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RESEARCH ARTICLE

A hierarchical model for jointly assessing ecological and anthropogenic impacts on animal demography

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Abstract

1. The management of sustainable harvest of animal populations is of great ecological and conservation importance. Development of formal quantitative tools to estimate and mitigate the impacts of harvest on animal populations has positively impacted conservation efforts.
2. The vast majority of existing harvest models, however, do not simultaneously estimate ecological and harvest impacts on demographic parameters and population trends. Given that the impacts of ecological drivers are often equal to or greater than the effects of harvest, and can covary with harvest, this disconnect has the potential to lead to flawed inference.
3. In this study, we used Bayesian hierarchical models and a 43-year capture–mark–recovery dataset from 404,241 female mallards *Anas platyrhynchos* released in the North American midcontinent to estimate mallard demographic parameters. Furthermore, we model the dynamics of waterfowl hunters and habitat, and the direct and indirect effects of anthropogenic and ecological processes on mallard demographic parameters.
4. We demonstrate that density dependence, habitat conditions and harvest can simultaneously impact demographic parameters of female mallards, and discuss implications for existing and future harvest management models.
5. Our results demonstrate the importance of controlling for multicollinearity among demographic drivers in harvest management models, and provide evidence for multiple mechanisms that lead to partial compensation of mallard harvest. We provide a novel model structure to assess these relationships that may allow for improved inference and prediction in future iterations of harvest management models across taxa.

KEYWORDS
Anas platyrhynchos, Bayesian, cause-specific mortality, demography, harvest, hierarchical model, mallard, multicollinearity, survival

1 | INTRODUCTION

The harvest of wild organisms for commercial and subsistence use has dramatically and negatively impacted animal populations. Although historical data that detail the realized impacts of harvest are generally lacking prior to the 19th century, poorly regulated harvest early in the industrial age has been consistently linked to severe declines in the abundances and geographic ranges of numerous taxa. For example, whales (Baker & Clapham, 2004), furbearers (Obbard et al., 1987), waders and shorebirds (Frohring et al., 1988), fish (Lear, 1998) and mussels (Anthony & Downing, 2001) all declined precipitously following historical overharvest, and many populations have never recovered. Ultimately, the absolute or functional extinction of a variety of bird and mammal populations (e.g. sea mink *Neovison macrodon*, passenger pigeon *Ectopistes migratorius*, heath hen *Tympanuchus cupido cupido* and bison *Bison bison*) following overharvest and landscape change provided a harsh lesson on the importance of conservation. These examples of unsustainable exploitation of supposedly inexhaustible resources spurred the development of wildlife management (Leopold, 1933), and the ensuing management of sport and commercial harvest of animals has been central to population recovery in some areas. Despite clear progress in our understanding and interest in the conservation of animals, many taxa remain susceptible to harvest-related exploitation (Bennett et al., 2002; Brashares et al., 2004; Hutchings & Myers, 1994), or continue to be harvested in the absence of a functional understanding of the relationship between harvest and population dynamics (e.g. upland gamebirds; Sands & Pope, 2010).

Despite a tremendous amount of research (e.g. Cooch et al., 2014; Péron, 2013; Servanty et al., 2010), much remains to be learned about the impacts and sustainability of harvest on animal populations. There are two primary hypotheses regarding the impacts of harvest. Harvest compensation occurs when increases in harvest have little to no effect on survival probabilities, as increases in harvest are associated with declines in other mortality sources. In contrast, harvest could add to the mortality process, when increases in harvest do not reduce other causes of mortality, and the overall mortality rate increases as harvest mortality increases. Harvest compensation is typically achieved through two biological mechanisms. The first of these is individual heterogeneity (Rexstad & Anderson, 1992). Individuals that are more likely to be harvested may be in poorer condition or of lower latent quality (Arnold, 2021; Hepp et al., 1986) and have lower survival probabilities and residual reproductive value. Thus, as hunters and anglers remove lower quality individuals from the population, the survival probability of the total population is relatively unaffected, as these individuals were putatively more likely to die from other causes even in the absence of harvest (Errington, 1945). The second compensation mechanism is the alleviation of density dependence (Gunnarsson et al., 2013; Sedinger & Herzog, 2012; Viljugrein et al., 2005), where the harvest of individuals competing for resources may increase the latent survival probabilities and/or fecundity (i.e. compensatory harvest natality; Boyce et al., 1999) of remaining individuals as competition is reduced. These mechanisms are not mutually exclusive and can occur synergistically (Péron, 2013). Models of additive harvest typically assume a negative relationship between harvest rate and survival or population growth rate, such that increases in harvest mortality do not affect natural mortality (Péron, 2013), leading to declines in survival. Finally, depensatory mortality can occur when increases in harvest mortality lead to increases in other sources of mortality as well.

Researchers have employed a variety of techniques to estimate harvest effects. Early analyses of harvest impacts compared survival probabilities between periods of restrictive and liberal harvest (e.g. Anderson & Burnham, 1976). Following this, researchers employed ultrastructure approaches that directly assessed the effect of harvest as a covariate on survival (Burnham et al., 1984; Smith & Reynolds, 1992). Subsequent simulation-based research demonstrated that random effects models that estimate second-order correlations between survival and harvest, or between natural mortality and harvest, are more effective at exposing underlying relationships (Otis & White, 2004). Thus, these model types have become the predominant analytical tool to assess harvest impacts (e.g. Péron, 2013). Critically, while decades of research have been directed towards assessing the relationship between harvest and survival, existing approaches often fail to account for multicollinearity among harvest regulations, ecological processes, life-history strategies and demographic rates (Sedinger & Rexstad, 1994). For instance, if both natural mortality and hunter effort are density dependent, density-dependent effects may confound our understanding of the relationship between survival and harvest (Sedinger & Herzog, 2012).

North American waterfowl populations are among the most extensively studied and managed terrestrial taxa (Cooch et al., 2014), and the midcontinent mallard population (*Anas platyrhnchos*) in North America is the most studied sport-harvested population world-wide. Substantial research has been conducted regarding the effects of harvest on the midcontinent mallard population (e.g. Anderson & Burnham, 1976; Burnham et al., 1984; Runge et al., 2002; Smith & Reynolds, 1992), and mallard harvest management models have often been used as a case study highlighting the successful implementation of adaptive resource management strategies (e.g. Nichols et al., 2015, 2018, 2019). Thus, this system is excellent for testing new ideas and model structures against established modelling frameworks. Currently, the population models underlying Adaptive Harvest Management (Runge et al., 2002) of North American mallards indicate that harvest is additive to the mortality process (Nichols et al., 2007; Runge & Johnson, 2002), meaning that the removal of individuals through harvest is not compensated by reduced natural mortality. Accordingly, harvest regulations track changes in North American mallard populations, where harvest rates are reduced when population size is low, and increased when population size increases.

North American duck populations exhibit density-dependent regulation of fecundity (Amundson & Arnold, 2011; Gunnarsson et al., 2013; Specht & Arnold, 2018; Viljugrein et al., 2005) and survival (Robinson et al., 2017; Zhao et al., 2018, 2020), as well as density-dependent harvest pressure, whereby hunter effort and harvest are strongly correlated with duck abundance (Anderson & Padding, 2015). Thus, there is potential for strong correlations among multiple covariates that affect demographic rates. Sedinger and Herzog (2012) demonstrated that this multicollinearity among demographic drivers has the potential to impact inference about the relationship between harvest mortality, survival and population growth rates. Additionally, recent (Arnold et al., 2016, 2017; Bartzen & Dufour, 2017; Péron, 2013; Péron et al., 2012) and previous research (Anderson & Burnham, 1976; Rexstad & Anderson, 1992; Sedinger & Rexstad, 1994) has indicated that harvest mortality may not be completely additive in North American duck populations, or in populations of other wild organisms (Bartmann et al., 1992; Sedinger et al., 2010; Stenglein et al., 2018). An equally large body of research has questioned the biological realism of purely compensatory or purely additive models of harvest effects on survival (e.g. Lebreton, 2005; Runge & Johnson, 2002; Smith & Reynolds, 1992), and recent research has demonstrated that existing models of the impacts of harvest on mallards are not predictive (Koons et al., 2022).

In this study, we use a hierarchical mark–recovery model (Cubaynes et al., 2012; Gimenez et al., 2012), to partition the effects of ecological (e.g. density dependence, habitat availability; Sedinger et al., 2019) and anthropogenic (e.g. harvest regulations, number of hunters) processes on natural and harvest mortality rates of female mallards marked in the Prairie Pothole Region of the North American midcontinent over more than four decades (1974–2016; Figure 1). We estimate harvest mortality hazard rate as a function of ecological processes and anthropogenic actions that occur prior to and during the hunting season, and natural mortality hazard rate as a function of ecological processes that occur during the breeding season, when the vast majority of natural mortality occurs in ducks (Hoekman et al., 2002). Thus, we control for the potential confounding effects of ecological processes on our understanding of anthropogenic effects by modelling relationships among habitat conditions, mallard abundance, hunter abundance, harvest regulations, reproductive effort and harvest and natural mortality rates (Figure 2). We then compare our estimates to predictions generated from existing Adaptive Harvest Management models (Runge et al., 2002). Our results

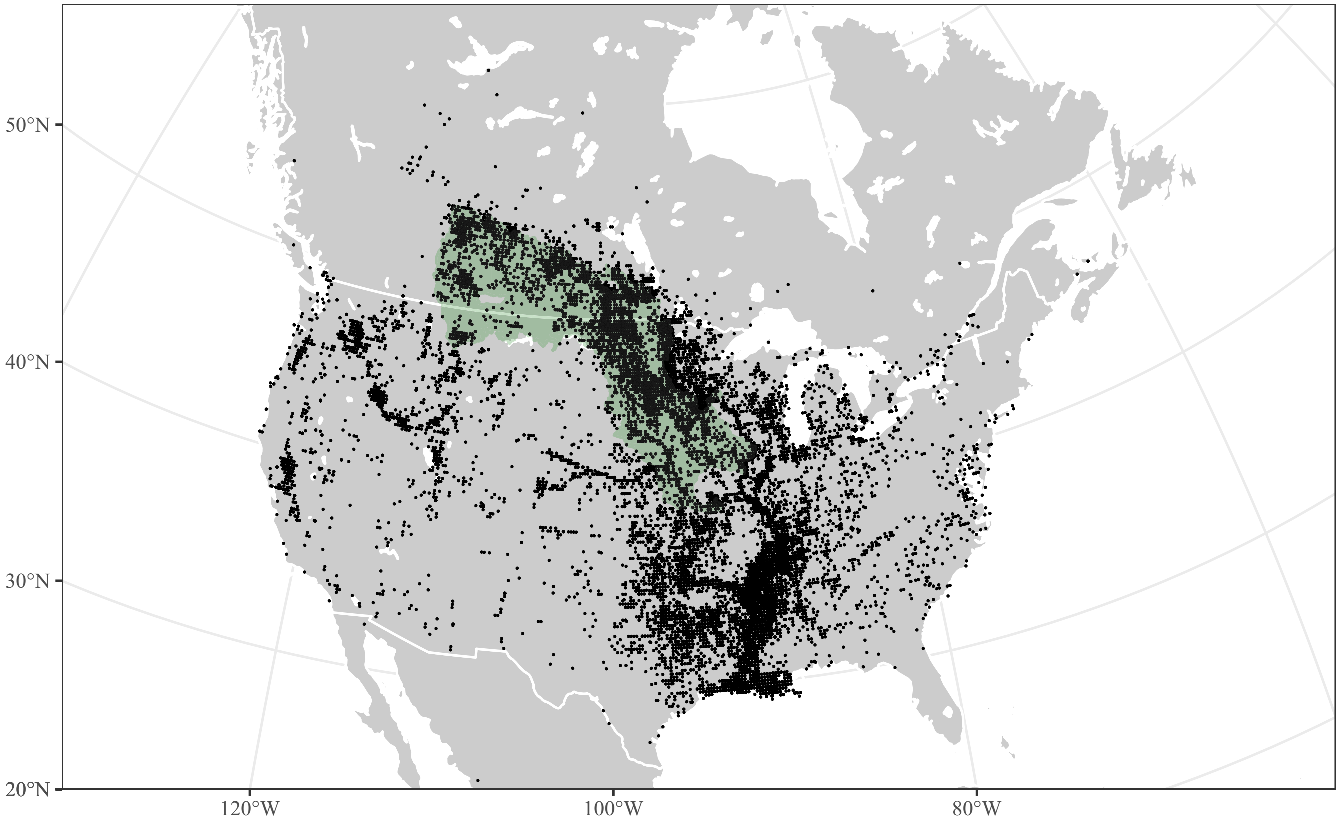


FIGURE 1 Map of band recovery locations (black points) for juvenile and adult female mallards marked and released (1974–2016) in EPA Level III Ecoregions 9.2.1, 9.2.2, 9.2.3 and 9.3.1 (transparent forest green, Omernik & Griffith, 2014)

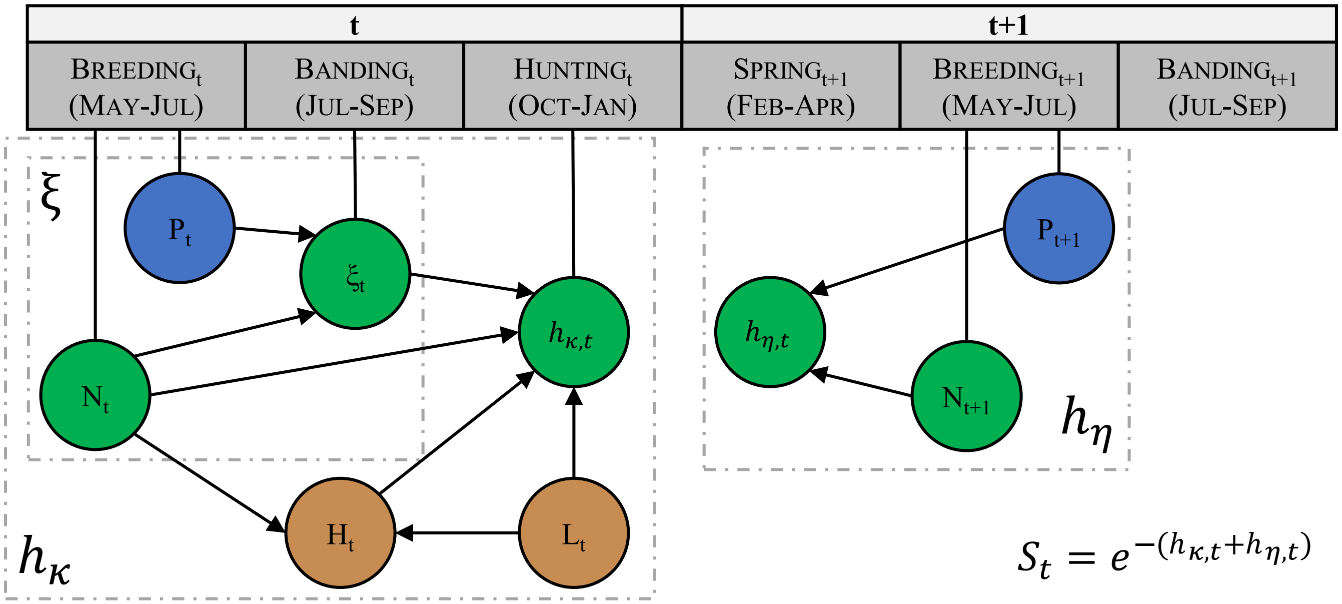


FIGURE 2 Directed acyclic graph demonstrating the hypothesized relationships among mallard breeding pair abundance (N), the number of ponds (P), harvest limits (L), the abundance of duck hunters (H), fecundity (ξ), harvest mortality hazard rate (h_κ), natural mortality hazard rate (h_η) and survival (S) for mallards marked and released in the Prairie Pothole Region of the United States and Canada, 1974–2016. Arrows represent covariate effects, grey dashed lines enclose separate generalized linear models and vertical solid lines denote the time period or interval when parameters were estimated, where survival (S) and natural mortality in year t are estimated from banding in year t to banding in year $t+1$. We estimated age-specific band recovery probabilities (f) as a function of age-specific harvest probability (κ), reporting rate (r) and crippling rate (c), $f = \kappa(1-c)r_t$. We note that we hypothesized the same relationships among demographic components for both juvenile and adult females.

demonstrate that questions regarding the effects of harvest on mallard demographic rates have not been fully resolved, and that novel approaches may improve existing inference.

2 | MATERIALS AND METHODS

2.1 | Field methods and data acquisition

Juvenile (*jv*) and adult (*ad*) female mallards were captured in swim-in traps, during drive-trapping, by hand, and from airboats and skiffs from 1 July to 30 September (1974–2016). Mallards were marked with metal leg rings. We subset these mark–release data to female mallards marked and released in EPA Level III ecoregions 9.2.1, 9.2.2, 9.2.3 and 9.3.1 (Omernik & Griffith, 2014). These ecoregions are generally equivalent to the Prairie Pothole Region, an area rich in ephemeral shallow wetlands (i.e. ponds), and the most important breeding area for dabbling ducks in North America. Marked individuals were then harvested by hunters during the fall and winter (October—early February), and a portion of rings were reported to the USGS Bird Banding Lab (Figure 1). We restricted ring recoveries to hunter harvested individuals recovered during the hunting season. Mark–recovery data were downloaded from the GameBirds Database CD (Bird Banding Lab, USGS Patuxent Wildlife Research Center; Celis-Murillo et al., 2020). In addition, we accessed estimates of mallard abundance and pond abundance from the Waterfowl Breeding Population and Habitat Survey (U.S. Fish and Wildlife Service, 2021), as well as data on federal duck stamp sales, which are required to hunt for waterfowl in the United States. Third party data were used for this study, collection of which followed appropriate ethical guidelines. No additional ethical approval was required from our institution.

We used a hierarchical capture–mark–recovery model (Cubaynes et al., 2012; Gimenez et al., 2012) to model the relationships among mallard, pond and hunter abundance, mallard fecundity, and cause-specific mortality hazard rates (see Figure 2 for a directed acyclic graph). We first modelled the estimates of mallards ($y_{N,t}$) and ponds ($y_{P,t}$) in millions as normal variation around the underlying true values (Kéry & Schaub, 2012), and we approximated the estimate error (ς_y) using time-varying standard errors from the Waterfowl Breeding Population and Habitat Survey (U.S. Fish and Wildlife Service, 2019),

$$\begin{aligned} y_{N,t} &\sim \text{Normal}\left(N_t,\ \varsigma^2_{y_N}\right), \\ y_{P,t} &\sim \text{Normal}\left(P_t,\ \varsigma^2_{y_P}\right). \end{aligned} \tag{1}$$

We modelled the true underlying number of ponds (***P***) and mallard abundance (***N***) in millions as first-order auto-regressive processes with variance,

$$\begin{aligned} N_{t+1} &\sim \text{Normal}\left(N_t,\ \sigma^2_{\text{N}}\right), \\ P_{t+1} &\sim \text{Normal}\left(P_t,\ \sigma^2_{\text{P}}\right). \end{aligned} \tag{2}$$

We defined fecundity (ξ) as the number of juvenile females captured per adult female at banding during each year. We modelled fecundity as a function of *z*-standardized number of ponds, *z*-standardized breeding pair abundance and random annual variation ($\epsilon_{\xi,t}$) given the number of juvenile females marked and released in each year ($r_{\mathrm{jv,t}}$), and the number of adult females ($r_{\mathrm{ad,t}}$) marked and released in each year.

$$\begin{aligned} r_{\mathrm{jv,t}} &\sim \mathrm{Poisson}\left(r_{\mathrm{ad,t}} \times \xi_{\mathrm{t}}\right), \\ \log\left(\xi_{\mathrm{t}}\right) &= \beta_{\xi,1} + \beta_{\xi,2} \times N_{\mathrm{t}} + \beta_{\xi,3} \times P_{\mathrm{t}} + \epsilon_{\xi,\mathrm{t}}, \\ \epsilon_{\xi,\mathrm{t}} &\sim \mathrm{Normal}\left(0,\ \sigma_{\xi}^{2}\right). \end{aligned} \tag{3}$$

We modelled the number of hunters (*H*) in millions during each year given the number of duck stamps sold ($y_{H,\mathrm{t}}$) as a function of mallard breeding pair abundance (*N*), a long-term trend (Anderson & Padding, 2015) and harvest limits (L_{t}); restrictive limits were enacted during a major drought and period of low mallard abundance (1985–1994),

$$\begin{aligned} y_{\mathrm{H,t}} &\sim \mathrm{Normal}\left(H_{\mathrm{t}},\ \sigma_{\mathrm{H}}^{2}\right), \\ H_{\mathrm{t}} &= \beta_{H,1} + \beta_{H,2} \times N_{\mathrm{t}} + \beta_{H,3} \times t + \beta_{H,4} \times L_{\mathrm{t}} \end{aligned} \tag{4}$$

2.2 | Estimating cause-specific mortality rates

We then estimated the effects of these interrelated covariates on natural (h_{η}) and harvest (h_{κ}) mortality hazard rates for each age class (*a*). In this system, ringing occurs in late summer (July—September), followed by a hunting season during autumn and winter (October—January). The majority of natural mortality occurs during the ensuing breeding season (Hoekman et al., 2002), and the survival interval is from ringing to ringing (Figure 2). We hypothesized that harvest mortality rate would increase as abundance and fecundity during the breeding season prior to harvest increased (Sedinger & Herzog, 2012) given the strong correlation between duck abundance and hunter participation (Anderson & Padding, 2015), that restrictive harvest limits (*L*) from 1985 to 1994 would reduce harvest rates (Otis, 2004), and that long-term declines in duck hunter numbers (*H*) would lead to a long-term reduction in harvest rates (Anderson & Padding, 2015). We modelled the effects of pond abundance and breeding mallard abundance on natural mortality hazard rates, and the effects of fecundity and breeding mallard abundance on harvest mortality hazard rates. For harvest mortality, we modelled the effects of fecundity and abundance during the breeding season prior to harvest, whereas we hypothesized that mallard and pond abundance during the breeding season following harvest would be most important for natural mortality (Figure 2). We hypothesized that increased reproductive allocation during wet years and increased abundance during the breeding season would lead to increased natural mortality hazard rates associated with energetic allocation to breeding (Arnold & Howerter, 2012; Dufour & Clark, 2002; Johns, 2019) in addition to the increased predation risk suffered by breeding females (Arnold et al., 2012; Sargeant et al., 1984),

$$\begin{aligned} \log\left(h_{\kappa_{\mathrm{a}},\mathrm{t}}\right) &= \beta_{\kappa_{\mathrm{a}},1} + \beta_{\kappa_{\mathrm{a}},2} \times N_{\mathrm{t}} + \beta_{\kappa_{\mathrm{a}},3} \times \xi_{\mathrm{t}} + \beta_{\kappa_{\mathrm{a}},4} \times L_{\mathrm{t}} + \beta_{\kappa_{\mathrm{a}},5} \times H_{\mathrm{t}} + \epsilon_{\kappa_{\mathrm{a}},\mathrm{t}}, \\ \log\left(h_{\eta_{\mathrm{a}},\mathrm{t}}\right) &= \beta_{\eta_{\mathrm{a}},1} + \beta_{\eta_{\mathrm{a}},2} \times N_{\mathrm{t+1}} + \beta_{\eta_{\mathrm{a}},3} \times P_{\mathrm{t+1}} + \epsilon_{\eta_{\mathrm{a}},t}, \end{aligned} \tag{5}$$

We used vague priors for all parameters in the previously described linear models,

$$\begin{aligned} \boldsymbol{\beta} &\sim \mathrm{Normal}(0, 100), \\ \boldsymbol{\sigma} &\sim \mathrm{Uniform}(0, 3). \end{aligned} \tag{6}$$

We derived age-specific harvest mortality probabilities (κ) as a function of harvest mortality hazard rates, $\kappa_{\mathrm{a,t}} = 1 - e^{-h_{\kappa_{\mathrm{a,t}}}}$. We derived age-specific natural mortality probability (η) as a function of natural mortality hazard rate conditional on surviving harvest, $\eta_{\mathrm{a,t}} = \left(1 - \kappa_{\mathrm{a,t}}\right) \times \left(1 - e^{-h_{\eta_{\mathrm{a,t}}}}\right)$. We then derived annual survival probability as a function of harvest and natural mortality hazard rate,

$$S_{\mathrm{a,t}} = \ e^{-\left(h_{\eta_{\mathrm{a,t}}} + h_{\kappa_{\mathrm{a,t}}}\right)}. \tag{7}$$

Finally, we derived ring-recovery probabilities ($f_{\mathrm{a,t}}$) for the two age classes (*a*) given harvest mortality probability (Zhao et al., 2018). To avoid inducing bias in parameter estimates due to crippling mortality (Péron, 2013) and temporal variation in band reporting rates associated with band type, we developed an informative prior for crippling rate (*c*) (Bellrose, 1953; Nieman et al., 1987) and used time-varying band reporting probabilities for mallards (ρ_{t}) estimated by Arnold et al. (2020),

$$\begin{aligned} f_{\mathrm{a,t}} &= \kappa_{\mathrm{a,t}}(1 - c)\rho_{\mathrm{t}}, \\ c &\sim \mathrm{Beta}(20, 80). \end{aligned} \tag{8}$$

We note that estimates of harvest are thus directly dependent on estimates of reporting rate and crippling rate; higher values of crippling rate or lower values of reporting rate would lead to increased estimates of harvest, and vice versa.

2.3 | Parameterizing the mark–recovery model

We formatted the mark–recovery data in $T \times T+1$ matrices (i.e. m-arrays), where *T* is the number of years of ringing and surveying the population ($T = 43$). Each row (*i*) of the m-array denotes year of release, each column (*j*) denotes year of recovery, and the final column is the number of individuals never recovered. Thus, the main diagonal of each m-array (Williams et al., 2002) is the number of individuals released during a given year and recovered during the ensuing hunting season (i.e. 'direct' recoveries), and the cells above the main diagonal are the number of individuals that survived one or more years and were then recovered (i.e. 'indirect' recoveries). We then defined the probabilities of being recovered in each year as a function of survival probability (*S*) and band-recovery probability (*f*) for juvenile (Ψ) and adult (Ω) female mallards following Brownie (1978). The cell probabilities were therefore,

$$\begin{aligned} \psi_{\mathrm{i,j}} &= \begin{cases} 0, & \mathrm{i} < \mathrm{j} \\ f_{\mathrm{jv,i}}, & \mathrm{i} = \mathrm{j} \\ S_{\mathrm{jv,i}} f_{\mathrm{ad,j}}, & \mathrm{i}+1 = \mathrm{j} \\ S_{\mathrm{jv,i}} \left(\prod_{k=i+1}^{k=j-1} S_{\mathrm{ad,k}} \right) f_{\mathrm{ad,j}}, & \mathrm{i}+1 < \mathrm{j} < \mathrm{T}+1 \\ 1 - \sum_{k=1}^{k=T} \psi_{\mathrm{i,k}}, & \mathrm{j} = \mathrm{T}+1 \end{cases}, \\ \omega_{\mathrm{i,j}} &= \begin{cases} 0, & \mathrm{i} < \mathrm{j} \\ f_{\mathrm{ad,i}}, & \mathrm{i} = \mathrm{j} \\ \prod_{k=i}^{k=j-1} S_{\mathrm{ad,k}} \left(f_{\mathrm{ad,j}}\right), & \mathrm{i} < \mathrm{j} < \mathrm{T}+1 \\ 1 - \sum_{k=1}^{k=T} \omega_{\mathrm{i,k}}, & \mathrm{j} = \mathrm{T}+1 \end{cases}. \end{aligned} \tag{9}$$

We modelled each row in the m-arrays for juvenile (M_{jv}) and adult (M_{ad}) female mallards using multinomial distributions given the respective cell probabilities and the number of juvenile ($r_{\mathrm{jv,t}}$) and adult ($r_{\mathrm{ad,t}}$) females marked and released during each year.

$$\begin{aligned} m_{\mathrm{jv,t,1:(T+1)}} &\sim \mathrm{multinomial}\left(r_{\mathrm{jv,t}},\ \psi_{\mathrm{t,1:T}}\right), \\ m_{\mathrm{ad,t,1:(T+1)}} &\sim \mathrm{multinomial}\left(r_{\mathrm{ad,t}},\ \omega_{\mathrm{t,1:T}}\right). \end{aligned} \tag{10}$$

2.4 | Assessing efficacy of existing harvest management models

To assess the ability of existing mid-continent mallard harvest management models (Runge et al., 2002) to predict survival probabilities, we used the equations described in the 2019 Adaptive Harvest Management report (U.S. Fish and Wildlife Service, 2019) and estimates of age-class-specific (*a*) harvest mortality probability from this study to predict survival rates under existing deterministic additive and compensatory models of harvest effects on survival,

$$S_{a,t,Compensatory} = \begin{cases} 0.5965, & \text{if } \kappa_{\mathrm{a,t}} \le 0.4035, \\ 1 - \kappa_{\mathrm{a,t}}, & \text{if } \kappa_{\mathrm{a,t}} > 0.4035, \end{cases} \tag{11}$$

$$S_{a,t,Additive} = 0.6886 - 0.6886 \times \kappa_{\mathrm{a,t}}.$$

We then calculated the mean signed difference (MSD) between the estimates of temporal variation in age-class-specific survival probabilities in this study and predicted values of survival probabilities from existing harvest management models.

2.5 | Computational details

All analyses were conducted in R (R Core Team, 2020) and JAGS (Plummer, 2003) using the JAGSUI package (Kellner, 2016). We sampled three MCMC chains for 500,000 iterations, where we discarded the first 250,000 iterations and retained every 100th saved iteration. We ensured all posterior distributions had $\hat{R}$ values <1.01 (Brooks & Gelman, 1998), and visually inspected trace plots for convergence (Kéry & Schaub, 2012). In the following text, tables and figures, we report medians of posterior distributions, 95% Bayesian credible intervals and υ, the proportion of the posterior distribution on the same side of zero as the mean.

3 | RESULTS

Over the 43 years of the study, 157,089 juvenile and 247,152 adult female mallards were captured, marked and released, and 34,869 individuals (8.6%) were shot by hunters, retrieved and reported to the USGS Bird Banding Lab.

3.1 | Mallard, pond and hunter abundance and mallard fecundity

We estimated temporal variation (Figure 3) and positive autocorrelation in both breeding pair abundance and the number of ponds (Figure 4). There was a positive effect of the number of ponds on fecundity ($\beta_{\xi,3} = 0.311$; $\upsilon = 1$; Table 1), and evidence for negative density dependence in fecundity ($\beta_{\xi,2} = -0.101$; $\upsilon = 0.926$; Figure 4). We estimated a long-term decline in the number of hunters ($\beta_{H,3} = -0.227$; $\upsilon = 1$). Mallard breeding pair abundance had a positive effect ($\beta_{H,2} = 0.148$; $\upsilon = 1$) on the number of hunters, and restrictive harvest regulations had a negative effect on the number of hunters ($\beta_{H,4} = -0.223$; $\upsilon = 1$).

3.2 | Ecological and anthropogenic impacts on cause-specific mortality rates

Natural and harvest mortality probability varied over time (Figure 5; Table 2). Ecological processes had strong effects on natural mortality rates of both adult and juvenile female mallards. Increased mallard abundance ($\beta_{\eta_{\mathrm{ad}},2} = 0.045;\ \upsilon = 0.848$) and pond abundance ($\beta_{\eta_{\mathrm{ad}},3} = 0.051;\ \upsilon = 0.863$) were both weakly associated with increased natural mortality probability for adult females (Figure 6). Breeding pair abundance was not associated with natural mortality rates of juvenile females ($\beta_{\eta_{\mathrm{jv}},2} = -0.062;\ \upsilon = 0.766$). However, increased pond abundance led to increases in natural mortality hazard rates of juvenile females ($\beta_{\eta_{\mathrm{jv}},3} = 0.153;\ \upsilon = 0.968$; Figure 6).

Similarly, both ecological and anthropogenic processes had direct effects on harvest mortality rates of both adult and juvenile female mallards (Figure 7). Increased breeding pair abundance reduced adult female harvest mortality hazard rate ($\beta_{\kappa_{\mathrm{ad}},2} = -0.090;\ \upsilon = 0.979$) once the number of hunters and harvest regulations were controlled for, but did not strongly affect juvenile harvest mortality hazard rate ($\beta_{\kappa_{\mathrm{jv}},2} = -0.011;\ \upsilon = 0.605$). There was evidence for a positive effect of fecundity on both juvenile ($\beta_{\kappa_{\mathrm{jv}},3} = 0.082;\ \upsilon = 0.996$) and adult harvest rate ($\beta_{\kappa_{\mathrm{ad}},3} = 0.036;\ \upsilon = 0.959$). Restrictive harvest regulations had a strong negative effect on harvest mortality rate of both juveniles ($\beta_{\kappa_{\mathrm{jv}},4} = -0.600;\ \upsilon = 1$) and adults ($\beta_{\kappa_{\mathrm{ad}},4} = -0.210;\ \upsilon = 0.961$). The number of hunters positively affected harvest mortality rate for both juveniles ($\beta_{\kappa_{\mathrm{jv}},5} = 0.101;\ \upsilon = 0.996$) and adults ($\beta_{\kappa_{\mathrm{ad}},5} = 0.324;\ \upsilon = 1$; Figure 7), leading to direct and indirect effects of restrictive regulations on harvest rate (Figure 8).

3.3 | Fit of existing harvest management models

There were substantive differences between current predictive models used in Adaptive Harvest Management of midcontinent mallards (U.S. Fish and Wildlife Service, 2018; Runge et al., 2002) and survival estimates from this study. Additive ($\mathrm{MSD} = -0.060$; 95% BCI −0.081, −0.039) and compensatory ($\mathrm{MSD} = -0.049$; 95% BCI

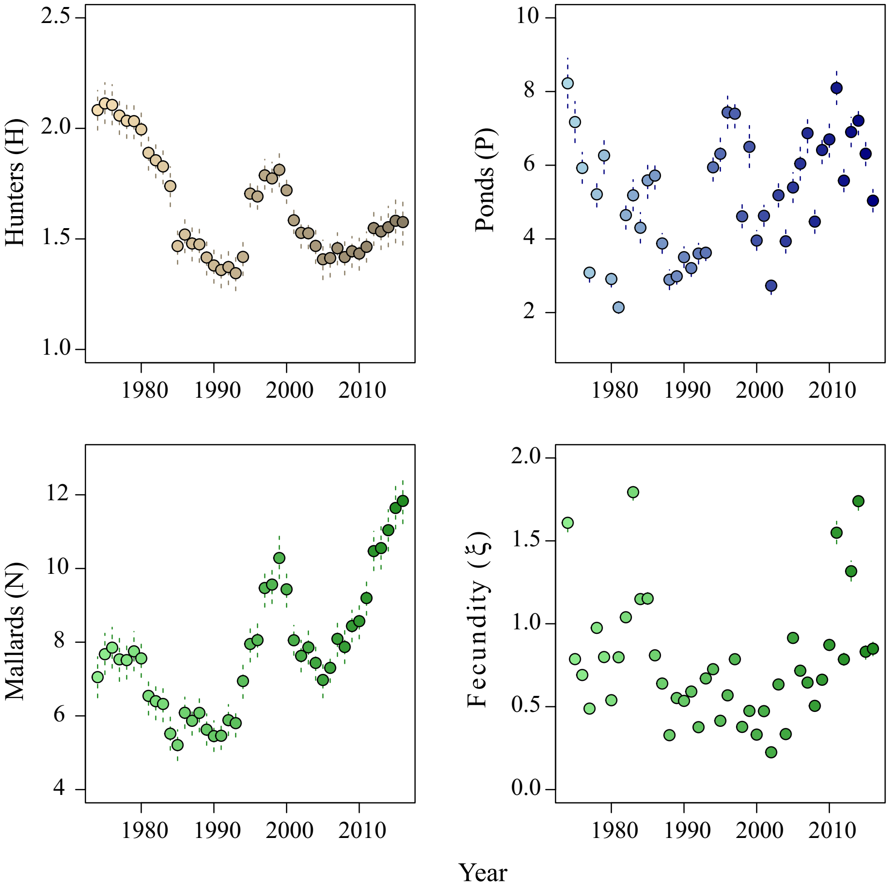


FIGURE 3 Medians (coloured points) and 95% Bayesian credible intervals (dashed lines) of hunter abundance (*H*), pond abundance (*P*), breeding pair abundance (*N*) and fecundity (ξ), for female mallards marked in the Prairie Pothole Region of North America (1974–2016). The gradients of colours corresponds to time, where darker points represent later years in the study.

−0.068, −0.031) models underpredicted survival probability of juvenile females. The additive model overpredicted (MSD = 0.040; 95% BCI 0.032, 0.047) survival probability of adult females, while the compensatory model was unbiased (MSD = − 0.001; 95% BCI −0.007, 0.003), albeit with substantial variance (Figure 9). We estimated more temporal variation in survival probabilities than predicted by either of the AHM models of survival, and harvest appeared to predict survival less effectively as the ratio of natural to harvest mortality risk increases (Figure 9).

4 | DISCUSSION

The literature on ecological and evolutionary drivers of demographic parameters is vast (Gaillard et al., 1989; Stearns, 1992), yet studies examining harvest impacts on survival typically restrict inference to a single covariate, harvest (Péron, 2013). In this study, we simultaneously modelled ecological and anthropogenic drivers of cause-specific mortality rates. Our study revealed strong direct and indirect effects of ecological processes on cause-specific mortality rates of female mallards marked in the North American midcontinent (Figures 6–8). For example, mallard breeding pair abundance indirectly affected harvest mortality hazard rates through hunter abundance, and directly affected both adult harvest and natural mortality hazard rates. Furthermore, we demonstrate that existing compensatory and additive models used in Adaptive Harvest Management (Runge et al., 2002) do not accurately predict survival of adult or juvenile female mallards in the North American midcontinent, and the underlying causes of these discrepancies may differ among age classes (Figure 9). Thus, we suggest that the effects of harvest may be intermediate between full compensation and full additivity, and that the interplay among ecological and evolutionary processes and anthropogenic actions confounds our current understanding of this process in this and other systems.

4.1 | On the importance of modelling variation in natural mortality

Life-history trade-offs and age-specific variation in demographic rates are fundamental components of ecology and evolution (Stearns, 1992). Numerous studies have demonstrated that female mallards greater than 1 year of age may experience increased breeding season mortality relative to first-time breeders at 1 year of age (Dufour & Clark, 2002; Reynolds et al., 1995), presumably as a function of increased reproductive allocation by older individuals (Dufour & Clark, 2002; Johns, 2019), and associated increases in mortality during nesting attempts (Arnold et al., 2012; Sargeant et al., 1984). This leads to differences in natural mortality rates between the age classes. Critically, our results provide strong evidence for differences in survival among age classes; juvenile survival was greater than adult survival during 35 of the

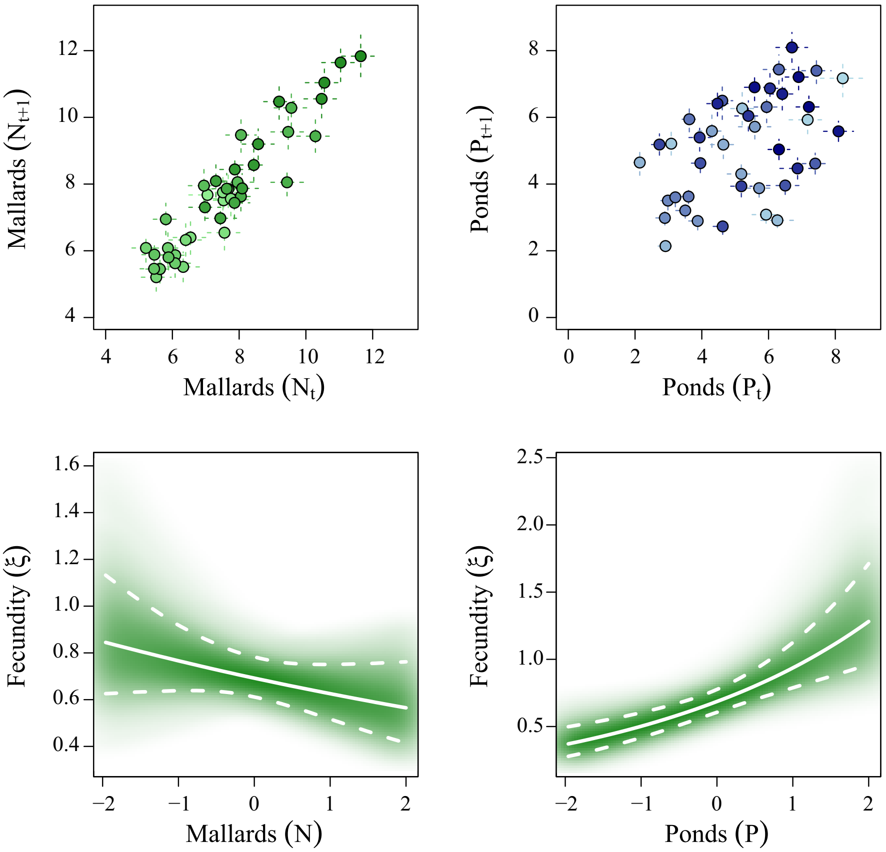


FIGURE 4 Scatterplots of medians mallard breeding pair abundance (*N*) and the number of ponds (*P*) during each season regressed against estimates from the previous breeding season, where darker shaded points represent later years of the study (top), and medians (solid white line), 95% Bayesian credible intervals (dashed white lines), and posterior distribution density (shaded green) of relationships among fecundity (ξ) and breeding pair (*N*) and pond (*P*) abundance for female mallards marked in the Prairie Pothole Region of North America (1974–2016; bottom)

TABLE 1 Medians, 95% Bayesian credible intervals (2.5% CrI and 97.5% CrI), and the proportion of the posterior distribution on the same side of zero as the median (υ) for regression parameters in models estimating annual variation in fecundity (ξ), hunter abundance (*H*), harvest mortality (h_κ), natural mortality (h_η) hazard rates and the effects of mallard abundance (*N*), ponds (*P*), long-term trends (*T*) and harvest limits (*L*) on these parameters for female mallards marked in the North American midcontinent (1974–2016)

β	Response	Predictor	Median	2.5%	97.5%	υ
$\beta_{\xi,1}$	ξ_t	Intercept	−0.370	−0.495	−0.247	—
$\beta_{\xi,2}$	ξ_t	N_t	−0.101	−0.237	0.035	0.926
$\beta_{\xi,3}$	ξ_t	P_t	0.311	0.179	0.441	1.000
$\beta_{H,1}$	H_t	Intercept	1.689	1.646	1.732	—
$\beta_{H,2}$	H_t	N_t	0.148	0.086	0.208	1
$\beta_{H,3}$	H_t	T	−0.227	−0.268	−0.185	1
$\beta_{H,4}$	H_t	L_t	−0.223	−0.333	−0.114	1
$\beta_{\kappa_{ad},1}$	$h_{\kappa_{ad},t}$	Intercept	−2.596	−2.701	−2.475	—
$\beta_{\kappa_{ad},2}$	$h_{\kappa_{ad},t}$	N_t	−0.090	−0.171	−0.004	0.979
$\beta_{\kappa_{ad},3}$	$h_{\kappa_{ad},t}$	ξ_t	0.036	−0.005	0.078	0.959
$\beta_{\kappa_{ad},4}$	$h_{\kappa_{ad},t}$	L_t	−0.210	−0.411	0.026	0.961
$\beta_{\kappa_{ad},5}$	$h_{\kappa_{ad},t}$	H_t	0.324	0.269	0.387	1
$\beta_{\kappa_{jv},1}$	$h_{\kappa_{jv},t}$	Intercept	−1.739	−1.855	−1.606	—
$\beta_{\kappa_{jv},2}$	$h_{\kappa_{jv},t}$	N_t	−0.011	−0.091	0.071	0.605
$\beta_{\kappa_{jv},3}$	$h_{\kappa_{jv},t}$	ξ_t	0.082	0.022	0.143	0.996
$\beta_{\kappa_{jv},4}$	$h_{\kappa_{jv},t}$	L_t	−0.600	−0.815	−0.373	1
$\beta_{\kappa_{jv},5}$	$h_{\kappa_{jv},t}$	H_t	0.101	0.028	0.178	0.996
$\beta_{\eta_{ad},1}$	$h_{\eta_{ad},t}$	Intercept	−0.838	−0.911	−0.771	—
$\beta_{\eta_{ad},2}$	$h_{\eta_{ad},t}$	N_{t+1}	0.044	−0.043	0.135	0.848
$\beta_{\eta_{ad},3}$	$h_{\eta_{ad},t}$	P_{t+1}	0.051	−0.042	0.148	0.863
$\beta_{\eta_{jv},1}$	$h_{\eta_{jv},t}$	Intercept	−1.308	−1.473	−1.169	—
$\beta_{\eta_{jv},2}$	$h_{\eta_{jv},t}$	N_{t+1}	−0.062	−0.238	0.106	0.766
$\beta_{\eta_{jv},3}$	$h_{\eta_{jv},t}$	P_{t+1}	0.153	−0.010	0.318	0.968

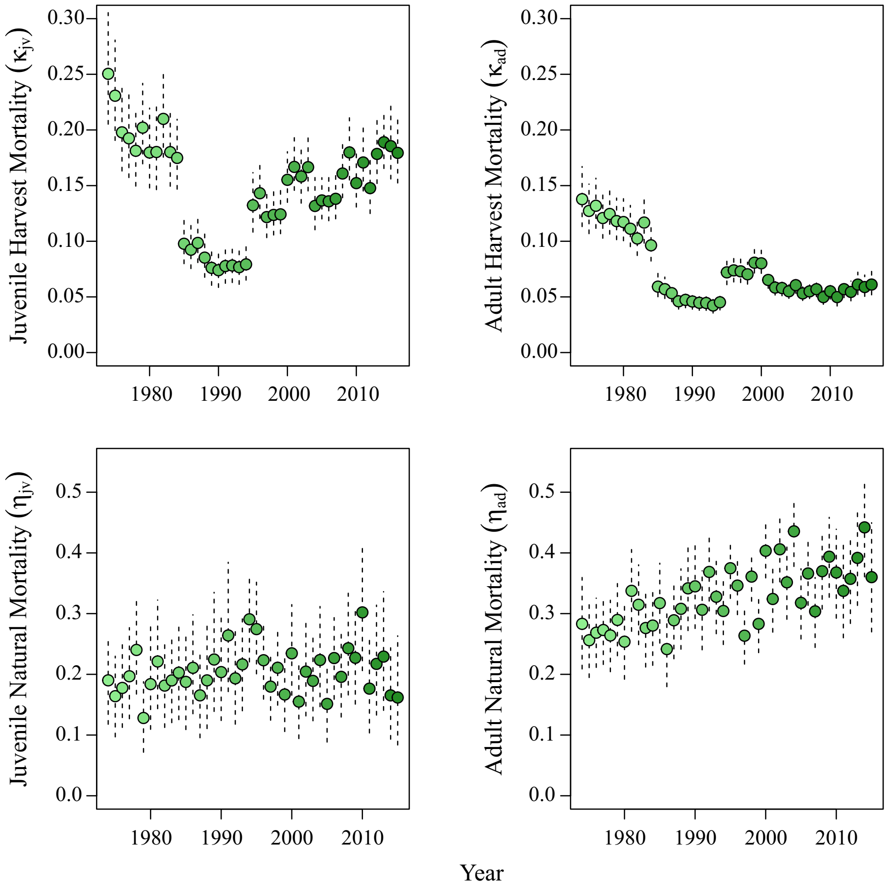


FIGURE 5 Medians (points) and 95% Bayesian credible intervals (dashed lines) of harvest mortality (κ; top) and natural mortality (η; bottom) probabilities for juvenile (jv; left) and adult (ad; bottom) female mallards marked in the Prairie Pothole Region of North America (1974–2016). The gradients of colours corresponds to time, where darker points represent later years in the study.

TABLE 2 Medians and 95% Bayesian credible intervals (2.5% CrI and 97.5% CrI) of variance parameters (σ) for mallard abundance (N), pond abundance (P), fecundity (ξ), hunter abundance (H) and harvest (h_κ) and natural (h_η) mortality hazard rates of adult (ad) and juvenile (jv) female mallards marked in the North American midcontinent (1974–2016)

σ	Parameter	Median	2.5%	97.5%	Link function
σ_N	Mallards	0.696	0.540	0.915	Identity
σ_P	Ponds	1.643	1.317	2.129	Identity
σ_ξ	Fecundity	0.401	0.325	0.511	Log
σ_H	Hunters	0.113	0.090	0.145	Identity
$\sigma_{\kappa_{ad}}$	Adult harvest mortality hazard rate	0.087	0.050	0.131	Log-Hazard
$\sigma_{\kappa_{jv}}$	Juvenile harvest mortality hazard rate	0.163	0.121	0.221	Log-Hazard
$\sigma_{\eta_{ad}}$	Adult natural mortality hazard rate	0.203	0.146	0.284	Log-Hazard
$\sigma_{\eta_{jv}}$	Juvenile natural mortality hazard rate	0.258	0.109	0.432	Log-Hazard

42 survival intervals (83.3%, Figure 9), despite juveniles experiencing more than double the average harvest mortality of adults (Table 1), and higher harvest mortality during every year of the study (Figure 5). We also demonstrate that natural mortality rates of adult females may be affected by ecological processes; increased abundance and breeding habitat conditions during breeding seasons led to increased natural mortality of adult females, while only breeding habitat condition impacted natural mortality rates of juvenile females (Table 1). Furthermore, substantial unexplained variation remained in natural mortality rates of juveniles and adults after accounting for covariate effects (Table 2). One might consider the variation in natural mortality described in this paper as variation in the intercept of existing predictive survival models, which are currently fixed as constant values (e.g. Runge et al., 2002). Thus, variation in reproductive allocation and associated effects on natural mortality of juvenile and adult mallards (Dufour & Clark, 2002, Johns, 2019) may reduce the efficacy of existing predictive models for harvest management (Figure 9). Importantly, in this manuscript we do not partition mortality seasonally (e.g. Arnold et al., 2016; Devers et al., 2021). While harvest mortality is obviously constrained to occur within the hunting season, natural mortality can occur throughout the survival interval. Although the majority of mortality occurs during the breeding season for adult female mallards (Hoekman et al., 2002; Reynolds et al., 1995), density dependence and other ecological effects may affect mortality differentially over the annual cycle. Future research might seasonally partition the mortality process to more effectively

FIGURE 6 Medians (points), 95% Bayesian credible intervals (dashed lines) and posterior distribution density (shaded green) of relationships among natural (h^{η}) mortality hazard rates and pond abundance (*P*; left) and mallard breeding pair abundance (*N*; right) for juvenile (jv; top) and adult (ad; bottom) female mallards marked in the Prairie Pothole Region of North America (1974–2016).

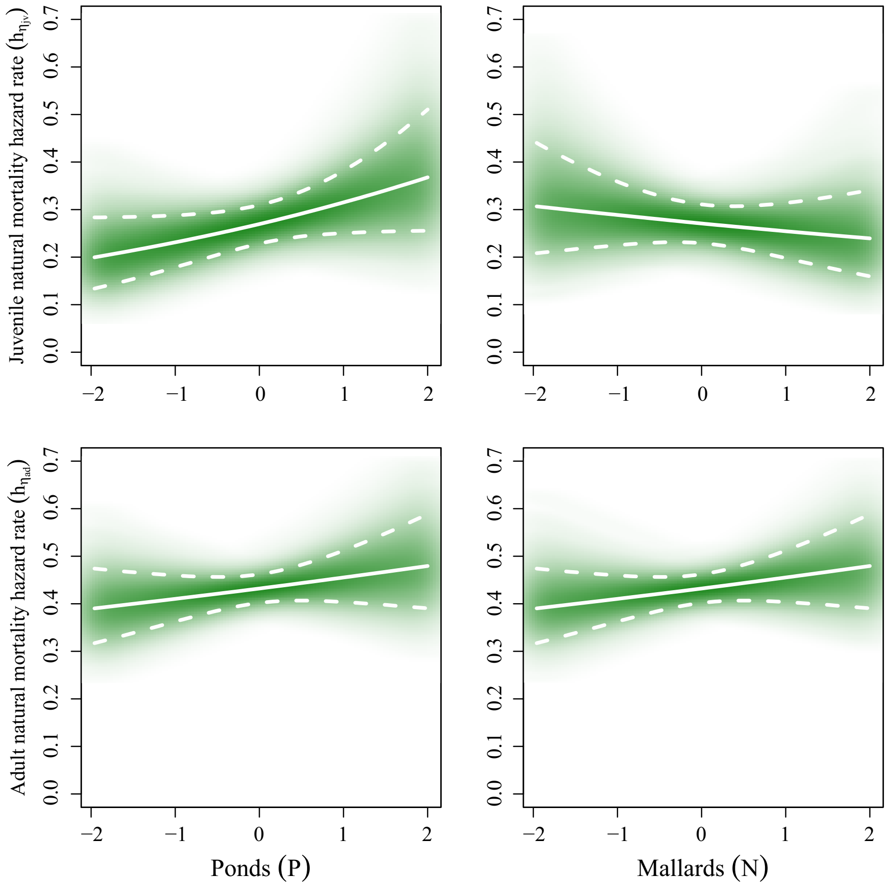
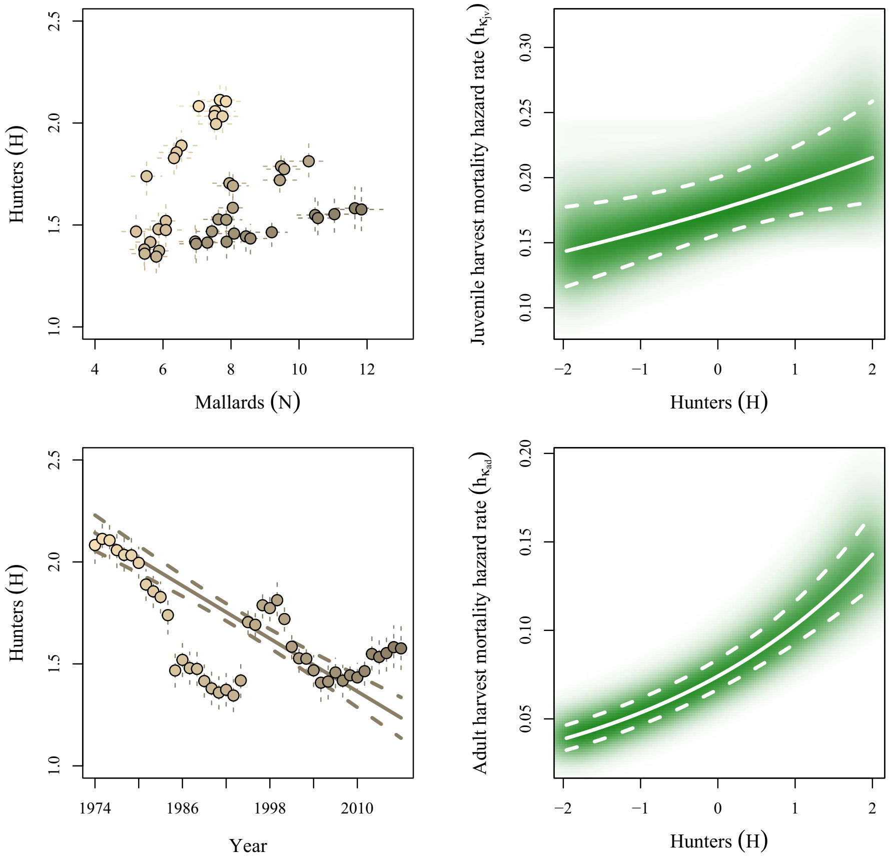


FIGURE 7 Scatterplots of the number of hunters (*H*) as a function of mallard breeding pair abundance (*N*), a long-term trend and the effects of hunter and breeding pair abundance on harvest mortality hazard rates (h^{κ}) for juvenile and adult female mallards marked in the Prairie Pothole Region of North America (1974–2016).



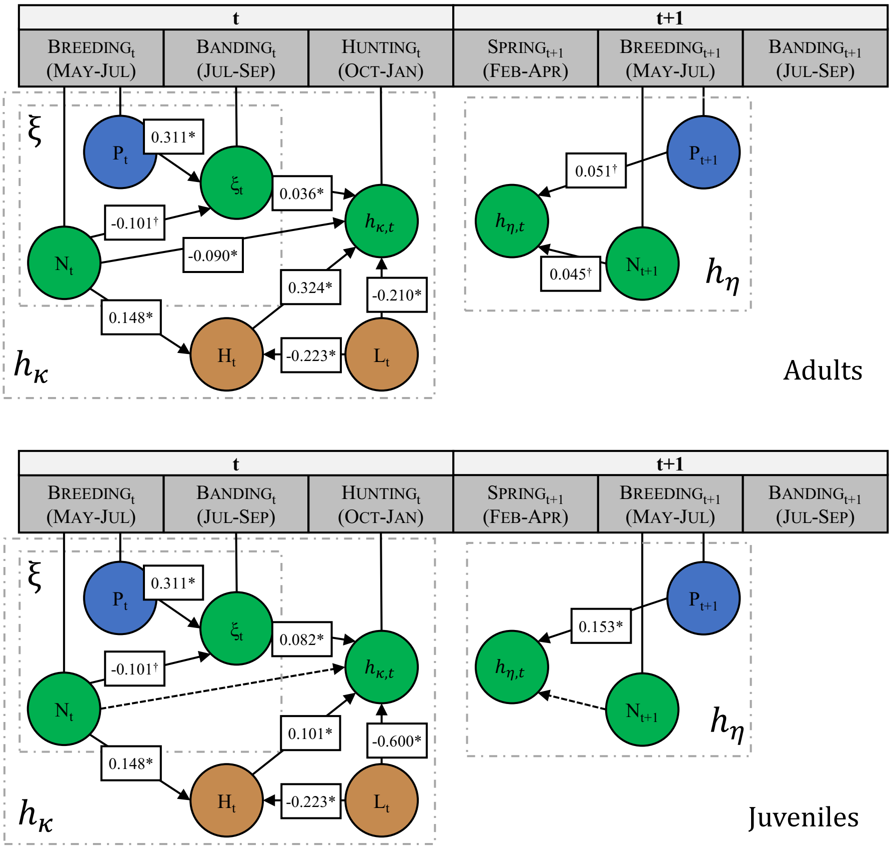


FIGURE 8 Directed acyclic graphs and parameter estimates from a Bayesian hierarchical model estimating relationships among mallard breeding pair abundance (N), the number of ponds (P), harvest limits (L), the number of hunters (H), fecundity (ξ), harvest mortality hazard rate (h_κ), natural mortality hazard rate (h_η) and survival (S) for adult (top) and juvenile (bottom) female mallards marked and released in the Prairie Pothole Region of the United States and Canada, 1974–2016. Arrows represent covariate effects, where dashed arrows represent covariate effects with little support. Parameter estimates denoted with * indicate when >0.95 of the posterior distribution is on the same side of zero as the median, and parameter estimates denoted with † indicate when >0.8 of the posterior distribution is on the same side of zero as the median.

understand these relationships in mallards and other harvested species, and further explore relationships between reproductive effort, success and mortality (e.g. Arnold et al., 2012; Arnold & Howerter, 2012). Furthermore, future research may examine variation in cause-specific mortality rates in juvenile and adult males, where we expect that the effects of harvest may be more apparent in males as they experience reduced natural mortality risk relative to females.

4.2 | Direct and indirect effects on harvest mortality

Beyond harvest regulations, we also noted substantial effects of ecological and anthropogenic processes on harvest mortality probabilities of both age classes. Breeding pair abundance had an indirect effect on harvest mortality by increasing the number of hunters, as mallard abundance increased hunter abundance, and hunter abundance had a strong positive effect on harvest mortality of both adults and juveniles (Figure 7). After controlling for the number of hunters and harvest regulations, greater population size had a negative effect on the per capita risk of harvest for adult females (Figure 8). Furthermore, long-term declines in the number of hunters may impact inference regarding the effects of harvest regulations as currently implemented in mallard adaptive management models (Runge et al., 2002), because declining hunter numbers are analogous to slowly enacting more restrictive regulations.

As the risk of natural mortality relative to harvest mortality increased over time, adult survival was consistently overpredicted by AHM additive models of survival (Figure 9). As expected, restrictive regulations both reduced the number of hunters and the harvest probability of mallards (Figure 7). However, collinearity between regulations and mallard abundance may affect our understanding of this relationship, as we did not explicitly model the effects of mallard abundance on harvest regulations. In other words, if harvest is always high when abundance is high, and low when abundance is low, it will remain difficult to separate the effects of abundance from the effects of harvest (Sedinger & Herzog, 2012; Sedinger & Rexstad, 1994). Finally, we observed substantial age-related variation in harvest mortality probability; juvenile females were more than twice as likely to be harvested than adults and this difference was increasing over time (Figure 5), despite ultimately experiencing higher survival rates due to lower rates of natural mortality.

4.3 | Mechanisms for partial harvest compensation

Smith and Reynolds (1992) noted that relationships among harvest and natural mortality may be more complex than completely

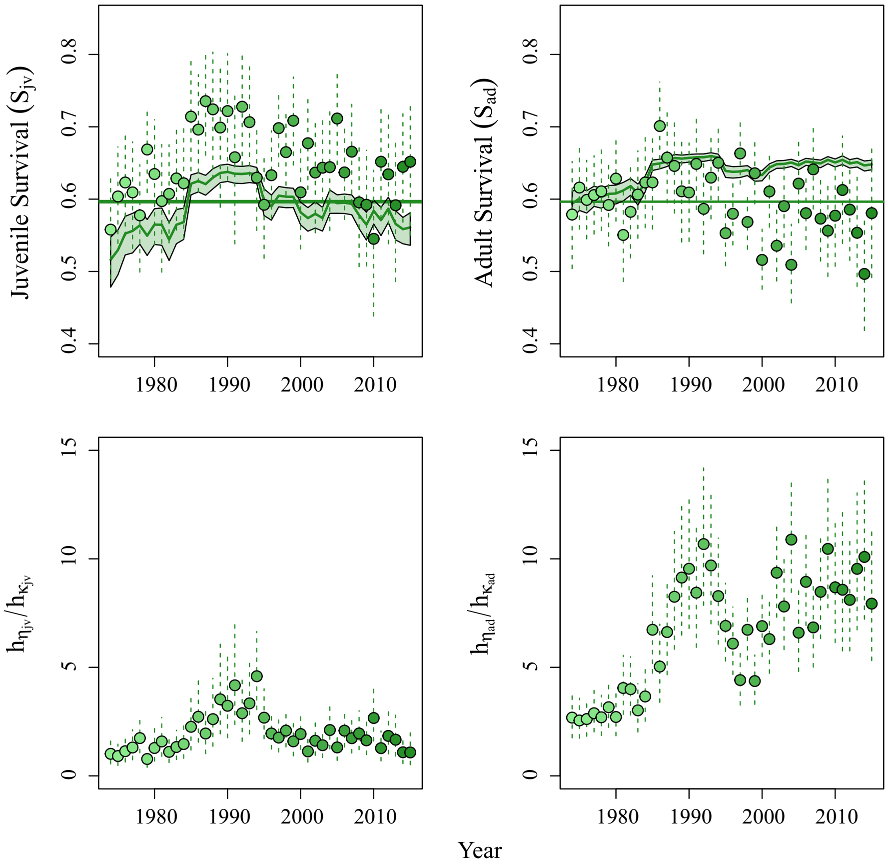


FIGURE 9 Medians (points) and 95% Bayesian credible intervals (dashed lines) for juvenile (left) and adult (right) female survival (top) and the ratio of natural (h_{η}) to harvest (h_{κ}) mortality hazard rate (bottom) for mallards marked in the Prairie Pothole Region of North America (1974–2015). In the upper survival plots, the horizontal line with an intercept of 0.5965 depicts predictions from compensatory models of harvest mortality, and the solid line and associated shaded 95% Bayesian credible intervals represent predictions from additive models used to predict hatch year and after hatch year female mallard survival rates in mid-continent mallard Adaptive Harvest Management (U.S. Fish and Wildlife Service, 2018).

additive or completely compensatory models of harvest mortality in mallards. Furthermore, Conn and Kendall (2004) demonstrated that if the functional form of the relationship between harvest and survival was not included in the model set, model selection errors might favour additive models of harvest effects. Our results provide evidence for partial compensation through multiple mechanisms. First, increased breeding pair abundance led to increased natural mortality rates in adult females, consistent with a density-dependent mechanism for partial compensation of hunting mortality (Table 1; Figure 6). Second, we observed density dependence in fecundity, where harvest may increase the reproductive potential of surviving individuals, leading to compensatory harvest natality. Perhaps most importantly, our results indicate that the drivers of harvest and natural mortality are often collinear (e.g. abundance), where harvest increases when abundance and fecundity increases, and increases in abundance and fecundity also lead to increases in natural mortality. These collinear processes will affect inference in traditional (e.g. Anderson & Burnham, 1976; Runge et al., 2002) models of harvest effects on survival, as the effects of harvest will appear more severe due to these multicollinear processes. These complex relationships have important implications for future efforts to model the impacts of changes in harvest regulations on harvest, and the impacts of changes in harvest on survival probability. Specifically, if the effects of harvest are overestimated under existing models, managers might: (a) prescribe overly restrictive harvest regulations, and (b) overestimate the ability of restrictive harvest regulations to mitigate population declines.

4.4 | Hierarchical models for assessing harvest impacts

A large number of animal studies have set out to test the additive and compensatory mortality hypotheses with the aim of guiding management or better understanding population ecology. Here we show that controlling for multiple drivers of mortality is key to understanding the effects of harvest on population trajectories, and demonstrate the use of general methods (Cubaynes et al., 2012; Gimenez et al., 2012; van de Pol & Brouwer, 2021) that can be applied to a wide variety of taxa and systems. While our approach to simultaneously assessing ecological and anthropogenic effects on demographic rates is highly useful, it requires: (a) long-term capture–recapture or capture–recovery and survey data that allow for reliably estimating demographic rates, habitat conditions and population abundance, and (b) a working knowledge of the key ecological drivers of cause-specific mortality rates. Furthermore, there is substantial statistical literature addressing limitations on inference drawn from the approaches described herein. For instance, the relationships we estimate in our analyses can be interpreted as estimates from a causal hypothesis, not as proof of causation (Cubaynes et al., 2012; Gimenez et al., 2012; Pearl, 2000; Shipley, 2009). Despite these constraints, we believe similar models might be constructed to great effect in other systems where researchers model the effects of harvest on demographic rates, or in other 'allowable take' frameworks (Runge et al., 2009). Researchers may simply model demographic rates of interest as well as relationships among drivers of demographic rates (see Gimenez et al., 2012). We particularly highlight the importance of modelling density-dependent effects separately from harvest effects, as *a large number of terrestrial and aquatic harvest management programs link harvest regulations to population abundance, coupling density-dependent and harvest effects on demographic rates*. Finally, we note the importance and continued relevance of harvest experiments (see Sandercock et al., 2011 for an excellent example), where long-term carefully designed experiments across a range of taxa have the potential to address many of the concerns with existing systems we raise in this paper.

Science- and evidence-based decision making is at the root of successful conservation policy and management (Nichols et al., 2019), and the integration of science and policy is critical for the continued success and improvement of harvest management models (Nichols et al., 2015). Adaptive models for mallard harvest management have often been promoted as a highly successful example of the integration of science and policy (e.g. Nichols et al., 2019, 2021). In this study, we present evidence that existing models can be substantially improved, and demonstrate a potential alternative method that could be extended to directly assess the impacts of harvest on demographic processes in an integrated population modelling framework (Schaub & Kéry, 2022). We note that the auto-regressive nature of the models we describe also allows for predictive inference in the face of uncertainty. While we acknowledge that model developers face constraints and trade-offs between the complexity of models and their utility and implementation, we have demonstrated that model types similar to the one developed herein have the potential to improve inference, and that this type of model can be applied to a broad range of taxa given sufficient data. Given our results, we suggest a new paradigm for models of harvest impacts on demographic rates of animal populations. Novel models and harvest management frameworks should simultaneously consider ecological and anthropogenic drivers of demographic rates.

AUTHORS' CONTRIBUTIONS

T.V.R. led the writing of the manuscript; T.V.R., B.S.S. and J.S.S. designed the analysis with thoughtful contributions from D.N.K. and T.W.A.; D.G., M.S., M.G.L. and P.J.W. were critical to parameterizing the model described in the text, and parameter interpretation. All authors contributed critically to manuscript revisions and editing.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Mallard band-recovery data (https://doi.org/10.5066/P9R1L6Q7; Celis-Murillo et al., 2020) are publicly available. Data on pond and breeding pair abundance and duck stamp sales are published in U. S. Fish and Wildlife Service and U. S. Geological Survey annual reports (U.S. Fish and Wildlife Service, 2021). R script for analysing the data in JAGS and producing figures as well as the input file used for this analysis are available from Dryad Digitial Repository (https://doi.org/10.5061/dryad.k98sf7m80; Riecke et al., 2022).

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