Received: 15 August 2024 | Revised: 12 October 2024 | Accepted: 21 October 2024

DOI: 10.1002/jwmg.22702

THE JOURNAL OF WILDLIFE MANAGEMENT

THE WILDLIFE SOCIETY

RESEARCH ARTICLE

Great Lakes mallard population dynamics

Benjamin Z. Luukkonen[1] | Scott R. Winterstein[1] | Daniel B. Hayes[1] | Drew N. Fowler[2] | Gregory J. Soulliere[3] | John M. Coluccy[4] | Amy A. Shipley[5] | John Simpson[6] | Brendan Shirkey[6] | Jason M. Winiarski[5] | Benjamin J. O'Neal[7] | Barbara A. Avers[8] | Gerald R. Urquhart[9] | Philip Lavretsky[10]

[1]Department of Fisheries and Wildlife, Michigan State University, 480 Wilson Road, East Lansing, MI 48824, USA

[2]U.S. Geological Survey, Louisiana Cooperative Fish and Wildlife Research Unit, 4174 Highland Road, Baton Rouge, LA 70803, USA

[3]U.S. Fish and Wildlife Service, Upper Mississippi/Great Lakes Joint Venture, 2651 Coolidge Road, Suite 101, East Lansing, MI 48823, USA

[4]Ducks Unlimited Inc., 7322 Newman Boulevard Building 2, Dexter, MI 48130, USA

[5]Wisconsin Department of Natural Resources, Office of Applied Science, 2801 Progress Road, Madison, WI 53716, USA

[6]Winous Point Marsh Conservancy, 3500 South Lattimore Road, Port Clinton, OH 43452, USA

[7]Department of Biology, Franklin College, 101 Branigin Boulevard, Franklin, IN 46131, USA

[8]Michigan Department of Natural Resources, Wildlife Division, 4166 Legacy Parkway, Lansing, MI 48910, USA

[9]Lyman Briggs College and Department of Fisheries and Wildlife, Michigan State University, 919 E Shaw Lane, East Lansing, MI 48825, USA

Abstract

Breeding mallard (*Anas platyrhynchos*) populations in the Great Lakes region (Michigan, Minnesota, Wisconsin, USA) declined by >40% between 2000–2022 based on abundance data collected during spring aerial surveys. Mallards are an important waterfowl species in this region, where an estimated 60–80% of the mallard harvest is composed of locally banded birds. Extensive population monitoring datasets are available for mallards, presenting an opportunity to address complex questions such as estimating productivity at large spatial and temporal scales, identifying the effects of harvest on mallard demography, quantifying mechanisms for harvest compensation, and integrating multiple datasets to quantify the demographic drivers of population change. Our objective was to simultaneously examine factors affecting demographic parameters and their relative contribution to Great Lakes mallard population dynamics. We used 32 years of banding, band recovery, and aerial survey data collected for mallards from Michigan and Wisconsin to develop an integrated population model (IPM). We used age ratios at banding to estimate productivity, band recoveries from hunter-harvested birds to estimate annual survival and cause-specific mortality (i.e., harvest or non-hunting), and modeled abundance using aerial survey and

---

[10]Department of Biological Sciences, University of Texas El Paso, 500 W University, El Paso, TX 79902, USA

Correspondence
Benjamin Z. Luukkonen, Michigan State University, 480 Wilson Road, East Lansing, MI 48824, USA.
Email: luukkon3@msu.edu

Funding information
AgBioResearch, Michigan State University; Illinois Natural History Survey Forbes Biological Station; US Fish and Wildlife Service Upper Mississippi Great Lakes Joint Venture; Great Lakes Fish and Wildlife Restoration Act, Grant/Award Number: GG 751210000001883; Winous Point Marsh Conservancy; Indiana Department of Natural Resources; Franklin College; Ducks Unlimited Inc.; Michigan Department of Natural Resources

demographic parameter estimates from 1991–2022. The IPM results indicated the decline in Great Lakes mallard abundance was caused by increased non-hunting mortality and a decline in productivity. Productivity varied spatially but temporally declined with the loss of Conservation Reserve Program area. Moreover, our productivity assessment provided evidence of density dependence in reproduction. Non-hunting mortality was 3.5–6.7 times and 1.3–4.2 times greater than harvest mortality for adult and juvenile female mallards, respectively, indicating environmental factors during spring and summer, not harvest, most greatly influenced annual mortality for female mallards. Our IPM reduced uncertainty in the factors affecting Great Lakes mallard population dynamics and indicated management actions that address non-hunting mortality and productivity would be most effective in increasing Great Lakes mallard abundance.

KEYWORDS

Anas platyrhynchos, Great Lakes, integrated population model, mallard, productivity, survival

The first goal of the North American Waterfowl Management Plan (NAWMP) is to maintain abundant and resilient waterfowl populations to support hunting and other uses (NAWMP 2018). To that end, researchers and managers have long invested in waterfowl population monitoring and management, with North American waterfowl being some of the most intensively monitored species in the world (Arnold et al. 2018). At a continental scale, annual waterfowl monitoring includes aerial surveys to estimate abundance (U.S. Fish and Wildlife Service [USFWS] 2023*a*), banding and systematic recording of band recoveries (Celis-Murillo et al. 2022), and waterfowl hunter surveys to estimate quantity and composition of the annual harvest (Raftovich et al. 2022). This wealth of data allows scientists to predict the effects of management actions on population dynamics (Cowardin and Johnson 1979), estimate productivity at large spatial and temporal scales (Specht and Arnold 2018), identify the effects of harvest (Burnham and Anderson 1984, Rexstad 1992), quantify mechanisms for harvest compensation (Riecke et al. 2022*b*), and quantify the demographic drivers of population change (Koons et al. 2017). Integrated population models (IPMs) are particularly well suited to applied population research when multiple datasets are available to estimate one or more population parameters (Schaub and Abadi 2011).

The application of IPMs in waterfowl research has become more common (Arnold et al. 2018), providing a framework to jointly analyze ≥2 datasets that inform population size or structure (Besbeas et al. 2002, Schaub and Abadi 2011). Benefits from IPMs relative to separate or isolated data analyses can include reduced parameter uncertainty, the ability to estimate unmonitored parameters, incorporation of uncertainty from multiple sources in population projection, and increased understanding of relationships between demographic parameters and abundance (Schaub and Abadi 2011, Arnold et al. 2018, Zipkin and Saunders 2018, Riecke et al. 2022*a*). Therefore, the ability to provide insight into complex demographic questions is increasing for well-monitored wildlife species such as the mallard (*Anas platyrhynchos*; Wiegers et al. 2022, Roberts et al. 2023).

In North America, mallards have been delineated into 3 populations to facilitate harvest management, which are defined by breeding geography and administrative flyway. These include eastern, midcontinent, and western mallards (USFWS 2023*b*). The midcontinent mallard population is the largest and comprises mallards nesting from the Northwest Territories in Canada to the Great Lakes region in the United States. The Waterfowl Breeding Population and Habitat Survey (WBPHS) and Great Lakes state (Michigan, Minnesota, and Wisconsin, USA) breeding waterfowl surveys are conducted annually to estimate breeding abundance of midcontinent mallards (USFWS 2022). Mallard abundance in the Great Lakes region historically followed the same trend as the remainder of the midcontinent population (USFWS 2023*a*). However, prairie-nesting mallard abundance increased following a decline in the early 2000s, whereas mallard abundance in the Great Lakes region continued to decline. Mallard abundance in the Great Lakes region exceeded 1 million during most years in the late 1990s based on state aerial surveys but had declined to around 0.5 million in 2023 (USFWS 2023*b*). Regionally produced mallards are particularly important to hunters in the Great Lakes region, as an estimated 58–83% of their mallard harvest is derived from mallards banded within the region (Arnold and De Sobrino 2010). Declining mallard abundance is thus a concern for wildlife management agencies involved in waterfowl harvest management and those implementing the NAWMP (Soulliere et al. 2017).

Although the causes of Great Lakes mallard population decline are unknown, several factors are of concern and interest to waterfowl managers, such as the relationship between harvest and abundance. During the early 1990s, duck hunting regulations were liberalized, reflecting increased duck abundance across North America. Season lengths increased in the Mississippi Flyway from 30 to 60 days, and in 2011, 2014, and 2020, the female mallard daily harvest limit increased from 1 to 2 in Minnesota, Michigan, and Wisconsin, respectively. Some stakeholders voiced concern that liberalization of female mallard harvest was contributing to population decline in the Great Lakes region (B. A. Avers, Michigan Department of Natural Resources, personal communication), although recent research suggests harvest is a relatively small component of total mortality in female midcontinent mallards (Riecke et al. 2022*b*) and harvest rates were not considered unsustainable for Great Lakes mallards (Singer 2014).

There have also been substantial changes in landscapes used for nesting by mallards and other grassland-nesting birds in the Great Lakes region. Between 2001 and 2016, the area of developed land, classified as low, medium, and high intensity developed in the National Land Cover Database (NLCD; Yang et al. 2018) expanded by 338,000 ha (8% increase) and the area of cultivated cropland increased by 987,000 ha (3% increase) in the Upper Mississippi/Great Lakes Joint Venture (UMGLJV) region. In contrast, the area of land cover categorized as grassland-herbaceous and hay-pasture declined by 1.4 million ha (9% decrease; Soulliere et al. 2020). The loss of grassland is expected to reduce the quantity and quality of upland nesting habitat for mallards. Expansion and intensification of agriculture during this period, including increasing use of systemic pesticides (i.e., neonicotinoid insecticides), potentially reduces availability of invertebrate food resources and reproductive capacity for upland and wetland birds, including mallards (Hopwood et al. 2013, Morrissey et al. 2015, Soulliere et al. 2020). Intensive monitoring of Great Lakes mallards through aerial population surveys and annual banding provide an opportunity to reduce uncertainty regarding these varied complex and potentially confounding factors contributing to population decline.

We developed an IPM to identify how ecological and anthropogenic factors affect Great Lakes mallard population dynamics. Our objectives were to examine factors affecting demographic parameters and their relative contribution to population growth rate for Great Lakes mallards. We used abundance estimates derived from spring aerial surveys, estimated productivity from age ratios at banding (Specht and Arnold 2018), and estimated survival, harvest mortality, and non-hunting mortality probabilities (Riecke et al. 2022*b*) for female mallards surveyed and banded in Michigan and Wisconsin from 1991–2022. Among the demographic drivers of population growth rate, we hypothesized that productivity and adult female survival would be the parameters most strongly linked to population dynamics but expected productivity to be more annually variable than adult survival (Koons et al. 2014). We predicted harvest would be a small component of mortality relative to non-hunting mortality (Riecke et al. 2022*b*).

STUDY AREA

We considered mallards nesting across Michigan and Wisconsin representative of the Great Lakes mallard component of the midcontinent mallard population and defined these states as the study area. Aerial breeding waterfowl surveys and annual pre-season (1 July–30 September) mallard banding in Michigan, Minnesota, and

Wisconsin support monitoring of the Great Lakes component of the midcontinent mallard population (USFWS 2023*a*) and contribute to adaptive harvest management models (USFWS 2023*b*). However, 27% of Minnesota is within the Prairie Pothole Region (PPR; Bird Studies Canada and North American Bird Conservation Initiative 2014), where land cover and mallard population dynamics differ from the Great Lakes region (Coluccy et al. 2008), and aerial surveys for breeding waterfowl cover about 40% of the state (Cordts 2023). Further, a vital assumption of IPMs is that all data sources are derived from the same population (Schaub and Abadi 2011, Arnold et al. 2018). To achieve spatial congruence, we used data from mallards surveyed and banded in Michigan and Wisconsin only and assumed that population demography for this sample was representative of mallards nesting within Great Lakes states Bird Conservation Regions (BCRs) 12, 22, and 23.

Aerial surveys and mallard banding were conducted in Michigan and Wisconsin and band recoveries from hunter harvest occurred throughout North America (Figure 1). Michigan and Wisconsin are primarily composed of BCRs 23 (Prairie Hardwood Transition) and 12 (Boreal Hardwood Transition; Bird Studies Canada and North American Bird Conservation Initiative 2014). These BCRs are dominated by extensive forests and lakes in the north (BCR 12) that transition to a landscape of forests, lakes, and herbaceous wetlands mixed with human-modified land cover types (agricultural and developed) in the south (BCR 23; Soulliere et al. 2017). Regional temperatures and precipitation are influenced by the Great Lakes and generally consist of cold, snowy winters and hot, humid summers (Scott and Huff 1996). Moderating lake effects result in wetland conditions that are generally more stable

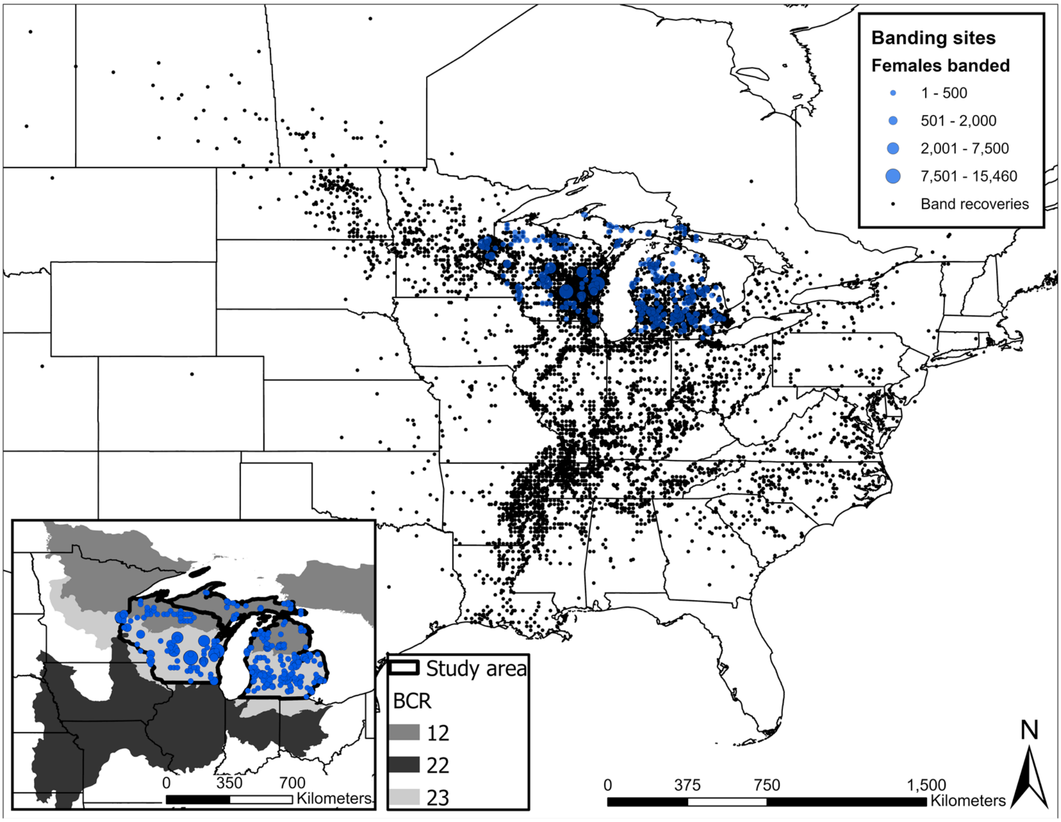

FIGURE 1 Female mallard banding locations and effort (total female mallards banded) in Michigan and Wisconsin, USA, and resulting harvest locations of banded mallards, 1991–2022. The Michigan and Wisconsin study area is shown in relation to Bird Conservation Regions (BCRs) within the Upper Mississippi/Great Lakes Joint Venture region.

and less seasonally dynamic than in the midcontinent prairies and parklands (Euliss et al. 2004, Simpson et al. 2005). Mallards were the most abundant nesting duck in the Great Lakes region (USFWS 2023*a*) and nesting densities were estimated to be greatest in BCR 23 (Soulliere et al. 2017).

METHODS

We developed an IPM to examine factors affecting annual survival and productivity and the influence of these demographic parameters on population growth rate of Great Lakes mallards. Additionally, we estimated annual harvest mortality and non-hunting mortality probabilities to determine the relative contribution of cause-specific mortality to annual survival (Riecke et al. 2022*b*). We derived annual productivity indices from female age ratios at banding (Specht and Arnold 2018). We estimated abundance as a function of annual survival and productivity and using information from aerial survey abundance estimates. We assumed that emigration and immigration were negligible at the spatial scale of this analysis (Lavretsky and Sedinger 2023, Luukkonen 2024).

Banding, recovery, population, and habitat survey data

Annually during April and May, pilots flew stratified random transects with fixed wing aircraft in Michigan and Wisconsin and trained observers recorded waterfowl and wetland counts according to the WBPHS protocol (USFWS 1987). Visibility correction factors accounted for imperfect detection from the fixed wing aircraft via a modified ground count method in Wisconsin (March et al. 1973) and via helicopter surveys in Michigan (Soulliere and Chadwick 2003). These surveys provide estimates of total abundance of waterfowl species (Smith 1995), and total wetlands suitable for waterfowl on a statewide scale (USFWS 2023*b*). We modeled true wetland (pond) abundance ($\mathrm{P_t}$) in year *t* in a state-space framework as an auto-regressive process where the sum of observed wetland counts in Michigan and Wisconsin ($\mathrm{v_t}$) was normally distributed with observation variance ($\sigma^2_{\mathrm{P,obs}}$) and true wetland abundance in the next year was a function of current wetland abundance and process variance (σ^2_{P}):

$$\mathrm{v_t} \sim \mathrm{Normal}\left(\mathrm{P_t},\ \sigma^2_{\mathrm{P,obs}}\right)$$

$$\mathrm{P_{t+1}} \sim \mathrm{Normal}\left(\mathrm{P_t},\ \sigma^2_{\mathrm{P}}\right)$$

$$\sigma_{\mathrm{P}} \sim \mathrm{Uniform}(0,\ 5)$$

$$\sigma_{\mathrm{P,\ obs}} \sim \mathrm{Uniform}(0,\ 10)$$

We obtained banding and recovery data for mallards marked in Michigan and Wisconsin during 1991–2022 from the United States Geological Survey (USGS) Bird Banding Laboratory (BBL) Gamebirds database (Celis-Murillo et al. 2022). Researchers captured mallards from 1 July to 30 September using baited traps, rocket nets, night-lighting, and by hand. Researchers identified age and sex of birds using plumage characteristics (Carney 1992) and banded them with a size 7 USGS aluminum leg band. We included female mallards released in the same 10-minute block (standard spatial areas used by USGS BBL that are 10 minutes of latitude by 10 minutes of longitude) as captured (BBL status code = 003) and marked with standard aluminum or control bands (i.e., standard bands paired with reward bands in studies to estimate band reporting probability) in analyses (we excluded birds marked with transmitters and blood-sampled birds from analyses). We retained only hunter-harvested band recoveries (BBL how obtained code = 01) to enable estimation of cause-specific mortality hazard rates (Riecke et al. 2022*b*).

Survival and mortality models

We first modeled time-specific harvest ($h_{\kappa,\,t}$) and non-hunting ($h_{\eta,\,t}$) mortality hazard rates for each age class (a; adult = AHY [after hatching year], juvenile = HY [hatching year]). Hazard rates are the instantaneous intensity of lethal events that individuals are exposed to in continuous time and are measured on a ratio scale. Hazard rates are particularly useful when modeling competing risks (Chiang 1991) of mortality (e.g., harvest vs. non-hunting) and when modeling the effects of covariates on mortality (Ergon et al. 2018). Whereas harvest mortality occurs only during the hunting season, non-hunting mortality could occur throughout the annual cycle. We partitioned mortality sources by assuming the majority of female mallard non-hunting mortality occurred outside of the hunting season, primarily during the nesting and brood-rearing periods (Hoekman et al. 2002, Arnold et al. 2012). We predicted that non-hunting mortality hazard rate would be affected by annual wetland abundance (Devries et al. 2003) and mallard abundance (N_t; Riecke et al. 2022*b*), where η_a subscripts denoted β parameter estimates correspond to non-hunting mortality hazard rate and are age (a) specific, and ε_{η_a} represented random error:

$$\log(h_{\eta,\,t_a}) = \beta_{\eta_a 1} + \beta_{\eta_a 2} \times P_t + \beta_{\eta_a 3} \times N_t + \varepsilon_{\eta_a}$$

We were also interested in determining the effects of the total number of duck hunters in Michigan and Wisconsin (H_t), an index of harvest regulations (R_t), and mallard abundance on female mallard harvest mortality hazard rate, where κ_a subscripts denoted age-specific β parameter estimates for harvest mortality hazard rate, and ε_{κ_a} represented random error:

$$\log(h_{\kappa,\,t_a}) = \beta_{\kappa_a 1} + \beta_{\kappa_a 2} \times H_t + \beta_{\kappa_a 3} \times N_t + \beta_{\kappa_a 4} \times R_t + \varepsilon_{\kappa_a}$$

We retrieved annual estimates of duck hunter abundance provided by the Harvest Information Program (HIP) in Michigan and Wisconsin (Raftovich et al. 2022). To characterize female mallard harvest regulations, we developed a harvest regulation index as the duck hunting season length in days multiplied by the female mallard daily harvest limit in each state (Luukkonen et al. 2021), then summed the values for Michigan and Wisconsin. Thus, higher values of the harvest regulation index indicated more liberal female mallard harvest regulations (longer seasons and higher daily limits). We z-standardized all mortality hazard rate covariates. We used the following priors for regression parameters in the non-hunting and harvest mortality hazard rate models so likely β parameter means were between −6.2 and 6.2 on the log scale (Lemoine 2019):

$$\beta \sim \mathrm{Normal}(0,\ 100)$$

$$\sigma_\beta \sim \mathrm{Uniform}(0,\ 2)$$

$$\varepsilon \sim \mathrm{Normal}(0,\ \sigma_\varepsilon)$$

$$\sigma_\varepsilon \sim \mathrm{Uniform}(0,\ 2)$$

We then estimated annual survival probability (S; the probability that an individual alive at banding in year *i* is alive at banding in year *i* + 1) for each age class (a) using the Brownie dead recovery parameterization, with banding release and recovery data in an m-array format with cell probabilities a function of survival and recovery probabilities (Brownie et al. 1978). First, we converted harvest mortality hazard rate to annual harvest mortality probability (κ_{t_a}; the probability an individual alive in year *t* is shot and killed by a hunter during the duck hunting season in year *t*):

$$\kappa_{t_a} = 1 - e^{-h_{\kappa,t_a}}$$

We calculated non-hunting mortality probability (η_{t_a}) conditional on surviving harvest (Riecke et al. 2022*b*):

$$\eta_{t_a} = (1 - \kappa_{t_a}) \times (1 - e^{h_{\eta,\, t_a}})$$

We estimated annual band recovery probability (f_{t_a}), or Brownie dead recovery probability (Brownie et al. 1978), as the probability a banded individual alive in year *t* is shot, retrieved (1 − c), and the band is reported (ρ_t) to the BBL:

$$f_{t_a} = \kappa_{t_a}(1 - c)\rho_t$$

We assumed a time-constant wounding loss for unretrieved hunter-shot birds of c = 0.2 (Anderson and Burnham 1976, Ellis et al. 2022, USFWS 2023*b*), used estimates of mallard band reporting probability (ρ) from 1991–2016 from Arnold et al. (2020), and used $\rho_{2017} = 0.833$ (SD = 0.03), $\rho_{2018} = 0.84$ (0.03), $\rho_{2019} = 0.849$ (0.03), $\rho_{2020} = 0.898$ (0.03), $\rho_{2021} = 0.906$ (0.03), and $\rho_{2022} = 0.906$ (0.03) from a recent reward band analysis (P. Garrettson and S. Boomer, U.S. Fish and Wildlife Service, unpublished data). Finally, we used non-hunting and harvest mortality hazard rates to calculate annual survival probability:

$$S_{t_a} = e^{-(h_{\kappa,\, t_a} + h_{\eta,\, t_a})}$$

Productivity model

We defined mallard productivity (γ_t) as the ratio of juvenile females to adult females captured and banded (Specht and Arnold 2018, Riecke et al. 2022*b*) during pre-season banding (1 July–30 September). However, we modeled the proportion of juvenile females captured and banded (J) because this parameterization was bounded between 0 and 1 and allowed J at a given banding site to be modeled as a binomial random variable weighted by the total number of mallards banded annually at a given site, thus accounting for spatial and temporal variation in banding effort (Specht and Arnold 2018).

$$J = \frac{\text{juvenile females}}{\text{juvenile females + adult females}}$$

Proportion juveniles can be converted to the traditional productivity estimate of juvenile females per adult female (γ):

$$\gamma = \frac{J}{1 - J}$$

If capture probability is equal for juvenile and adult females, we obtain a direct estimate of productivity. If capture probability varies by age, for example if juveniles were more susceptible to capture, γ is an unbiased index of fecundity as long as capture probability varies randomly across years and sites, and independently of covariates (Specht and Arnold 2018). We assumed γ was an unbiased index of productivity and thus accounted for spatial and temporal variation in captures using fixed and random effects. We modeled J with a mixed-effects logistic regression model.

We predicted that z-standardized annual mallard and wetland abundance could influence productivity and considered 2 banding site-level (b) covariates. We included z-standardized banding site latitude (L_b) to account for potential latitudinal variation in productivity. Michigan and Wisconsin account for the northern 30% of the UMGLJV region, where periodic landscape change and bird habitat assessments have been completed. A recent Joint Venture evaluation documented loss of an estimated 1.4 million ha of grassland and hay-pasture between 2001-2016 (Soulliere et al. 2020). To annualize change in potential production habitat, we included the z-standardized area (G_t) in Michigan and Wisconsin enrolled in the United States Department of Agriculture's (USDA) Conservation Reserve Program (CRP) as an index of regional grassland abundance (Reynolds et al. 2001) to assess if productivity was related to loss of grassland nesting habitat (U.S. Department of Agriculture 2024). In the UMGLJV region, CRP consists of largely herbaceous upland cover, with >80% considered beneficial to grassland-nesting birds (Soulliere et al. 2020).

We hypothesized that mallards using urban areas would have lower productivity related to the greater prevalence of wild × game-farm mallard hybrids at developed sites (Luukkonen 2024); however, other factors could also result in reduced mallard productivity in urban settings. Thus, we used the proportion of developed land cover (U_b), classified as developed open space or low, medium, and high intensity developed in the 2021 NLCD database (Dewitz 2023), in a 7-km radius (Luukkonen 2024) of each banding site as a site covariate:

$$\mathrm{logit}(J_{t,b}) = \beta_{\gamma 1} + \beta_{\gamma 2} \times U_b + \beta_{\gamma 3} \times L_b + \beta_{\gamma 4} \times N_t + \beta_{\gamma 5} \times P_t + \beta_{\gamma 6} \times G_t + \varepsilon_{t,b}$$

We modeled all productivity coefficients as normal random variables with priors of $\mu = 0$ and $\sigma = 2$, resulting in likely β parameter means between −3.9 and 3.9 on the logit scale. Priors on coefficient standard deviations were uniform from 0 to 5. The residual random effect of banding site and year ($\varepsilon_{t,b}$) was considered normal:

$$\varepsilon_{t,b} \sim \mathrm{Normal}\left(0,\ \sigma_b^2\right)$$

$$\sigma_{t,b} \sim \mathrm{Uniform}(0,\ 5)$$

Use of age ratios to estimate fecundity assumes that banding captures and capture methods do not target mallards of a specific age, or that the ratio of juveniles per adult in the banded sample is representative of the ratio in the population. While we were unaware of any age-specific banding operations, we excluded any combination of banding site and year where only adults or only juvenile female mallards were banded (Specht and Arnold 2018), which totaled 163 site-year combinations, or 1.3% of banded female mallards.

Abundance model

We modeled an index of annual mallard abundance in Michigan and Wisconsin where the mallard abundance index in the next year equals the number of adult (AHY) females alive in the current year that survive to the next year, plus the number of juvenile (HY) females that are produced and survive to the next year:

$$N_{t+1} = N_t\left(1 - \kappa_{AHY_t} - \eta_{AHY_t}\right) + \left(N_t \times \gamma_t\right)\left(1 - \kappa_{HY_t} - \eta_{HY_t}\right)$$

We considered the sum of estimated mallard abundance in Michigan and Wisconsin from spring breeding aerial surveys (y_t) to be normally distributed around a mean of true mallard abundance with observation variance ($\sigma^2_{y,\ obs}$):

$$y_t \sim \mathrm{Normal}\left(N_t,\ \sigma^2_{y,obs}\right)$$

$$\sigma_{y,\ obs} \sim \mathrm{Uniform}(0,\ 2)$$

We did not separately estimate abundance by sex or the proportion of the female population composed of adult and of juvenile female mallards. We expected females in their second or subsequent nesting season to have higher productivity (Coluccy et al. 2008, Devries et al. 2008), although productivity estimates using the ratio of juvenile to adult females provide an aggregate index of productivity across all female ages. Further, aerial survey observations do not distinguish between juvenile and adult females. Therefore, our population model provided annual indices of total breeding abundance of adult and juvenile females combined. Aerial survey abundance estimates included male mallards (paired and unpaired; Smith 1995), but we assumed males outnumbered females (Alisauskas et al. 2014) and were non-limiting, and that population abundance estimates provided an index of total female mallard abundance (Riecke et al. 2022*a*, *b*). Finally, we estimated annual population growth rate (λ_t) as a derived parameter:

$$\lambda_t = \frac{N_{t+1}}{N_t}$$

Model implementation

We fit all models using Bayesian Markov chain Monte Carlo (MCMC) in JAGS (Plummer 2003) through program R (R Core Team 2022) using package jagsUI (Kellner 2016). We sampled 3 chains for 500,000 iterations, including 250,000 burn-in iterations and retained every twenty-fifth iteration. We checked that all posterior distributions had $\hat{R} < 1.01$ (Brooks and Gelman 1998) and inspected trace plots to assess convergence. We report medians of posterior distributions and 95% credible intervals unless otherwise indicated and the proportion of the posterior distribution on the same side of zero as the mean (υ) as an estimate of the probability that a coefficient is greater than or less than 0. When 95% credible intervals included zero, we assessed evidence for a weak relationship when $|\upsilon| > 0.7$.

RESULTS

There were 30,148 adult and 70,128 juvenile female mallards banded during the pre-season period in Michigan and Wisconsin from 1991–2022. The mean number of female mallards banded per year was 942 (range = 219–1819) and 2,192 (range = 763–3183) for adults and juveniles, respectively. Female mallards were captured at 316 sites throughout the study area. Hunters recovered and reported 3,752 adult and 12,167 juvenile female mallards with bands (Figure 1). Indices of mallard abundance (in 100,000 s) increased from 5.16 (3.78, 6.87) in 1991 to 7.43 (5.11, 9.35) in 2000, then declined to 3.41 (1.18, 5.76) in 2022.

The area in Michigan and Wisconsin enrolled in CRP during 1991–2022 peaked in the 1990s and declined after the early 2000s (Figure 2). Pond counts during 1991–2022 spring breeding waterfowl surveys were variable but increased beginning around 2015 (Figure 2). The number of duck hunters during this period increased to a peak in the early 2000s then declined to lows comparable to the early 1990s (Figure 2). Duck hunting season lengths increased from 30 days in 1991 to the first 60-day season in both Michigan and Wisconsin in 1997 and remained 60 days throughout the rest of the study period. The female mallard daily limit increased from 1 to 2 females in Michigan in 2014 and in Wisconsin in 2020, representing a general liberalization of regulations from 1991–2022 (Figure 2). Spring mallard abundance estimates from aerial surveys were positively correlated with CRP area ($r = 0.758$) and hunter abundance ($r = 0.521$), and negatively correlated with pond abundance ($r = -0.315$) and the harvest regulation index ($r = -0.615$).

Survival and mortality

Adult female mallard survival probability estimates steadily declined from 0.56 (0.52, 0.61) to 0.47 (0.41, 0.53) during 1991–2022, while juvenile female mallard survival declined from 0.52 (0.45, 0.59) to 0.45 (0.36, 0.54) during the study (Figure 3). Adult female mallard harvest mortality probability estimates remained relatively constant

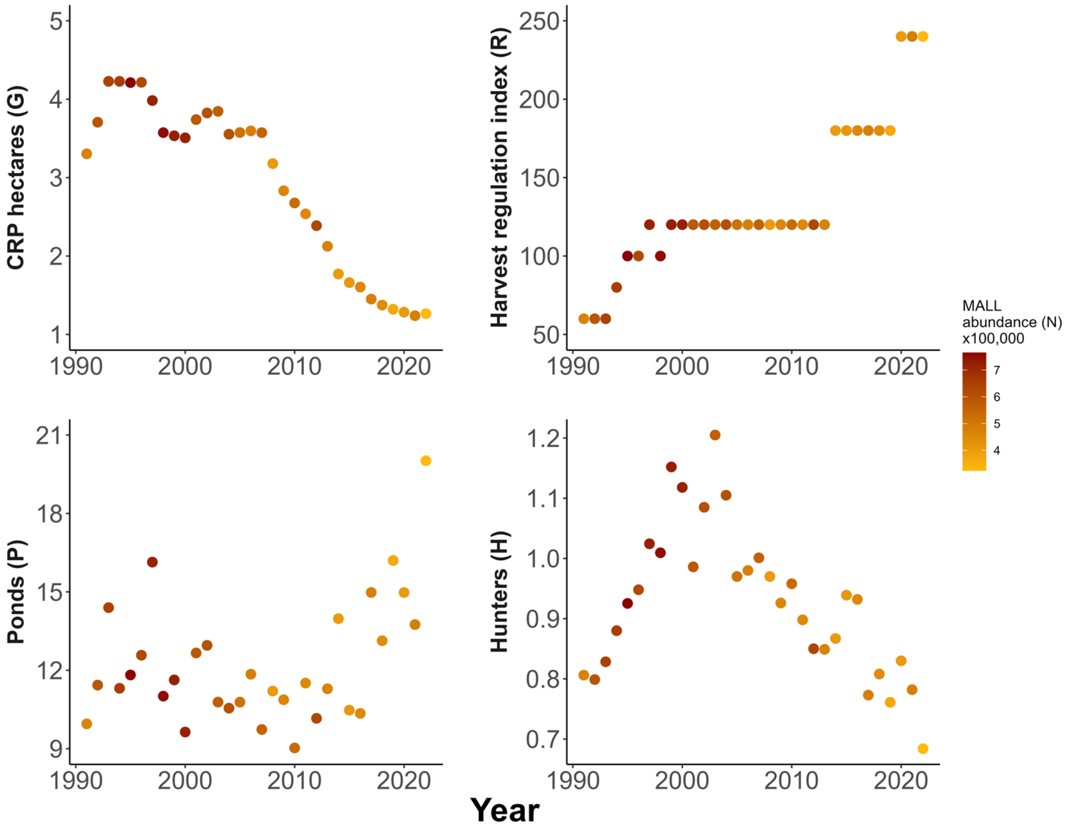

FIGURE 2 Annual hectares enrolled in the Conservation Reserve Program (CRP) within Michigan and Wisconsin, USA, duck hunting regulation indices (season length × female mallard daily bag limit in Michigan + Wisconsin), pond (wetland) counts from spring breeding waterfowl aerial surveys, and total licensed duck hunters in Michigan and Wisconsin, 1991–2022. Point color represents total estimated mallard abundance in Michigan and Wisconsin from the spring breeding waterfowl surveys. The CRP hectares, ponds, duck hunters, and mallard abundance scales are in 100,000s and vary by panel.

(range = 0.09–0.13), while non-hunting mortality steadily increased from 0.32 (0.27, 0.36) to 0.43 (0.37, 0.50). Juvenile female mallard harvest (range = 0.15–0.27) and non-hunting mortality (range = 0.24–0.44) increased initially, but harvest mortality declined beginning in 2010 while non-hunting mortality continued to increase (Figure 3).

Adult female non-hunting mortality was negatively related to mallard abundance ($\beta_{\eta,AHY,2} = -0.08$ [−0.13, −0.03]; $\upsilon = 1.00$) and directly to pond abundance ($\beta_{\eta,AHY,3} = 0.04$ [−0.02, 0.10]; $\upsilon = 0.91$). Juvenile female non-hunting mortality was negatively related to mallard abundance ($\beta_{\eta,HY,2} = -0.16$ [−0.26, −0.06]; $\upsilon = 1.00$) and was weakly related to pond abundance ($\beta_{\eta,HY,3} = -0.07$ [−0.07, 0.03]; $\upsilon = 0.92$). Adult female harvest mortality was not strongly related to hunter abundance ($\beta_{\kappa,AHY,2} = 0.01$ [−0.05, 0.08]; $\upsilon = 0.66$) or mallard abundance ($\beta_{\kappa,AHY,3} = -0.02$ [−0.09, 0.06]; $\upsilon = 0.66$), and there was a weak negative relationship with duck hunting regulations ($\beta_{\kappa,AHY,4} = -0.05$ [−0.12, 0.03]; $\upsilon = 0.90$). Juvenile female harvest mortality was most strongly related to hunter abundance ($\beta_{\kappa,HY,2} = 0.13$ [0.05, 0.21]; $\upsilon = 1.00$), negatively related to mallard abundance ($\beta_{\kappa,HY,3} = -0.06$ [−0.15, 0.04]; $\upsilon = 0.89$), and was unrelated to harvest regulations ($\beta_{\kappa,HY,4} = -0.05$ [−0.12, 0.03]; $\upsilon = 0.56$; Table 1). Changes in the number of duck hunters and increases in duck hunting season lengths and female mallard daily harvest limits did not result in changes to adult female harvest mortality (Table 1; Figure 3). The increase in duck hunters

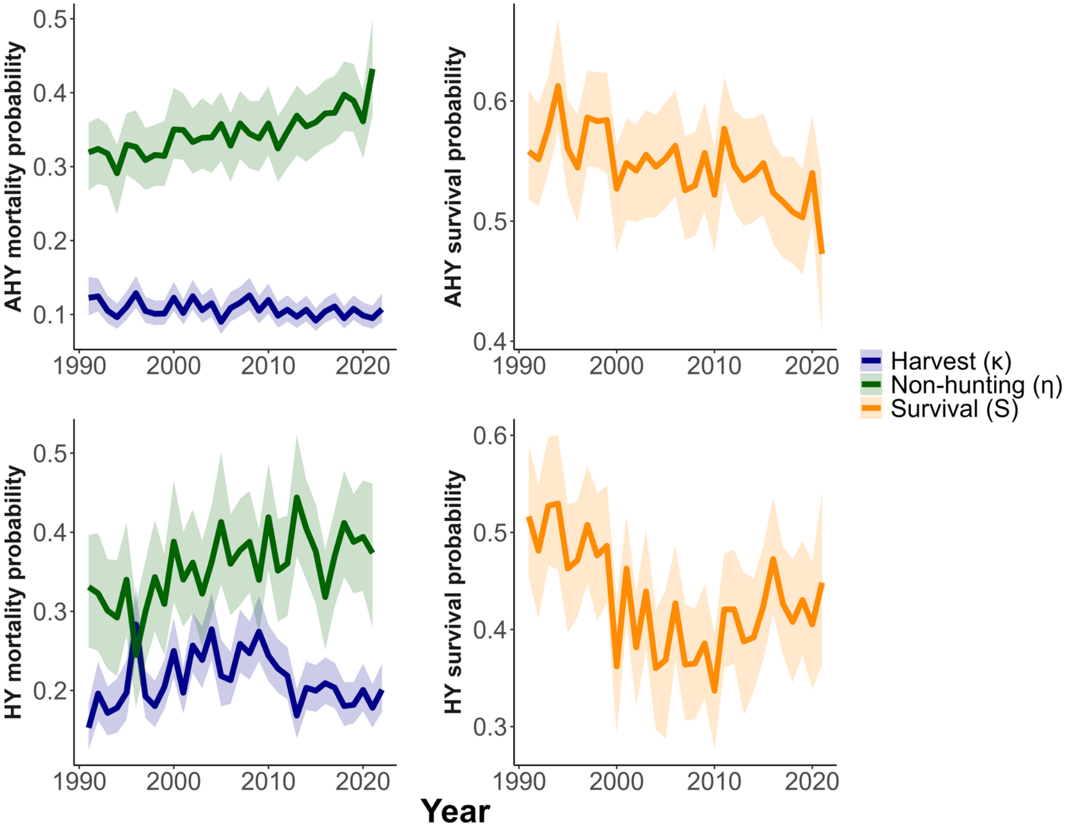

FIGURE 3 Posterior medians (lines) and 95% credible intervals (shaded regions) of annual survival (S), non-hunting (η) mortality, and harvest (κ) mortality probabilities for adult (AHY) and juvenile (HY) female mallards banded in Michigan and Wisconsin, USA, 1991–2022.

corresponded to an increase in juvenile female harvest mortality, although harvest mortality then declined with hunter numbers and did not substantially change with the increase from a 1 to 2 female mallard daily limit in Michigan and Wisconsin (Table 1; Figure 3). Non-hunting mortality was on average 4.4 (range = 3.5–6.6) times greater and 2.6 (range = 1.3–4.2) times greater than harvest mortality for adult and juvenile female mallards, respectively.

Productivity

Productivity estimates varied with temporal and spatial factors during the study (Table 1; Figure 4). Annual productivity indices increased from 1991 into the early 2000s, then generally declined (Figure 5). Productivity increased with latitude ($\beta_{\gamma,3}$ = 0.25 [0.15, 0.35]) and was higher in years when more area was enrolled in CRP ($\beta_{\gamma,6}$ = 0.25 [−0.31, 0.70]), though most CRP enrollment was likely in the southern portion of the study area where cultivated cropland is a dominate land cover (U.S. Department of Agriculture 2024). Productivity declined with an increasing proportion of developed land cover within a 7-km radius of banding sites ($\beta_{\gamma,2}$ = −1.02 [−1.50, −0.55]), increasing mallard abundance ($\beta_{\gamma,4}$ = −0.14 [−0.26, −0.02]), and increasing pond abundance ($\beta_{\gamma,5}$ = −0.38 [−0.69, −0.31]). Thus, for the average annual mallard abundance, pond abundance, and CRP area, per capita productivity was estimated to be lowest at developed sites in the southern Great Lakes region (Figure 4).

TABLE 1 Regression coefficient (β) medians, 95% credible intervals (CRI), and the proportion of the posterior distribution on the same side of zero as the mean (υ) for models estimating parameters for adult (AHY) and juvenile (HY) female mallards in Michigan and Wisconsin, USA, during 1991–2022: non-hunting mortality hazard rate (h_η; log-link), harvest mortality hazard rate (h_κ; log-link), and age ratio (J; proportion juveniles; logit-link). Covariates include z-standardized mallard abundance (N), wetland abundance (P), waterfowl hunter abundance (H), duck hunting regulation index (R), proportion urban land cover (U) at banding sites (b), banding site latitude (L), and annual hectares of land enrolled in the Conservation Reserve Program in Michigan and Wisconsin (G).

β	Response	Predictor	Median	Lower 95% CRI	Upper 95% CRI	υ
$\beta_{\eta,AHY,1}$	$h_{\eta,\,t_{AHY}}$	Intercept	−0.71	−0.77	−0.67	
$\beta_{\eta,\;AHY,2}$	$h_{\eta,\,t_{AHY}}$	N	−0.08	−0.13	−0.03	1.00
$\beta_{\eta,AHY,3}$	$h_{\eta,\,t_{AHY}}$	P	0.04	−0.02	0.10	0.91
$\beta_{\eta,HY,1}$	$h_{\eta,\,t_{HY}}$	Intercept	−0.51	−0.62	−0.41	
$\beta_{\eta,HY,2}$	$h_{\eta,\,t_{HY}}$	N	−0.16	−0.26	−0.06	1.00
$\beta_{\eta,HY,3}$	$h_{\eta,\,t_{HY}}$	P	−0.07	−0.16	0.03	0.92
$\beta_{\kappa,AHY,1}$	$h_{\kappa,\,t_{AHY}}$	Intercept	−2.18	−2.30	−2.04	
$\beta_{\kappa,AHY,2}$	$h_{\kappa,\,t_{AHY}}$	H	0.01	−0.05	0.08	0.66
$\beta_{\kappa,AHY,3}$	$h_{\kappa,\,t_{AHY}}$	N	−0.02	−0.09	0.06	0.66
$\beta_{\kappa,AHY,4}$	$h_{\kappa,\,t_{AHY}}$	R	−0.05	−0.12	0.03	0.90
$\beta_{\kappa,HY,1}$	$h_{\kappa,\,t_{HY}}$	Intercept	−1.45	−1.57	−1.29	
$\beta_{\kappa,HY,2}$	$h_{\kappa,\,t_{HY}}$	H	0.13	0.05	0.21	1.00
$\beta_{\kappa,HY,3}$	$h_{\kappa,\,t_{HY}}$	N	−0.06	−0.15	0.04	0.89
$\beta_{\kappa,HY,4}$	$h_{\kappa,\,t_{HY}}$	R	−0.01	−0.09	0.08	0.56
$\beta_{\gamma,1}$	$J_{t,\,b}$	Intercept	0.92	0.77	1.07	
$\beta_{\gamma,2}$	$J_{t,\,b}$	U	−1.02	−1.50	−0.55	1.00
$\beta_{\gamma,3}$	$J_{t,\,b}$	L	0.25	0.15	0.35	1.00
$\beta_{\gamma,4}$	$J_{t,\,b}$	N	−0.14	−0.26	−0.02	0.99
$\beta_{\gamma,5}$	$J_{t,\,b}$	P	−0.38	−0.69	−0.31	1.00
$\beta_{\gamma,6}$	$J_{t,\,b}$	G	0.25	−0.31	0.70	0.81

Abundance

Model indices of mallard abundance tracked estimates from spring breeding aerial surveys and showed a consistent decline in abundance since the early 2000 s (Figure 6). Abundance generally increased from 1991 to 2000 owing to increased productivity, despite declines in adult and juvenile survival during that time. Population declines since 2000 occurred with declines in survival and productivity. Population growth rate was >1 in 9 of 11 years from 1991–2001 and was <1 in 9 of 20 years from 2002–2021. Population growth rate was more strongly correlated with adult non-hunting mortality ($r = -0.45$) and juvenile non-hunting mortality ($r = -0.44$) than with adult harvest mortality ($r = -0.14$) or juvenile harvest mortality ($r = -0.27$). Further, population growth rate had higher correlation with adult survival ($r = 0.51$) and juvenile survival ($r = 0.53$) than with productivity ($r = 0.12$).

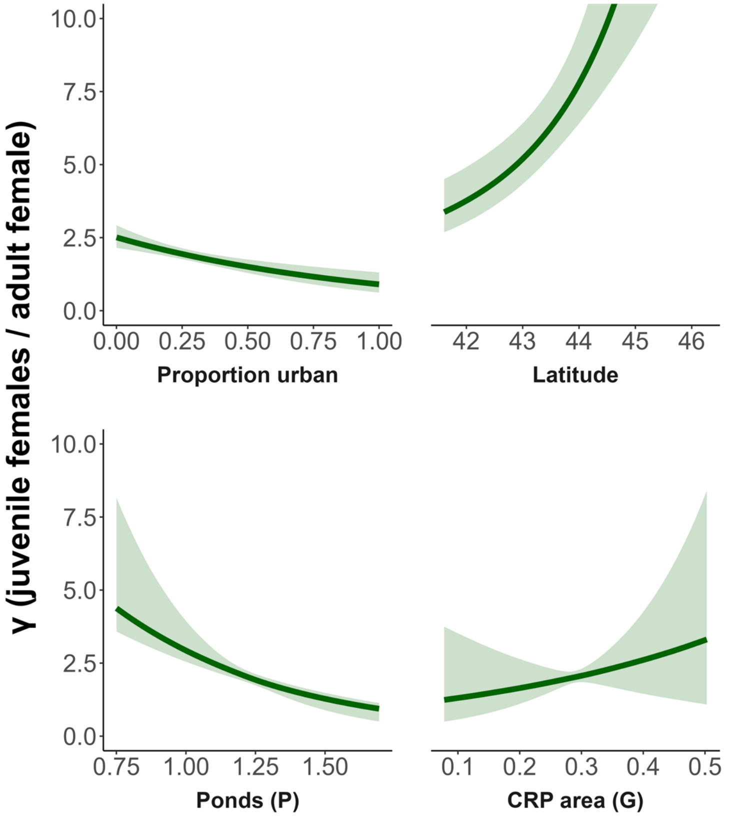

FIGURE 4 Covariate relationships (lines) and 95% credible intervals (shaded regions) with productivity (γ; juvenile females per adult female) for mallards banded in Michigan and Wisconsin, USA, 1991–2022. Mallard abundance, pond abundance, and Conservation Reserve Program (CRP) area (ha) are in millions. Proportion urban denotes the proportion of urban developed land cover within a 7-km radius of banding sites.

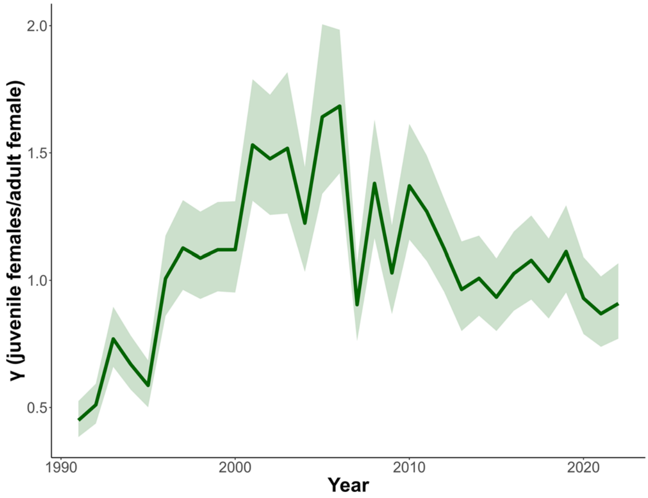

FIGURE 5 Posterior medians (line) and 95% credible intervals (shaded regions) of annual productivity (γ; juvenile females per adult female mallard) for mallards banded in Michigan and Wisconsin, USA, 1991–2022.

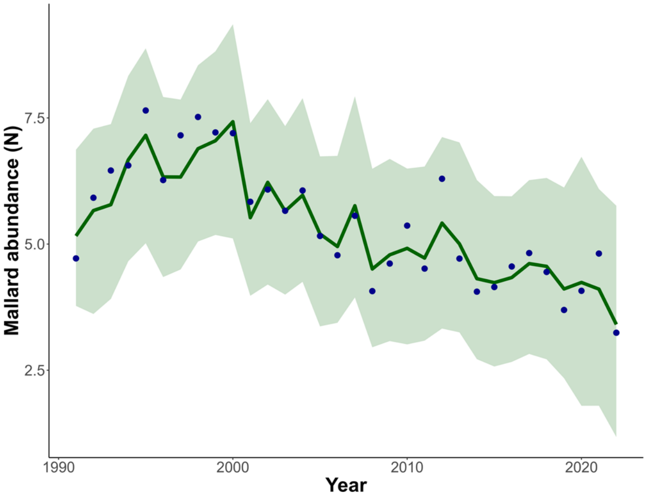

FIGURE 6 Posterior medians (line), 95% credible intervals (shaded region) of estimated mallard abundance (N), and mallard abundance (in 100,000 s) from the Michigan and Wisconsin, USA, spring breeding aerial waterfowl surveys (points), 1991–2022.

DISCUSSION

We analyzed 32 years of banding, band recovery, and population abundance data to identify factors affecting non-hunting mortality, harvest mortality, and productivity, and the subsequent influence of these parameters on mallard population dynamics in the Great Lakes region. Mallard population growth from 1991 to 2000 was driven by a 3-fold increase in productivity and relatively high adult and juvenile female survival. Mallard abundance in Michigan and Wisconsin peaked near 750,000 in the year 2000. Declining productivity and declining adult and juvenile survival contributed to a steady decrease in abundance from 2000 to 2022. Cause-specific mortality probabilities revealed that declines in survival were primarily driven by increases in non-hunting mortality. Further, adult and juvenile non-hunting mortality probabilities were the parameters most highly correlated with population growth rate. Given our modeling assumption that non-hunting mortality is conditional on surviving harvest, and that non-hunting mortality primarily occurs outside of the duck hunting season for female mallards, we suggest that processes acting in the late winter, spring, and or summer portion of the annual cycle have most affected population size. This corresponds to previous work indicating duckling production and breeding female mortality during the breeding period drive upland-nesting dabbling duck population dynamics (Cowardin and Johnson 1979; Hoekman et al. 2002; Arnold et al. 2012; Riecke et al. 2022*a*, *b*; Roberts et al. 2023). Decreasing non-hunting mortality, increasing productivity, or both would positively influence mallard abundance in the Great Lakes region if emigration were negligible (Luukkonen 2024).

Non-hunting mortality of adult and juvenile female mallards was negatively related to mallard abundance, indicating that as abundance increases, the risk of non-hunting mortality declines. Under density dependence in non-hunting mortality, we expect non-hunting mortality risk to increase with increasing population size (e.g., because of declining per capita resource availability), a relationship observed for adult but not for juvenile midcontinent mallards (Riecke et al. 2022*b*). In this study, increasing pond abundance was related to increased non-hunting mortality for adult females but decreased non-hunting mortality for juvenile females. Adult females make a larger investment in reproduction than juvenile females through higher probability of nesting (Devries et al. 2008) and re-nesting (Arnold et al. 2010). If adult females increased reproductive effort when wetlands were more abundant, the tradeoff between exposure to mortality during incubation in terrestrial environments and nesting effort (Arnold et al. 2012) may explain increased adult non-hunting mortality in years with wetter conditions. Alternately, the pond count parameter could simply be a poor reflection of breeding habitat abundance in the Great Lakes region. Compared to the PPR, where the pond count typically reflects natural wetland basins (potholes) suitable for duck reproduction, surveys completed in the far more heterogenous Great Lakes states included a variety of wet areas recorded as ponds that were likely unsuitable for mallard production (G. J. Soulliere, U.S. Fish and Wildlife Service, personal observation), reducing the value of these data as a habitat indicator.

In a previous study in the Great Lakes, breeding period survival for female mallards was negatively related to the amount of forest cover in home ranges, with predation considered the leading cause of mortality (Boyer et al. 2018). However, the proportion of forest cover in the Great Lakes region remained relatively constant during the study (Oswalt et al. 2019, Soulliere et al. 2020). The expansion of agriculture and loss of grassland (Soulliere et al. 2020) could have direct and indirect (Murphy 2003, Stanton et al. 2018) effects on non-hunting mortality through reduction in the quantity and quality of nesting habitat, leading to increased predation risk, or to a reduction in aquatic invertebrate prey (Nebel et al. 2010, Hallmann et al. 2014) required to meet nutrient demands of reproduction (Alisauskas and Ankney 1992). Hybridization of wild with domestic game-farm mallards (Lavretsky et al. 2020) could additionally be a factor contributing to increased non-hunting mortality (Schladweiler and Tester 1972) as domestic mallards typically suffered higher predation rates and lower survival (Smith 1999, Osborne et al. 2010, Söderquist et al. 2013) in free-ranging environments. Recent work demonstrating that mallards harvested in Ohio (Schummer et al. 2023) and a large component of the breeding population in the Great Lakes region are composed of wild × game-farm mallard hybrids (Luukkonen 2024) warrants further investigation into the demographic consequences of hybridization. The interactions between nesting and brood-rearing habitat quantity and quality, predation pressure, and anthropogenic factors such as agricultural intensification, urban development, and release of game-farm mallards are likely complex and additional work is needed to understand mechanisms associated with increased non-hunting mortality.

Adult female harvest mortality was remarkably constant from 1991–2022 despite changes in the number of duck hunters and liberalization of harvest regulations. There was limited evidence of a negative relationship of adult and juvenile female harvest mortality with spring mallard abundance, suggesting that harvest risk declines when the population is larger, a trend also detected in wood ducks (*Aix sponsa*) banded in the UMGLJV region (Greenawalt 2023). Harvest mortality of juvenile female mallards increased with the number of duck hunters but was not closely tied to harvest regulations (Figure S1, available in Supporting Information). In contrast, Palumbo and Shirkey (2022) found juvenile female direct recovery rates were about 3 times greater among mallards banded in areas with substantially more liberal regulations (daily limit of 6 female mallards and 107-day season compared to daily limit of 1 female mallard and 62-day season). However, our results indicated limited ability to reduce female mallard harvest probability, particularly for adult females, via regulation changes to the hunting season framework for the United States portion of the Mississippi Flyway. Singer (2014) found female mallard kill rates in the Great Lakes region peaked in the 1960s and 1970s and then declined with declining numbers of duck hunters and liberalization of regulations in the 1990s, concluding female mallard harvest had not been unsustainable in the early 2000s. Given partial controllability of harvest mortality, opportunities for partial compensation of harvest through non-hunting mortality, and density dependence in productivity (described below), restricting female mallard harvest regulations may be ineffective in increasing female mallard abundance in the Great Lakes region relative to other management actions that address non-hunting mortality or productivity.

Harvest was a small component of total annual mortality for adult and juvenile females, consistent with findings that dabbling duck population growth rates are primarily influenced by environmental factors rather than harvest (Sedinger et al. 2019; Riecke et al. 2022*a*, 2022*b*). While harvest regulations were not closely tied to Great Lakes female mallard survival, determining the effects of the number of hunters, regulations, and ultimately harvest on population dynamics requires accounting for potentially confounding effects of environmental factors and population density (Riecke et al. 2022*a*). Although mallard abundance in the Great Lakes region has declined since harvest regulations were liberalized, harvest mortality is a fraction of non-hunting mortality and declines in survival were primarily related to increasing non-hunting mortality. Further, harvest is likely partially compensated by non-hunting mortality, as adult females were approximately 3.5 to 6.5 times more likely to die from non-hunting causes than from harvest. During the study period, increasing non-hunting mortality relative to harvest mortality indicates a mechanism for harvest to become more compensatory over time.

The survival and mortality models used in this study rely on the assumptions that non-hunting mortality occurs outside of the hunting season, band reporting probability estimates are unbiased, banded female mallards have the same probability of being reported as male mallards, and that wounding loss remained constant at 20% during the study. Although unavailable for this study, post-season or winter banding can provide additional data required to fit seasonal survival models. Joint analysis of pre- and post-season banding allows estimation of seasonal survival (e.g., hunting season vs. non-hunting season) without the assumption that non-hunting mortality occurs only outside of the hunting season. Seasonal survival models present an opportunity to further learn about mortality processes occurring throughout the annual cycle and their contribution to population dynamics (Roberts et al. 2023).

Temporal productivity trends identified in this study were generally similar to the trend and magnitude of mallard age ratios in the prairie pothole and prairie parklands (Specht and Arnold 2018), to the magnitude of mallard age ratios in the United States prairies and Saskatchewan (Weegman et al. 2024), and to long-term average mallard productivity in the Great Lakes region derived from Lincoln estimates (Singer et al. 2016). Hybridization of wild with domestic game-farm mallards likely contributes to lower incubation incidence in hybrids with predominantly domestic genes (Luukkonen 2024), and movement data collected from global positioning system (GPS) transmitters indicate hybrid mallards select for urban areas and are more prevalent in the southern Great Lakes region (Luukkonen 2024). These findings are consistent with lower female age ratios at developed and southern locations and raise concern regarding the impact of current game-farm mallard releases on Great Lakes mallard productivity.

Productivity was also related to habitat conditions and was higher during years when more hectares were enrolled in CRP. Because land cover types provided by CRP have been linked to increased nest success and production in upland-nesting ducks (Reynolds et al. 2001), we surmised the total area of CRP could provide a reasonable annual index of regional availability of upland nesting cover. The estimated loss of 1.4 million ha of grassland and pasture in the UMGLJV region since 2001 corresponds to the decline in CRP and subsequently mallard productivity. Because we did not include agricultural intensity as a covariate in our models, it is unclear whether declining productivity is primarily related to loss of upland nesting habitat, an increase in cropland area or pesticide use, or an interaction of these factors, which is an area for further research. There is a well-established link between wetland counts and mallard abundance in the PPR (USFWS 2023*a*). While the area enrolled in CRP declined, wetland counts during aerial surveys were variable annually with an increase in the last several years of this study. However, wetlands with stable hydrology may proceed to late successional stages where wetland area is dominated by emergent vegetation, reducing value to breeding mallards (Fowler et al. 2024). The relationship between wetlands and productivity for Great Lakes mallards warrants further research, especially the influence of hybridization, use of urban areas for nesting (Luukkonen 2024), and the consequences of intensive agricultural practices on brood-rearing wetlands.

Productivity was lower in years when mallard abundance was high, a key component of adaptive harvest management, suggesting the potential for density dependence in productivity. This is consistent with the hypothesis that resources such as quality nest sites, brood-rearing habitat, or food become more limiting when the number of breeding mallards increases relative to the supply of these resources, and therefore nest success is lower or fewer ducklings survive until fledging at high population density. Identification of density dependence varies among studies and likely depends on the scale at which density is measured (Singer et al. 2016, Specht and Arnold 2018, Riecke et al. 2022*b*, Devries et al. 2023). Density dependence in productivity would provide another mechanism for harvest compensation, in addition to compensation through the increasing non-hunting mortality observed in this study.

Our model indicates the Great Lakes mallard population is primarily limited by non-hunting mortality and productivity, resulting from environmental and anthropogenic factors, while female mallard harvest has likely not been the most influential factor in the population decline. Integrated analysis of multiple datasets will continue to be valuable to inform management actions and predict population dynamics under changing environmental conditions (Zhao et al. 2019, Weegman et al. 2022). High-priority questions for additional research including understanding how habitat changes and releases of game-farm mallards affect non-hunting mortality and productivity of Great Lakes mallards.

MANAGEMENT IMPLICATIONS

Continued investment in banding and population survey programs would contribute to valuable data sets that can be used for monitoring the effects of ecological and anthropogenic factors on waterfowl population dynamics. Management actions that reduce female mallard mortality during late winter, spring, and summer, and that increase productivity at large scales are most likely to positively influence mallard abundance in the Great Lakes region. Programs that increase the quantity and quality of upland nesting habitat (i.e., grassland) and brood-rearing wetlands in the southern (BCR 23) portion of the Great Lakes region would likely be most effective. Based on our analysis, reducing female mallard non-hunting mortality would likely be more effective in increasing abundance than would restricting female mallard harvest regulations. Additional research focused on identifying the primary causes of increasing non-hunting mortality and declining productivity would greatly inform future management actions given the uncertainty in the relative influences of environmental, habitat, and anthropogenic factors on decline in Great Lakes mallards.

ACKNOWLEDGMENTS

Funding was provided by grant GG 751210000001883 from the Great Lakes Fish and Wildlife Restoration Act, grant WLD2101 from the Michigan Department of Natural Resources Wildlife Division, and through contribution from Ducks Unlimited, Dave and Denise Bunning through the Sunshine Charitable Foundation, Michigan State University, Winous Point Marsh Conservancy, Franklin College, Indiana Department of Natural Resources, Upper Mississippi/Great Lakes Joint Venture, and by the Joseph Laurence Maison scholarship and Joseph G. Schotthoefer Memorial Student Award by Safari Club International, Michigan Involvement Committee. Transmitter purchase and deployment by the Wisconsin Department of Natural Resources was funded through the Federal Aid in Wildlife Restoration Act. Dr. Scott Winterstein's participation in this research was supported in part by the intramural research program of the United States Department of Agriculture and National Institute of Food and Agriculture through Michigan State University AgBioResearch Project MICL02588 (Modeling Wildlife Population Dynamics). We thank the numerous waterfowl banders, pilots, aerial survey observers, and waterfowl hunters whose contributions provided the data to make this work possible. Feedback provided by B. S. Sedinger and 2 anonymous reviewers greatly improved this manuscript. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

This study followed ethical guidelines provided by the Michigan State University institutional animal care and use committee (IACUC) permit PROTO202100046 and used publicly available banding and band recovery data collected under United States Geological Survey Bird Banding Laboratory permits.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the U.S. Geological Survey Bird Banding Laboratory, the U.S. Fish and Wildlife Service, and the U.S. Department of Agriculture. These data were derived from the following resources available in the public domain: https://www.fws.gov/library/collections/waterfowl-population-status-reports; https://www.usgs.gov/data/north-american-bird-banding-program-dataset-1960-2023-retrieved-2023-07-12; https://www.fsa.usda.gov/programs-and-services/conservation-programs/reports-and-statistics/conservation-reserve-program-statistics/index.

ORCID

Benjamin Z. Luukkonen http://orcid.org/0009-0001-4930-9004
Drew N. Fowler http://orcid.org/0000-0001-9347-4579
Philip Lavretsky http://orcid.org/0000-0002-5904-8821

REFERENCES

Alisauskas, R. T., and C. D. Ankney. 1992. The cost of egg laying and its relationship to nutrient reserves in waterfowl. Pages 30–61 *in* B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, editors. Ecology and management of breeding waterfowl. University of Minnesota Press, Minneapolis, USA.

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.

Anderson, D. R., and K. P. Burnham. 1976. Population ecology of the mallard. VI. The effect of exploitation on survival. U.S. Fish and Wildlife Service, Washington, D.C., USA.

Arnold, T. W., R. T. Alisauskas, and J. S. Sedinger. 2020. A meta-analysis of band reporting probabilities for North American waterfowl. Journal of Wildlife Management 84:534–541.

Arnold, T. W., R. G. Clark, D. N. Koons, and M. Schaub. 2018. Integrated population models facilitate ecological understanding and improved management decisions. Journal of Wildlife Management 82:266–274.

Arnold, T. W., J. H. Devries, and D. W. Howerter. 2010. Factors that affect renesting in mallards (*Anas platyrhynchos*). Auk 127:212–221.

Arnold, T. W., E. A. Roche, J. H. Devries, and D. W. Howerter. 2012. Costs of reproduction in breeding female mallards: predation risk during incubation drives annual mortality. Avian Conservation and Ecology 7(1):1.

Arnold, T. W., and C. De Sobrino. 2010. An updated derivation of mallard harvest for midwestern waterfowl hunters. Midwest Fish and Wildlife Conference, Indianapolis, Indiana, USA.

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.

Bird Studies Canada and North American Bird Conservation Initiative. 2014. Bird Conservation Regions. <https://www.birdscanada.org/bird-science/nabci-bird-conservation-regions>. Accessed 30 Apr 2021.

Boyer, R. A., J. M. Coluccy, R. A. Montgomery, K. M. Redilla, and S. R. Winterstein. 2018. The effect of habitat on the breeding season survival of mallards (*Anas platyrhynchos*) in the Great Lakes region. Canadian Journal of Zoology 96: 700–706.

Brooks, S. P., and A. Gelman. 1998. General methods for monitoring convergence of iterative simulations. Journal of Computational and Graphical Statistics 7:434–455.

Brownie, C., D. R. Anderson, K. P. Burnham, and D. S. Robson. 1978. Statistical inference from band recovery data. First Edition. U.S. Fish and Wildlife Service, Resource Publication 131, 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.

Carney, S. M. 1992. Species, age and sex identification of ducks using wing plumage. U.S. Department of the Interior, U.S. Fish and Wildlife Service, Washington, D.C., USA. <http://www.npwrc.usgs.gov/resource/tools/duckplum/duckplum.htm>.

Celis-Murillo, A., M. Malorodova, and E. Nakash. 2022. North American Bird Banding Program dataset 1960-2022. U.S. Geological Survey, Reston, Virginia, USA.

Chiang, C. L., 1991. Competing risks in mortality analysis. Annual Review of Public Health 12:281–307.

Coluccy, J. M., T. Yerkes, R. Simpson, J. W. Simpson, L. Armstrong, and J. Davis. 2008. Population dynamics of breeding mallards in the Great Lakes states. Journal of Wildlife Management 72:1181–1187.

Cordts, S. 2023. 2023 Waterfowl Breeding Population Survey, Minnesota. Minnesota Department of Natural Resources, St. Paul, USA.

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

Devries, J. H., L. M. Armstrong, D. W. Howerter, and R. B. Emery. 2023. Waterfowl distribution and productivity in the Prairie Pothole Region of Canada: tools for conservation planning. Wildlife Monographs 211:e1074.

Devries, J. H., R. W. Brook, D. W. Howerter, and M. G. Anderson. 2008. Effects of spring body condition and age on reproduction in mallards (*Anas platyrhynchos*). Auk 125:618–628.

Devries, J. H., J. J. Citta, M. S. Lindberg, D. W. Howerter, and M. G. Anderson. 2003. Breeding-season survival of mallard females in the prairie pothole region of Canada. Journal of Wildlife Management 67:551.

Dewitz, J. 2023. 2021 National Land Cover Database Products. Earth Resources Observation and Science Center, Sioux Falls, South Dakota, USA.

Ellis, M. B., C. A. Miller, and S. G. Pallazza. 2022. The effect of individual harvest on crippling losses. Wildlife Society Bulletin 46:1–6.

Ergon, T., Ø. Borgan, C. R. Nater, and Y. Vindenes. 2018. The utility of mortality hazard rates in population analyses. Methods in Ecology and Evolution 9:2046–2056.

Euliss, N. H., J. W. Labaugh, L. H. Fredrickson, D. M. Mushet, M. K. Laubhan, G. A. Swanson, T. C. Winter, D. O. Rosenberry, and R. D. Nelson. 2004. The wetland continuum: a conceptual framework for interpreting biological studies. Wetlands 24:448–458.

Fowler, D. N., J. M. Winiarski, C. D. Pollentier, and R. C. Gatti. 2024. The influence of landscape composition and configuration on breeding waterfowl pair abundance in Wisconsin. Wildlife Society Bulletin 48:1–17.

Greenawalt, A. C. 2023. Population ecology and migration chronology of wood ducks that breed in the upper Mississippi Great Lakes region. Thesis, University of Wisconsin, Stevens Point, USA.

Hallmann, C. A., R. P. B. Foppen, C. A. M. Van Turnhout, H. De Kroon, and E. Jongejans. 2014. Declines in insectivorous birds are associated with high neonicotinoid concentrations. Nature 511:341–343.

Hoekman, S. T., L. S. Mills, D. W. Howerter, J. H. Devries, and I. J. Ball. 2002. Sensitivity analyses of the life cycle of midcontinent mallards. Journal of Wildlife Management 66:883.

Hopwood, J., S. H. Black, M. Vaughan, and E. Lee-Mader. 2013. Beyond the birds and the bees: effects of neonicotinoid insecticides on agriculturally important beneficial invertebrates. The Xerces Society for Invertebrate Conservation, Portland, Oregon, USA.

Kellner, K. F. 2016. jagsUI: a wrapper around 'rjags' to streamline 'JAGS' analyses. <https://CRAN.R-project.org/package=jagsUI>.

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., G. Gunnarsson, J. A. Schmutz, and J. J. Rotella. 2014. Drivers of waterfowl population dynamics: from teal to swans. Wildfowl Special Issue Number 4:169–191.

Lavretsky, P., N. R. McInerney, J. E. Mohl, J. I. Brown, H. F. James, K. G. McCracken, and R. C. Fleischer. 2020. Assessing changes in genomic divergence following a century of human-mediated secondary contact among wild and captive-bred ducks. Molecular Ecology 29:578–595.

Lavretsky, P., and B. Sedinger. 2023. Migratory patterns of mallards in eastern North America as revealed from band-recovery data. Journal of Wildlife Management 87:e22421.

Lemoine, N. P. 2019. Moving beyond noninformative priors: why and how to choose weakly informative priors in Bayesian analyses. Oikos 128:912–928.

Luukkonen, B. Z. 2024. Movement and population dynamics of Great Lakes mallards. Dissertation, Michigan State University, East Lansing, USA.

Luukkonen, B. Z., O. E. Jones, and R. W. Klaver. 2021. Canada goose survival and recovery rates in urban and rural areas of Iowa, USA. Journal of Wildlife Management 85:283–292.

March, J. R., G. F. Martz, and R. A. Hunt. 1973. Breeding duck populations and habitat in Wisconsin. Technical Bulletin 68. Wisconsin Department of Natural Resources, Madison, USA.

Morrissey, C. A., P. Mineau, J. H. Devries, F. Sanchez-Bayo, M. Liess, M. C. Cavallaro, and K. Liber. 2015. Neonicotinoid contamination of global surface waters and associated risk to aquatic invertebrates: a review. Environment International 74:291–303.

Murphy, M. T. 2003. Avian population trends within the evolving agricultural landscape of eastern and central United States. Auk 120:20–34.

Nebel, S., A. Mills, J. D. McCracken, and P. D. Taylor. 2010. Declines of aerial insectivores in North America follow a geographic gradient. Avian Conservation and Ecology 5(2):1.

North American Waterfowl Management Plan [NAWMP]. 2018. North American Waterfowl Management Plan (NAWMP) update: connecting people, waterfowl, and wetlands. U.S. Department of Interior, Fish and Wildlife Service, Washington, D.C., USA; and Environment Canada, Canadian Wildlife Service, Ottawa, Ontario, Canada.

Osborne, C. E., B. L. Swift, and G. A. Baldassarre. 2010. Fate of captive-reared and released mallards on eastern Long Island, New York. Human-Wildlife Interactions 4:266–274.

Oswalt, S. N., W. B. Smith, P. D. Miles, and S. A. Pugh. 2019. Forest resources of the United States. USDA Forest Service General Technical Report WO-97, Washington, D.C., USA. <https://www.fs.usda.gov/treesearch/pubs/57903>.

Palumbo, M. D., and B. T. Shirkey. 2022. Harvest mortality of mallards (*Anas platyrhynchos*) banded at Lake St. Clair, CAN and western Lake Erie, USA. Waterbirds 45:51–61.

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, 20–22 March, Vienna, Austria.

R Core Team. 2022. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Raftovich, R. V., K. K. Fleming, S. C. Chandler, and C. M. Cain. 2022. Migratory bird hunting activity and harvest during the 2020-21 and 2021-22 hunting seasons. U.S. Fish and Wildlife Service, Laurel, Maryland, USA.

Rexstad, E. A. 1992. Effect of hunting on annual survival of Canada geese in Utah. Journal of Wildlife Management 56: 297–305.

Reynolds, R. E., T. L. Shaffer, R. W. Renner, W. E. Newton, and B. D. J. Batt. 2001. Impact of the conservation reserve program on duck recruitment in the U.S. Prairie Pothole Region. Journal of Wildlife Management 65:765–780.

Riecke, T. V., M. G. Lohman, B. S. Sedinger, T. W. Arnold, C. L. Feldheim, D. N. Koons, F. C. Rohwer, M. Schaub, P. J. Williams, and J. S. Sedinger. 2022*a*. Density-dependence produces spurious relationships among demographic parameters in a harvested species. Journal of Animal Ecology 91:2261–2272.

Riecke, T. V., B. S. Sedinger, T. W. Arnold, D. Gibson, D. N. Koons, M. G. Lohman, M. Schaub, P. J. Williams, and J. S. Sedinger. 2022*b*. A hierarchical model for jointly assessing ecological and anthropogenic impacts on animal demography. Journal of Animal Ecology 91:1612–1626.

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 87:e22405.

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

Schladweiler, J. L., and J. R. Tester. 1972. Survival and behavior of hand-reared mallards released in the wild. Journal of Wildlife Management 36:1118–1127.

Schummer, M. L., J. Simpson, B. Shirkey, S. R. Kucia, P. Lavretsky, and D. C. Tozer. 2023. Population genetics and geographic origins of mallards harvested in northwestern Ohio. PLoS One 18:e0282874.

Scott, R. W., and F. A. Huff. 1996. Impacts of the Great Lakes on regional climate conditions. Journal of Great Lakes Research 22:845–863.

Sedinger, B. S., T. V. Riecke, C. A. Nicolai, R. Woolstenhulme, W. G. Henry, and K. M. Stewart. 2019. Experimental harvest regulations reveal that water availability during spring, not harvest, affects change in a waterfowl population. Ecology and Evolution 9:12701–12709.

Simpson, J. W., T. J. Yerkes, B. D. Smith, and T. D. Nudds. 2005. Mallard duckling survival in the Great Lakes region. Condor 107:898–909.

Singer, H. V. 2014. Factors affecting productivity and harvest rates of Great Lakes mallards. Thesis, Michigan State University, East Lansing, USA.

Singer, H. V., D. R. Luukkonen, L. M. Armstrong, and S. R. Winterstein. 2016. Influence of weather, wetland availability, and mallard abundance on productivity of Great Lakes mallards (*Anas platyrhynchos*). Wetlands 36:969–978.

Smith, D. B. 1999. Survival, behavior, and movements of captive-reared mallards released in Dorchester County, Maryland. Dissertation, Louisiana State University, Baton Rouge, USA.

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

Söderquist, P., G. Gunnarsson, and J. Elmberg. 2013. Longevity and migration distance differ between wild and hand-reared mallards in Northern Europe. European Journal of Wildlife Research 59:159–166.

Soulliere, G. J., M. A. Al-Saffar, J. M. Coluccy, R. J. Gates, H. M. Hagy, J. W. Simpson, J. N. Straub, R. L. Pierce, M. W. Eichholz, and D. R. Luukkonen. 2017. Upper Mississippi River and Great Lakes Region Joint Venture waterfowl habitat conservation strategy – 2017 revision. U.S. Fish and Wildlife Service, Bloomington, Minnesota, USA

Soulliere, G. J., M. A. Al-Saffar, K. R. VanBeek, C. M. Tonra, M. D. Nelson, D. N. Ewert, T. Will, W. E. Thogmartin, K. E. O'Brien, S. W. Kendrick, et al. 2020. Upper Mississippi/Great Lakes Joint Venture landbird habitat conservation strategy – 2020 Revision. U.S. Fish and Wildlife Service, Bloomington, Minnesota, USA.

Soulliere, G. J., and S. B. Chadwick. 2003. Using helicopter sampling to estimate visibility bias on the Michigan spring waterfowl survey. Michigan Department of Natural Resources Wildlife Division Report 3408, Lansing, USA.

Specht, H. M., and T. W. Arnold. 2018. Banding age ratios reveal prairie waterfowl fecundity is affected by climate, density dependence and predator–prey dynamics. Journal of Applied Ecology 55:2854–2864.

Stanton, R. L., C. A. Morrissey, and R. G. Clark. 2018. Analysis of trends and agricultural drivers of farmland bird declines in North America: a review. Agriculture, Ecosystems and Environment 254:244–254.

U.S. Department of Agriculture. 2024. Conservation Reserve Program statistics. CRP enrollment and rental payments by state, 1986-2022. <https://www.fsa.usda.gov/programs-and-services/conservation-programs/reports-and-statistics/conservation-reserve-program-statistics/index>. Accessed 21 Mar 2024.

U.S. Fish and Wildlife Service [USFWS]. 1987. Standard operating procedures for aerial waterfowl breeding ground population and habitat surveys in North America. USFWS, Washington, D.C., USA.

U.S. Fish and Wildlife Service [USFWS]. 2022. Waterfowl population status, 2022. Washington, D.C., USA.

U.S. Fish and Wildlife Service [USFWS]. 2023*a*. Adaptive Harvest Management: 2024 Hunting Season. U.S. Department of the Interior, Washington, D.C., USA. <http://training.fws.gov/library/Bird_Publications/adapt_harvest_ducks98.pdf%5Cnhttp://www.lmvjv.org/library/WWG_literature/AHM_Final_Report-2008.pdf>.

U.S. Fish and Wildlife Service [USFWS]. 2023*b*. Waterfowl population status, 2023. USFWS, Washington, D.C., USA.

Weegman, M. D., R. T. Alisauskas, D. K. Kellett, Q. Zhao, S. Wilson, and T. Telenský. 2022. Local population collapse of Ross's and lesser snow geese driven by failing recruitment and diminished philopatry. Oikos 2022:e09184.

Weegman, M. D., J. H. Devries, R. G. Clark, D. W. Howerter, D. Gibson, J. P. Donnelly, and T. W. Arnold. 2024. Ecological and anthropogenic drivers of waterfowl productivity are synchronous across species, space, and time. Ecological Applications 34:e2979.

Wiegers, J. N. Y., E. Jongejans, C. A. M. Van Turnhout, L. Van Den Bremer, H. Van Der Jeugd, and E. Kleyheeg. 2022. Integrated population modeling identifies low duckling survival as a key driver of decline in a European population of the mallard. Ornithological Applications 124:1–12.

Yang, L., S. Jin, P. Danielson, C. Homer, L. Gass, S. M. Bender, A. Case, C. Costello, J. Dewitz, J. Fry, et al. 2018. A new generation of the United States National Land Cover Database: requirements, research priorities, design, and implementation strategies. ISPRS Journal of Photogrammetry and Remote Sensing 146:108–123.

Zhao, Q., T. W. Arnold, J. H. Devries, D. W. Howerter, R. G. Clark, and M. D. Weegman. 2019. Land-use change increases climatic vulnerability of migratory birds: insights from integrated population modelling. Journal of Animal Ecology 88: 1625–1637.

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: Anthony Roberts.

SUPPORTING INFORMATION

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

How to cite this article: Luukkonen, B. Z., S. R. Winterstein, D. B. Hayes, D. N. Fowler, G. J. Soulliere, J. M. Coluccy, A. A. Shipley, J. Simpson, B. Shirkey, J. M. Winiarski, et al. 2024. Great Lakes mallard population dynamics. Journal of Wildlife Management e22702. https://doi.org/10.1002/jwmg.22702