July–30 September; Pre) and post-season (15 January–31 March; Post) banding models of survival and harvest rate for 4 cohorts (adult male [AM], adult female [AF], juvenile male [JM], and juvenile female [JF]), age-ratios using hunter surveys (Wings), and a state-space model of abundance (BPOP). Data are from calendar years 1998–2018 in the eastern United States and Canada. Measures of fit included Bayesian *P*-values and $\hat{c}$. Bayesian *P*-values close to 0 or 1 suggest lack of fit and when $\hat{c}$ is greater than 1, it suggests overdispersion of the data compared to the model.

Sub-model	Bayesian *P*-value	$\hat{c}$
Pre AM	0.002	1.338
Pre AF	0.002	1.372
Pre JM	0	1.669
Pre JF	0	1.565
Post AM	0.319	1.107
Post AF	0.631	0.955
Post JM	0.001	1.729
Post JF	0.001	1.832
Wings	0.311	1.389
BPOP	0.8	0.779

landscapes may reduce the prevalence of suitable nesting sites. In contrast, mallards are more likely to nest in more developed areas than many waterfowl species so an increase in urbanization may improve mallard survival or reproduction (Heusmann 1991). The other hypothesis is that a changing genetic makeup of mallards may be resulting in lower survival or reproductive capacity. Captive-reared mallards have been released in many areas of the Atlantic Flyway for a hundred years or more, and released birds are from populations of mallards in Europe rather than North America (Lavretsky et al. 2020). Changing genetics may result in a maladapted population and declining abundance due to decreased juvenile survival or reproduction (Lavretsky et al. 2019*a*, 2020).

Despite a different trajectory between eastern mallard and mid-continent mallard populations, we observed similar population dynamics between the 2 populations. In our work, the recruitment parameter had the highest correlation with annual growth rate, similar to a mid-continent mallard population model where recruitment explained most of the variance in annual population growth (Zhao et al. 2019). We estimated population stability would occur at a juvenile ratio of 0.9 juvenile females to adult females. In our data set, recruitment was below the equilibrium value in 4 of the first 10 years of the time series and 6 of the last 10 years.

The top 2 sub-models in our model set included a juvenile-only negative trend in survival. When we included the top sub-model in the IPM, average adult female survival rate was estimated as 0.54 compared to female mid-continent mallard survival estimates of 0.55–0.60 (Anderson and Burnham 1976, Zhao et al. 2019). In contrast to adult survival, we found declining juvenile survival in eastern mallards through time, with no evidence that the decline has stopped. Estimated annual survival for juvenile females in 2018 (0.44; last year of our time series) was 25% lower than seen in the mid-continent population of about 0.55 (Anderson and Burnham 1976, Arnold and Clark 1996). Our highest estimate of juvenile female survival (0.53; first year of our time series) was close to mid-continent mallard estimates. Juvenile survival is the only demographic parameter that showed a pattern through time, suggesting this parameter may be related to the population decline. The difference in adult versus juvenile female non-hunting season survival may be a result of poor body condition leading to winter mortality or to increased predation of inexperienced nesters. Increasing harvest rates may also result in a declining population, but we did not find a change in harvest rates of eastern mallards through time. This is not surprising because all hunting seasons in our time series had the same harvest regulations: 60 days and a 4-bird bag limit. The one exception was the 2018–2019 hunting season, the first with a 2-bird bag limit. The 2 female cohorts each experienced the lowest harvest rate of the time series in this final year.

We used WAIC to select a mark-recovery sub-model for use in our IPM to address the uncertainty about the structure of the survival sub-model. A variety of model selection methods have been used with IPMs, including Akaike's information criterion (AIC; Besbeas et al. 2002), Bayesian information criterion (BIC; Stenglein et al. 2015), DIC (Baillie et al. 2009), indicator variable selection (Abadi et al. 2017, Hostetler et al. 2021), reversible jump Markov chain Monte Carlo (Cave et al. 2010), and WAIC (Davis et al. 2014); however, we are unaware of other IPM studies that use newly available diagnostic tools (Vehtari et al. 2017) to verify that their model selection picks the best model for out-of-data prediction in their model set. This combination of tools could be used more widely to test many population ecology hypotheses, including those related to population limitation and causes of decline for North America's depauperated avifauna (Rosenberg et al. 2019). It is important to note that simply because a model is the best out of a set of models does not necessarily indicate that a model is useful for management decisions (Koons et al. 2022). Null models or models that do not include a link between harvest rate and demographics are not appropriate for harvest management because they do not incorporate a control variable (e.g., harvest rate). We recommend future efforts conduct comparison to more simplified models and test the possible inclusion of new information about covariates that may affect survival in addition to harvest (Riecke et al. 2022).

Our measures of model fit are low, and we think there are significant research advances that can come from exploring long-term mark-recapture analysis and best methods for estimating model fit. Researchers have demonstrated the importance of considering covariates other than harvest when modeling survival and failure to include those variables results in inaccurate predictions (Zhao et al. 2019, Riecke et al. 2022). The lack of fit in our models may be a result of additional unmodeled mechanisms affecting survival, particularly environmental covariates or individual heterogeneity in survival. Alternatively, these fit statistics may be inappropriate for long-term mark-recapture studies. We plotted the observed lack of fit for each cell of the mark-recovery array and the fit was adequate for cells near the release occasion. As time since banding increased, the expected cell values become very small, and just a few recoveries can result in low Bayesian *P*-values. This suggests the model may fit well when nearly all recoveries occur in the first few years, but there is substantial lack of fit for the remaining cells due to a few long-lived individuals. For example, 9 juvenile male mallards released in 2006 were recovered in the 2016–2017 hunting season when 4.2 were expected. In contrast, 339 recoveries occurred in the hunting season following 2006 pre-season banding when 332 were expected. More recoveries than expected multiple years after release can have a major impact on model fit, even when the model is still performing well. The effect of these anomalies in long-term band-recovery data sets on model performance have not been tested, and we recommend future models report fit statistics to explore how widespread this issue is.

Adaptive harvest management consists of the annual process of setting regulations and learning about key parameters and sources of uncertainty by comparing model predictions to subsequent monitoring observations. The model we describe here is formulated to learn about included parameters through time and result in improved estimates of parameters that are poorly estimated. Our results demonstrated the partial compensation parameter to be imprecise, and that error is carried forward to the annual optimization, but more years of data with continued monitoring effort may improve that estimate. Our current model only considers the effect of harvest on survival, but if harvest is collinear with unmodeled covariates, our inference may be biased (Riecke et al. 2022). Future research may also identify covariates that influence survival and reproduction. The flexibility of an IPM and the associated adaptive harvest strategy allows additional research findings to be incorporated into the model to improve future decisions.

Mallard presence in eastern North America prior to European settlement was likely sporadic (Heusmann 1991, Lavretsky et al. 2019*b*). Prior to deforestation in eastern North America, mallards may have only been present during winter, migrating from mid-continent breeding areas (Heusmann 1991). Despite historical conditions, the current eastern North American landscape supports abundant mallards, and our work indicates a carrying capacity of over 1.3 million birds, with recently declining abundance. In harvest management, IPMs such as ours can help managers set abundance index thresholds that trigger changes in harvest regulations (Roberts et al. 2021) or use estimates in an adaptive management program (Johnson et al. 2014, USFWS 2019*a*). No matter the cause of the decline, or prospects to changing population trajectory, the use of this model in an eastern mallard harvest strategy provides a framework for population processes that can be used in its current form and improved as new information is obtained.

MANAGEMENT IMPLICATIONS

The information provided by our model, and the associated equilibrium analysis, allows managers to set state-dependent regulations that may allow for more liberal seasons than the current 2-bird bag without over-harvesting. If the cause of the decline is declining productivity or recruitment, then a larger daily bag limit, such as 4 birds allowed in previous years, may be sustainable in years of high recruitment. Further, habitat management can focus on increasing productivity. There is a strong need for more information about what variables affect productivity and juvenile survival of eastern mallards. Prior to finalizing a fully adaptive harvest management plan for eastern mallards, the results of the equilibrium analysis provided important information to managers. The most recent abundance estimate of 1.05 million birds is 22% below the estimated carrying capacity of 1.35 million, and above the estimate of the equilibrium population estimate at maximum sustainable yield of 800,000. These estimates suggest current harvest levels are currently sustainable and provide potential abundance thresholds to monitor.

ACKNOWLEDGMENTS

Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the United States Government. The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the USFWS or other respective agencies. We thank A. T. Pearse, T. V. Riecke, and one anonymous reviewer for their help improving this manuscript.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

This study adhered to relevant regulations and guidelines regarding the ethics of animal welfare. The original data collection followed protocols and guidelines related to use of vertebrate animals in effect at the time the data were collected.

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article. Additional data are openly available from the USGS Bird Banding Laboratory at https://www.usgs.gov/labs/bird-banding-laboratory.

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Associate Editor: Daniel Collins.

SUPPORTING INFORMATION

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How to cite this article: Roberts, A. J., J. A. Hostetler, J. C. Stiller, P. K. Devers, and W. A. Link. 2023. Population dynamics and harvest management of eastern mallards. Journal of Wildlife Management e22405. https://doi.org/10.1002/jwmg.22405