Received: 2 November 2021 | Accepted: 10 August 2022

DOI: 10.1111/1365-2656.13807

Journal of Animal Ecology | BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Density-dependence produces spurious relationships among demographic parameters in a harvested species

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Funding information
Delta Waterfowl; Colorado State University; National Science Foundation, Grant/Award Number: DEB 1252656; California Department of Water Resources; Institute for Wetland and Waterfowl Research, Ducks Unlimited Canada

Handling Editor: Fernando Colchero

[Correction added on 03-December-2022, after first online publication: funding statement has been added.]

Abstract

1. Harvest of wild organisms is an important component of human culture, economy, and recreation, but can also put species at risk of extinction. Decisions that guide successful management actions therefore rely on the ability of researchers to link changes in demographic processes to the anthropogenic actions or environmental changes that underlie variation in demographic parameters.
2. Ecologists often use population models or maximum sustained yield curves to estimate the impacts of harvest on wildlife and fish populations. Applications of these models usually focus exclusively on the impact of harvest and often fail to consider adequately other potential, often collinear, mechanistic drivers of the observed relationships between harvest and demographic rates. In this study, we used an integrated population model and long-term data (1973–2016) to examine the relationships among hunting and natural mortality, the number of hunters, habitat conditions, and population size of blue-winged teal *Spatula discors*, an abundant North American dabbling duck with a relatively fast-paced life history strategy.
3. Over the last two and a half decades of the study, teal abundance tripled, hunting mortality probability increased slightly (< 0.02), and natural mortality probability increased substantially (> 0.1) at greater population densities. We demonstrate strong density-dependent effects on natural mortality and fecundity as population density increased, indicative of compensatory harvest mortality and compensatory natality. Critically, an analysis that only assessed the relationship between survival and hunting mortality would spuriously indicate depensatory mortality due to multicollinearity between abundance, natural mortality and hunting mortality.

4. Our findings demonstrate that models that only consider the direct effect of hunting on survival or natural mortality can fail to accurately assess the mechanistic impact of hunting on population dynamics due to multicollinearity among demographic drivers. This multicollinearity limits inference and may have strong impacts on applied management actions globally.

KEYWORDS
blue-winged teal, density-dependence, harvest compensation, integrated population model, multicollinearity, population dynamics, *Spatula discors*, survival

1 | INTRODUCTION

The relationship between anthropogenic harvest and population growth rates of wild organisms is of major interest to population managers and resource consumers (Nichols et al., 1995; Péron, 2013; Sedinger & Herzog, 2012; Servanty et al., 2011) and has received considerable attention and debate (Anderson & Burnham, 1976; Burnham et al., 1984; Lebreton, 2005; Nichols et al., 1995; Péron, 2013; Riecke, Sedinger, et al., 2022). Overexploitation can catastrophically impact wildlife populations (e.g. *Bison bison* Freese et al., 2007; *Ectopistes migratorius* Halliday, 1980). However, the effects of harvest, especially when managed, may be mitigated through two primary mechanisms (Boyce et al., 1999). First, compensatory natality occurs when reductions in density due to exploitations lead to increases in reproductive rates because of density-dependent recruitment (Gunnarsson et al., 2013; Viljugrein et al., 2005) or shifts in life-history tactics, such as earlier reproductive maturity (Servanty et al., 2011). Second, compensatory mortality occurs when hunting removes individuals with lower inherent survival probabilities, diminishes density-dependent feedbacks on survival by reducing population size, or both of these processes occur simultaneously (Boyce et al., 1999; Lebreton, 2005). While compensatory natality is well understood for many North American waterfowl populations (Gunnarsson et al., 2013; Specht & Arnold, 2018), harvest compensation remains a topic of major debate (Arnold et al., 2016; Arnold et al., 2017; Bartzen & Dufour, 2017; Lindberg et al., 2017). Further, the potential for unmodelled density-dependent effects on survival creates uncertainty surrounding the direct effect of hunting on survival (Riecke, Sedinger, et al., 2022; Sedinger & Herzog, 2012; Sedinger & Rexstad, 1994). This occurs because regulations typically allow for greater hunting opportunity when populations are high, but increased abundance might also favour greater natural mortality and lower fecundity. Thus, if investigators only examine relationships between hunting mortality and survival (Anderson & Burnham, 1976), or hunting mortality and population growth rate, the impacts of hunting may be overestimated.

Density-dependent effects on the vital rates of wild organisms have been extensively researched for a variety of taxa (Bonenfant et al., 2009; Fowler, 1981), including waterfowl (Gunnarsson et al., 2013; Viljugrein et al., 2005). However, density-dependent adult survival in North American waterfowl populations remains poorly understood (Sedinger & Herzog, 2012; Sedinger & Rexstad, 1994; Zhao et al., 2018). For instance, a review of 54 peer-reviewed studies that examined the effects of density-dependence on waterfowl vital rates found no examples of density-dependent mortality of adult waterfowl (Gunnarsson et al., 2013), although recent research has found evidence of density-dependent declines in adult survival (Riecke, Sedinger, et al., 2022). Life-history trade-offs are also an important driver of demographic rates (Stearns, 1992), where increased reproductive allocation at the population level may reduce survival of female waterfowl (Devries et al., 2003; Dufour & Clark, 2002). In an attempt to decouple hunting from other processes to better understand the survival response to hunting, the U.S. Fish and Wildlife Service enacted stabilized (i.e. fixed) hunting regulations in the early 1980s (Sparrowe & Patterson, 1987). However, managers quickly restricted hunting regulations during a major drought in the 1980s (Smith & Reynolds, 1992), a period of low duck fecundity and abundance, in an attempt to allow hunted waterfowl populations to recover more rapidly. This action and subsequent harvest management plans effectively coupled harvest of waterfowl populations with their abundance in North America, increasing harvest when abundance is high, and vice versa (Runge et al., 2002). This confounding of hunting mortality with population size, which also affects natural mortality and fecundity, makes it impossible to assess the impacts of hunting on waterfowl populations without also considering alternative pathways for density-dependent population regulation (Sedinger & Herzog, 2012).

To decouple effects of abundance from hunting, researchers require study organisms with major variation in abundance and minimal variation in hunting mortality. Blue-winged teal (*Spatula discors*; hereafter, teal) are currently the second most abundant duck species in North America (U.S. Fish & Wildlife Service, 2018), and greater than 700,000 teal have been harvested annually since 1995 (mean = 1,051,204; Raftovich et al., 2017). The harvest potential of North American teal populations is of great interest to North American waterfowl biologists and hunters (Devink et al., 2013), and the Teal Harvest Potential Working Group, formed in 2009, prepared a report summarizing the potential for adaptive management of teal harvest (Devink et al., 2013). Teal migration begins early in autumn (Rohwer et al., 2002) prior to most other sympatric species of waterfowl, which has led to the creation of early teal hunting seasons (Schroeder, 1978). Teal primarily winter south of the continental

United States, confining most North American hunting opportunities to the relatively brief co-occurrence of teal migration and special teal hunting seasons (Rohwer et al., 2002). Thus, teal hunting is relatively unique among dabbling duck species.

Critically, teal hunting mortality probability had been low and stable compared to other abundant dabbling duck species (Devink et al., 2013). For example, adult female North American hunting mortality probability was < 0.06 from 1974–2015, and hunting mortality probability was < 0.03 in 32 of 42 years (this paper, Devink et al., 2013). Increases in hunting mortality of 0.01 to 0.02 should not have large (>0.1) effects on survival, even if the effects of hunting were additive or depensatory, which would be rare in species such as teal that have rapid life histories (Koons et al., 2014; Péron, 2013). Additionally, estimates of teal abundance in the North American mid-continent have almost tripled since the early 1990s (U.S. Fish & Wildlife Service, 2018). Thus, teal populations exhibit consistently low hunting mortality, and major variation in per capita recruitment and abundance, consistent with the goals of the stabilized hunting regulations experiment implemented in the early 1980s for mallards *Anas platyrhynchos* (Sparrowe & Patterson, 1987). These characteristics make teal an ideal candidate species to consider the potential for co-occuring density-dependent and hunting effects on mortality in a hunted species. In this manuscript, we use an integrated population model (Schaub & Kéry, 2022) to simultaneously examine relationships among hunting and natural mortality hazard rates (Ergon et al., 2018; Nater et al., 2020) and abundance.

2 | MATERIALS AND METHODS

2.1 | Data collection

Adult female blue-winged teal (n = 112,639) were captured in traps and nets prior to the hunting season (July–September) in the prairie potholes and aspen parklands of the North American midcontinent from 1973 to 2016 (Figure 1). Teal were ringed with uniquely engraved metal markers, and some marked individuals were killed by hunters. A portion of these markers were retrieved and reported to the USGS Bird Banding Lab (n = 2518; USGS Patuxent Wildlife Research Center). From 1974–2016, waterfowl breeding population and habitat surveys were flown at the beginning of the breeding season over the same area by the U.S. Fish and Wildlife Service and the Canadian Wildlife Service to estimate the total number of breeding pairs of teal ($y_{n,t}$) and other ducks, and the number of ponds ($y_{p,t}$), a landscape

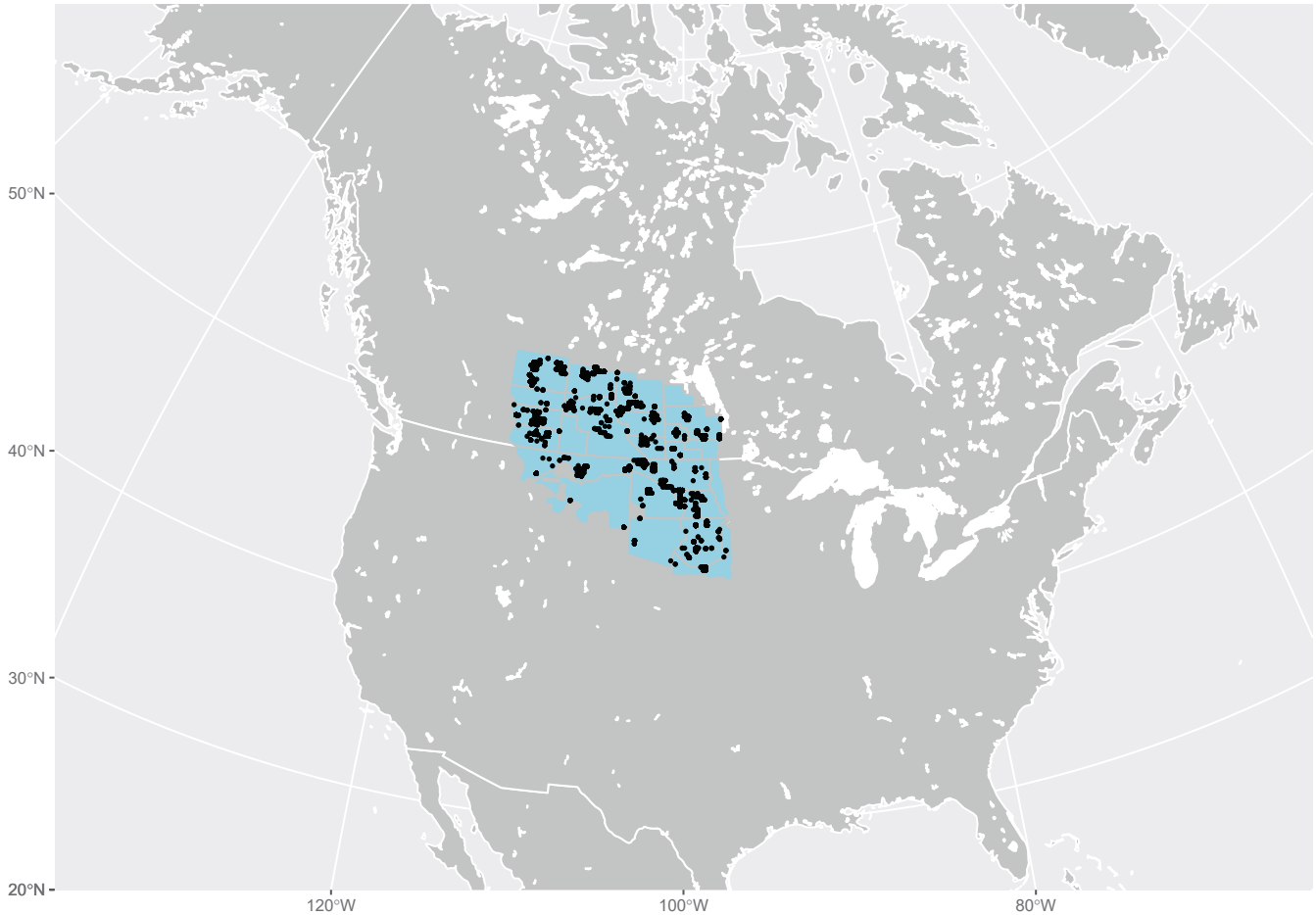

FIGURE 1 Locations (black points) where adult female blue-winged teal were captured, marked and released in Waterfowl Breeding Population and Habitat Survey (U.S. Fish & Wildlife Service, 2018) strata 20–49 (light blue; 1973–2016).

scale measure of habitat suitability for breeding waterfowl (U.S. Fish & Wildlife Service, 2018; Walker et al., 2013). We downloaded the ringing and recovery data from the GameBirds Database CD (Bird Banding Lab, USGS Patuxent Wildlife Research Center), and the Waterfowl Breeding Population and Habitat Survey data from the USFWS Migratory Birds Data Center. We retained females marked in Canada and the United States in Waterfowl Breeding Population and Habitat Survey strata 20–49 (U.S. Fish & Wildlife Service, 2018), and we restricted re-encounters to harvested individuals recovered and reported by hunters in the United States and Canada from September through early February, with half of all reported hunting mortality occurring in September. We excluded recoveries in Mexico, Central and South America, and the Carribean ($n = 316$) due to the inclusion of band reporting probabilities ($\boldsymbol{r} = r_{1973}, \ldots, r_{2016}$) in our analyses, which were not available for Latin America. Mark-recovery data were downloaded from the USGS Bird Banding Lab Celis-Murillo et al., 2020. We accessed estimates of teal abundance and pond abundance from the Waterfowl Breeding Population and Habitat Survey (U.S. Fish & Wildlife Service, 2018), 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 respective institutions. We formatted the capture-recovery data into a multinomial array to reduce computational requirements. Our notation follows Hobbs and Hooten (2015) in subsequent paragraphs, where lowercase symbols represent scalars, bold lowercase symbols represent vectors and uppercase bold symbols represent matrices or arrays.

2.2 | Data analysis

We modelled annual breeding pair abundance, $\boldsymbol{n} \equiv (n_{1974}, \ldots, n_{2016})'$, in thousands using point estimates from the Waterfowl Breeding Population and Habitat Survey ($y_{n,t}$; U.S. Fish & Wildlife Service, 2018), where $y_{n,t} \sim \text{Normal}\left(n_t, \varsigma^2_{n,t}\right)$. We used estimates of standard errors from the same surveys ($s_{n,t}$) to approximate the teal count variance, $\varsigma^2_{n,t} = s^2_{n,t}$. We modelled annual pond abundance, $\boldsymbol{p} \equiv (p_{1974}, \ldots, p_{2016})'$, in thousands in the same way, where $y_{p,t} \sim \text{Normal}\left(p_t, \varsigma^2_{p,t}\right)$ and the standard error of the pond abundance estimate ($s_{p,t}$) was used to approximate the variance of the count, $\varsigma^2_{p,t} = s^2_{p,t}$.

We modelled changes in pond abundance from year to year as an auto-regressive process, $p_{t+1} \sim \text{Normal}\left(p_t, \sigma^2_p\right)$. We modelled changes in teal abundance using an integrated population model (Figure 2; Schaub & Kéry, 2022), where the population in the next year (n_{t+1}; Table 1) was a function of the population in the previous year (n_t), natural mortality during the previous year (η_t), hunting mortality (κ_{t+1}) between the breeding seasons, and the mean number of female recruits produced per capita during the previous breeding season (ξ_t),

$$n_{t+1} = n_t \left(1 - \kappa_{t+1} - \eta_t\right) + n_t \, \xi_t. \tag{1}$$

We hypothesized that increases in hunter numbers would increase the hunting mortality hazard rate and increases in teal abundance would reduce hunting mortality hazard rate as each individual would be less susceptible to harvest (Riecke, Sedinger, et al., 2022). Thus, we modelled hunting mortality hazard rate ($h_{\kappa,t}$, Ergon et al., 2018, Nater et al., 2020) as a function of z-standardized $\left(z(x_i) = \frac{x_i - \bar{x}}{\text{sd}(\boldsymbol{x})}\right)$ breeding pair abundance, $z(\boldsymbol{n})$, the z-standardized number of hunters, $z(\boldsymbol{H})$, and random temporal variation (ϵ),

$$\log\left(h_{\kappa,t}\right) = \alpha_1 + \alpha_2 \times z\left(n_t\right) + \alpha_3 \times z\left(H_t\right) + \epsilon_t, \tag{2}$$

where mortality hazard rates are the instantaneous intensity of mortality events integrated over the exposure interval (Ergon et al., 2018). We hypothesized that natural mortality hazard rate would increase with increases in teal abundance, while fecundity would decline, and we hypothesized that both natural mortality and fecundity would increase with pond abundance (Riecke, Sedinger, et al., 2022). Thus, we modelled natural mortality hazard rate ($h_{\eta,t}$) and fecundity (ξ_t) as a function of z-standardized breeding pair abundance, $z(\boldsymbol{n})$, the z-standardized number of ponds, $z(\boldsymbol{p})$, and random temporal variation,

$$\begin{aligned} \log\left(h_{\eta,t}\right) &= \beta_1 + \beta_2 \times z\left(n_{t+1}\right) + \beta_3 \times z\left(p_t\right) + \omega_t, \\ \log\left(\xi_t\right) &= \gamma_1 + \gamma_2 \times z\left(n_t\right) + \gamma_3 \times z\left(p_t\right) + \delta_t. \end{aligned} \tag{3}$$

We modelled residual temporal variation in hunting and natural mortality hazard rates and fecundity as random effects,

$$\begin{aligned} \epsilon_t &\sim \text{Normal}\left(0, \sigma^2_\epsilon\right), \\ \omega_t &\sim \text{Normal}\left(0, \sigma^2_\omega\right), \\ \delta_t &\sim \text{Normal}\left(0, \sigma^2_\delta\right), \end{aligned} \tag{4}$$

and assigned vague priors for regression parameters and variances. We then derived hunting (κ) and natural (η) mortality probabilities as a function of respective hazard rates. Teal hunting primarily occurs in September and October (Devink et al., 2013), while natural mortality of adult female ducks primarily occurs during the breeding season (Arnold et al., 2012; Dufour & Clark, 2002; Hoekman et al., 2002; Riecke, Sedinger, et al., 2022). Thus, we modelled natural mortality probability as conditional on having survived previous hunting mortality,

$$\begin{aligned} \kappa_t &= 1 - e^{-h_{\kappa,t}}, \\ \eta_t &= \left(1 - \kappa_t\right)\left(1 - e^{-h_{\eta,t}}\right). \end{aligned} \tag{5}$$

To model the band-recovery data, we built modified band-recovery models following Brownie and Pollock (1985), Kéry and Schaub (2012), Ergon et al. (2018), Nater et al. (2020) and Riecke, Sedinger, et al. (2022), where recoveries of previously marked adult females occurred as a function of annual survival (s_t) and band-recovery (f_t) probabilities. We estimated annual band-recovery probability as a function of hunting mortality probability (κ), band-reporting probability (ρ), and the probability that birds killed by hunting are not retrieved, that is, crippling loss probability (c). We modelled c as $c \sim \text{Beta}(20, 80)$ given Bellrose (1953), Nieman et al. (1987), and Hicklin & Barrow, 2004. We incorporated uncertainty about

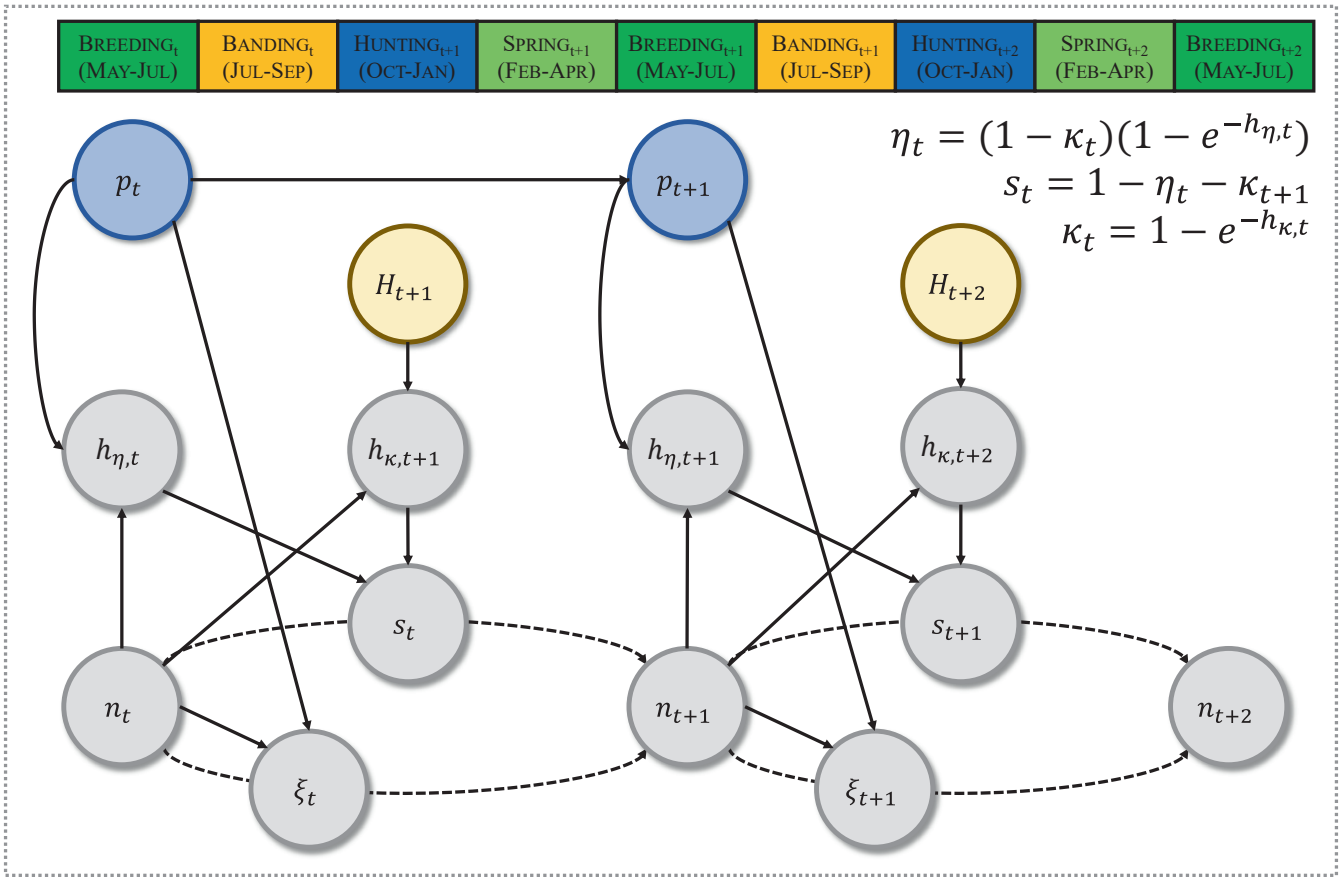

FIGURE 2 A directed acyclic graph demonstrating the relationships among abundance (***n***), ponds (***p***; blue), fecundity (ξ), hunting mortality hazard rate ($\boldsymbol{h}_\kappa$), natural mortality hazard rate ($\boldsymbol{h}_\eta$), survival (**s**) and the number of duck hunters (***H***; brown) for blue-winged teal breeding in the North American Prairie Pothole Region across the annual cycle (1973–3016). Solid arrows represent estimated directional relationships, and dashed arrows represent processes leading to changes in population abundance.

TABLE 1 Parameter symbols, definitions and temporal scale for parameters estimated in the integrated population model of relationships among abundance, hunting mortality and natural mortality for adult female blue-winged teal marked in the North American midcontinent (1973–2016)

Symbol	Definition	$t = 1$
h_κ	Hunting mortality hazard rate	1973–74
h_η	Natural mortality hazard rate	1974
s	Survival probability	1973
κ	Hunting mortality probability	1973–74
η	Natural mortality probability	1974
ξ	Fecundity; female recruits in $t+1$ produced per female in t	1974
n	The number of blue-winged teal pairs	1974
p	The number of May ponds	1974
α	Regression parameters for hunting mortality hazard	—
β	Regression parameters for natural mortality hazard	—
γ	Regression parameters for fecundity	—

band-reporting probabilities using estimates for mallards from Arnold et al. (2020) and moment matching (Hobbs & Hooten, 2015; Thompson et al., 2022). We then derived band recovery probability as $f_t = \kappa_t(\rho_t)(1-c)$. Major assumptions of our analyses were that crippling loss probability was time invariant, and band reporting probabilities for blue-winged teal were equivalent to mallard band-reporting probabilities estimated by Arnold et al. (2020). Higher crippling probabilities or lower reporting probabilities would increase our estimates of hunting mortality probability, and vice versa.

We modelled adult female survival (s_t) as a function of natural ($h_{\eta,t}$) and hunting ($h_{\kappa,t}$) mortality hazard rates (Ergon et al., 2018; Nater et al., 2020), where $s_t = e^{-(h_{\kappa,t}+h_{\eta,t})}$. We formatted the capture-recovery data (***M***) in a multinomial array (Brownie & Pollock, 1985), where the rows (i) represent the year of release, the columns (j) represented the year of recovery, and T is the number of years where individuals were released. Thus, the cell values in the data represent the number of individuals released in year i and shot, retrieved and reported in year j, and the last column in the m-array is the number of individuals that were never reencountered (Brownie & Pollock, 1985; Kéry & Schaub, 2012). The cell probabilities (***X***) for the m-array (***M***) were therefore,

$$x_{ij} = \begin{cases} 0 & i > j < T+1 \\ f_i & i = j < T+1 \\ \left(\prod_{k=i}^{k=j-1} s_k\right) f_j & i < j < T+1 \\ 1 - \sum_{k=1}^{T} x_{i,k} & j = T+1 \end{cases}, \quad (6)$$

and each row in the m-array, $\boldsymbol{m}_i = (m_{i,1}, \ldots, m_{i,T+1})$, was modelled with a multinomial distribution given the number of marked adult females released per year (r_t) and the cell probabilities for that release year ($\boldsymbol{x}_i$),

$$\begin{aligned} \boldsymbol{m}_i &\sim \text{Multinomial}(r_t, \boldsymbol{x}_i), \\ \boldsymbol{x}_i &= (x_{i,1}, \ldots, x_{i,T+1})'. \end{aligned} \quad (7)$$

We fit the integrated population model in JAGS (Plummer, 2003) using the `jagsUI` package (Kellner, 2016). We sampled three chains of 1,000,000 iterations using a MCMC algorithm, discarded the first 500,000 iterations, and retained every fiftieth saved iteration. We report medians of posterior distributions, 95% Bayesian credible intervals, and the proportion of the posterior distribution on the same side of zero as the median (υ) in the text, tables and figures. We visually assessed convergence, and all chains converged adequately ($\hat{R} < 1.01$; Brooks & Gelman, 1998).

3 | RESULTS

From 1973–2016, 112,639 adult female teal were marked and released in the Prairie Pothole Region of North America. Hunters shot, retrieved and reported 2518 individuals in the United States and Canada during the same time period. Breeding population abundance declined from 1974 through the 1980s and reached an all-time low in 1990 ($n_{1990} = 2.7$ million), at the end of a major drought (Figure 3). Following the beginning of a major wet cycle in 1993, populations doubled in four years, and remained high through the mid-2010s, reaching a peak in 2012 ($n_{2012} = 9.2$ million; Figure 3). Fecundity was positively influenced by the number of ponds ($\gamma_3 = 0.143$ proportion of the posterior on the same side of zero as the median (υ) = 0.972), and negatively density-dependent ($\gamma_2 = -0.010$; $\upsilon = 0.914$), consistent with some compensation of hunting mortality through increases in fecundity (i.e. compensatory natality). There was a strong positive effect of abundance on natural mortality hazard rate ($\beta_2 = 0.098$; $\upsilon = 0.993$), leading to a rapid increase in natural mortality hazard rate as populations

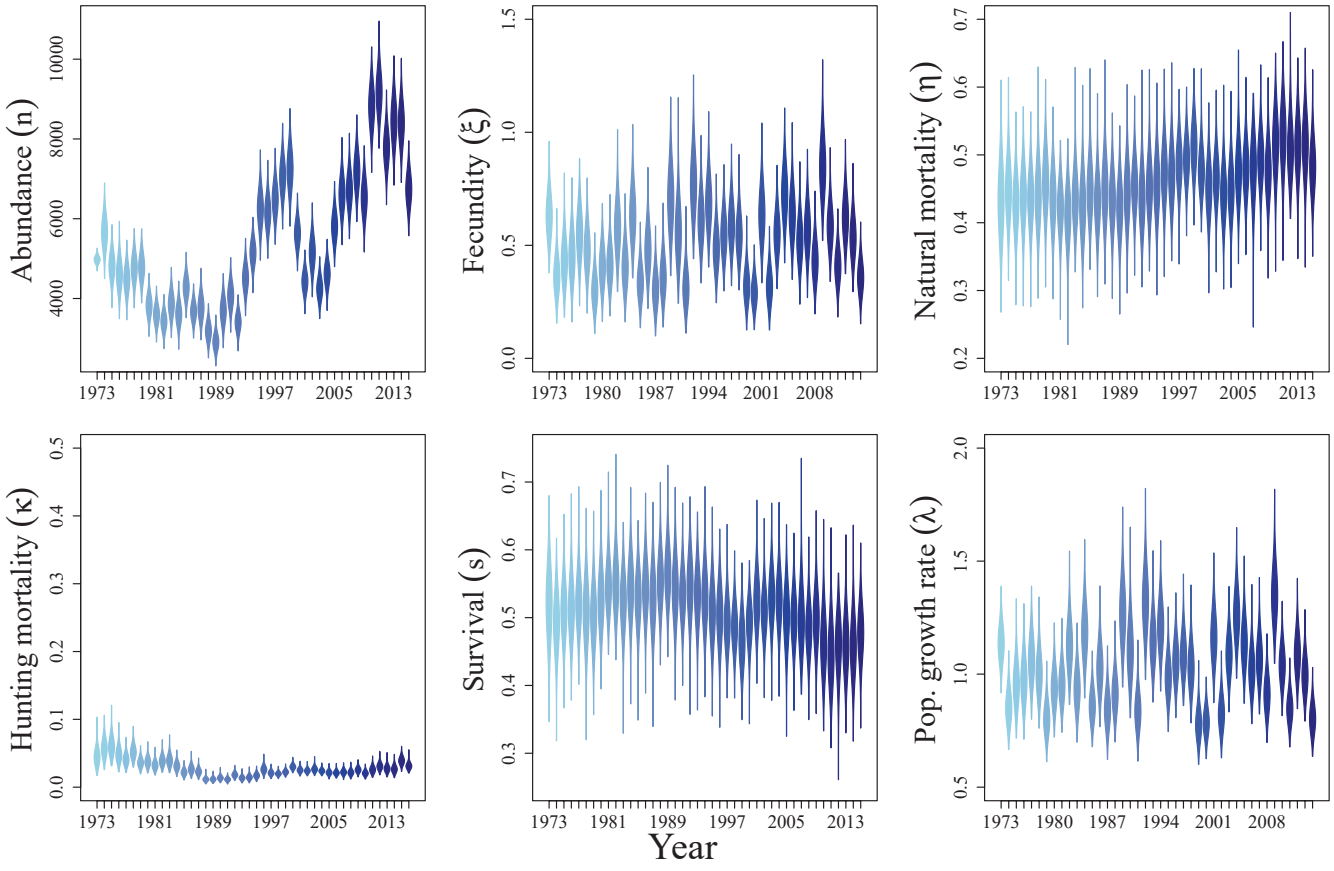

FIGURE 3 Posterior distributions of breeding pair abundance (n; upper left), fecundity (ξ; upper center), natural mortality probability (η; upper right), hunting mortality probability (κ; lower left), survival (s; lower center), and population growth rate (λ, lower right) of adult female blue-winged teal captured, marked and released in the North American midcontinent from 1973–2016. Note that darker shading of the violin plots represents later years in the time series to provide a temporal reference for subsequent bivariate plots.

increased (Figures 3 and 4). We did not observe an effect of pond abundance on the natural mortality hazard rate ($\beta_3 = -0.019$; $\upsilon = 0.658$). We estimated a positive relationship between hunting mortality hazard rate and abundance ($\alpha_2 = 0.093$; $\upsilon = 0.973$), and between hunting mortality hazard rate and the number of hunters ($\alpha_3 = 0.376$; $\upsilon = 1$; Figure 4). Thus, hunting mortality probability was high during a peak in total duck, hunter and pond numbers in the 1970s (U.S. Fish & Wildlife Service, 2018), and declined during a major drought and restrictive harvest regulations in the 1980s. Hunting mortality probability increased again as a long-term wet cycle began in the 1990s (Figure 3). Concurrently, teal and other duck populations increased (U.S. Fish & Wildlife Service, 2018), the number of hunters increased, and harvest regulations also became more liberal in parallel with abundant duck populations. Critically, we note that natural mortality hazard rates were at least an order of magnitude greater than hunting mortality hazard rates for the duration of the study (Figure 4). Since the turn of the century, the risk of mortality from hunting has never been greater than one-twentieth of the risk from natural mortality (Figure 4). Thus, density-dependent changes in natural mortality hazard rate led to the majority of the observed change in survival (Figure 5).

4 | DISCUSSION

We demonstrate that strong density-dependent natural mortality occurs in a species with a fast-paced life-history strategy. Our results have important implications for inference regarding the effects of hunting on the population dynamics of wild organisms. We show that natural mortality probability of adult female blue-winged teal increased > 0.1 as populations rapidly increased, with minimal (< 0.02) changes in hunting mortality probability. We also observed density-dependent effects on fecundity. Both of these mechanisms are consistent with demographic compensation of teal hunting, as removing individuals through harvest reduces density-dependent natural mortality, and increases fecundity. We suggest that the observed increases in cause-specific mortality do not indicate that hunting was the principal driver of the major decline in teal survival rates, but rather that intraspecific competition, reproductive allocation, predation and habitat availability may be important additional mechanisms that affect survival rates of teal and other hunted species (e.g. mallard, Riecke, Sedinger, et al., 2022). To illustrate this point, if we naively assume that hunting is the sole driver of temporal variability in survival, and that this relationship is linear (two assumptions inherent to existing additive and compensatory models of hunting mortality in waterfowl and other taxa), the observed linear relationship between survival and hunting mortality is biologically implausible (Figure 5) because survival declined five times faster than the rate at which hunting mortality increased.

Our results indicate that female dabbling ducks are prone to density-dependent effects on natural mortality (Figure 4), as natural mortality for females increased rapidly as populations increased (Figure 3). We hypothesize that density-dependent natural morality

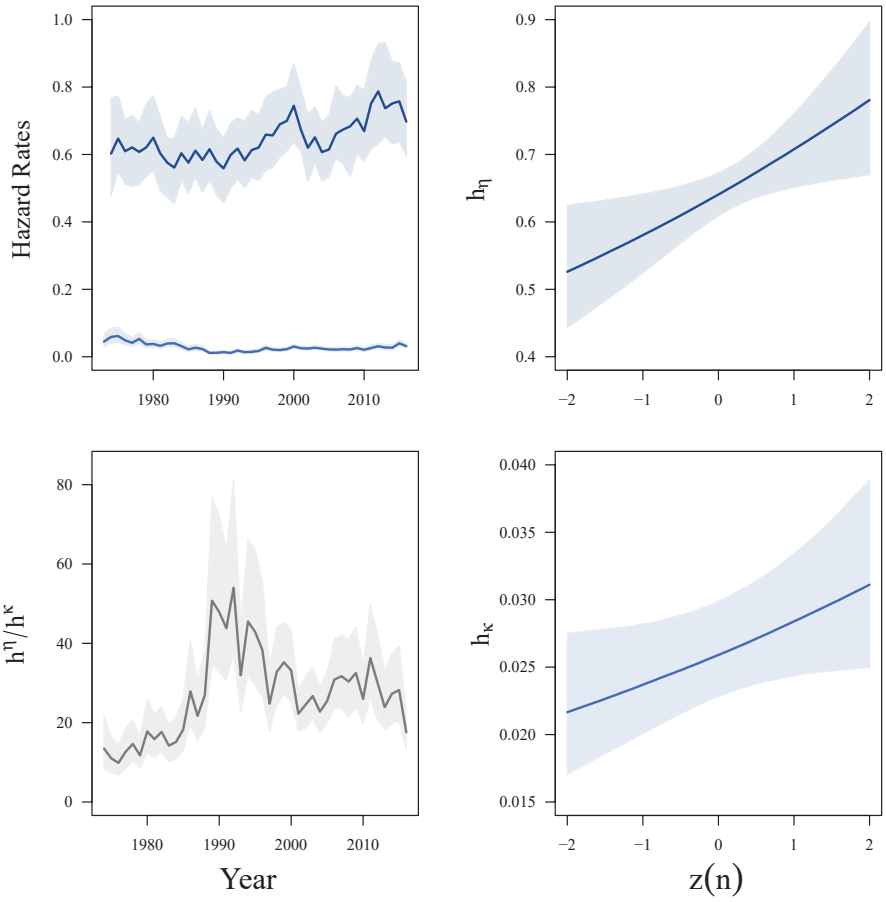

FIGURE 4 Estimates and 95% Bayesian credible intervals for natural (h_η; dark blue) and hunting (h_κ; blue) mortality hazard rates plotted against year (upper left) and *z*-standardized abundance (*z*[*n*]; right), and the ratio of natural mortality hazard rates to hunting mortality hazard rates (lower left) for adult female blue-winged teal captured, marked and released in the north American midcontinent from 1974–2016.

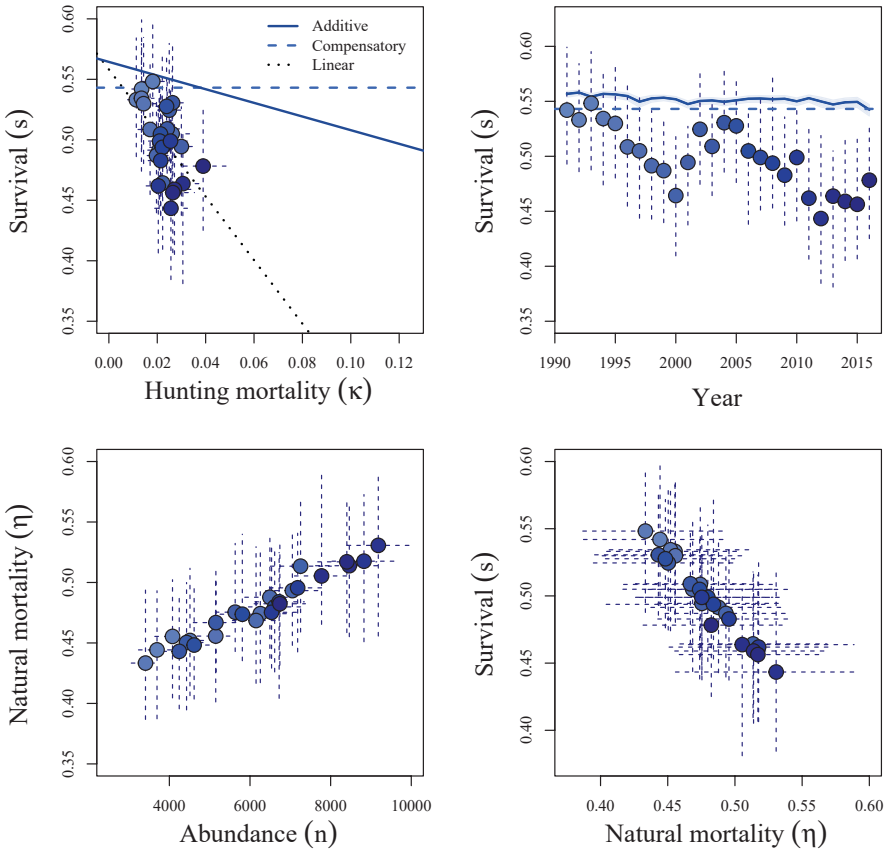

FIGURE 5 The estimated linear relationship (black dotted line) between survival (*s*) and hunting mortality (κ) compared to compensatory (light blue dashed line) and additive (dark blue solid line) models proposed by the Teal Harvest Potential Working Group (Devink et al., 2013) for adult female blue-winged teal captured, marked and released in the North American midcontinent during a major increase in teal abundance (top left; 1991–2016), as well as comparisons of our survival estimates to predictions from the additive and compensatory models over time (top right), the relationship between natural mortality probability and abundance (thousands; bottom left), and the relationship between survival and natural mortality (bottom right). Note that points are medians, navy coloured dashed lines are 95% credible intervals, and darker shading of the points represents later years in the time series.

could be attributable to both nutritional or energetic constraints and predation (Arnold et al., 2012; Dufour & Clark, 2002). Female dabbling ducks invest substantially in egg production, incubation, and brood care (Ankney et al., 1991; Gloutney & Clark, 1991; Lack, 1968), and incur increased predation risk during incubation (Arnold et al., 2012), leading to breeding season mortality (Brasher et al., 2006; Dufour & Clark, 2002). Wet-dry periods typically occur cyclically (Millett et al., 2009), where females may have increased breeding and re-nesting propensity and associated energy expenditure (Ankney et al., 1991; Gloutney & Clark, 1991; Lack, 1968) during wet cycles (Dufour & Clark, 2002; Krapu et al., 1983), which coincide with increased abundance due to increased suitability of nesting and brood-rearing habitats. Density-dependence might also operate classically, where increasing population size increases competition for food during breeding and non-breeding periods. Taken together, these processes may lead to a strong relationship between abundance and natural mortality.

The relationship between natural mortality and abundance may be energy independent as well (Arnold et al., 2012) if predation is density-dependent in this system (Ringelman et al., 2012, 2014; Sargeant et al., 1984). For example, prey selection is often linked to prey abundance for mesopredators, and mesopredators in the North American midcontinent may allocate more effort toward locating duck eggs and incubating females (Ringelman et al., 2012, 2014; Sargeant et al., 1984) as the abundance of nesting teal and other dabbling ducks increases (i.e. a type III functional response), adding increased predation risk (Arnold et al., 2012) to increased energy expenditure and competition when breeding populations are high. Additionally, predators may devote less attention to nest searching and predation as the availability of microtine rodents increases (Specht & Arnold, 2018). Increased or decreased nest predation would subsequently lead to shifts in mortality of breeding females.

Many researchers have discussed comparative fit of different (e.g. additive or compensatory) models of the impacts of hunting by comparing survival and hunting mortality or natural and hunting mortality estimates from mark-recapture-recovery data against expectation under competing models of the survival process for teal (Devink et al., 2013) and other wildlife species (Péron, 2013; Runge et al., 2002; Servanty et al., 2010). To highlight potential issues inherent in models only considering survival and hunting mortality parameters (i.e. ignoring density-dependence and other confounding processes), we derived the observed linear relationship between survival and hunting mortality rates for adult female blue-winged teal from 1990–2015, a period during which teal populations more than tripled, and roughly contemporaneous with the period Adaptive Harvest Management has been used to determine North American waterfowl harvest regulations. The observed linear relationship between survival and hunting mortality for adult female teal in this study (intercept = 0.558; slope = −2.63) would lead to survival rates of zero as hunting mortality probability approached 0.2 (Figure 5), which is clearly biologically implausible. We also note that as teal populations increased, the relationship between survival and harvest failed to fit either the compensatory or additive hypotheses of hunting mortality effects on survival, and instead fit an extremely

depensatory model of hunting effects (Figure 5), despite minimal temporal variation in hunting mortality (Figure 3).

We raise two important points regarding the continued use of such modelling strategies when researchers do not incorporate other potential sources of variation in survival rates. First, our findings strongly suggest that density-dependent processes can affect natural mortality of wild waterfowl populations (Figure 4; Riecke, Sedinger, et al., 2022), and a plethora of other research has demonstrated that density-dependence can affect survival across taxa (e.g. Cubaynes et al., 2014; He & Duncan, 2000). Second, duck abundance, hunter participation and harvest are strongly correlated in North American waterfowl populations (Sedinger & Herzog, 2012). Given multicollinearity among harvest, abundance and natural mortality, we suggest that existing models might inadequately explain the underlying relationship between hunting mortality and survival, and may lead to inappropriate management frameworks. The ecological literature is clear on the potential issues and challenges associated with multicollinearity (Hilborn & Stearns, 1982), particularly when biologically appropriate models are not included in the model set.

Literature regarding the role of adaptive management practices has focused on the potential for learning as systems and our knowledge of systems change (Berkes et al., 2000; Johnson et al., 2015). Current parameterizations of fully compensatory models have faced substantial and well-founded criticism (Lebreton, 2005; Runge & Johnson, 2002), and do not appear to be biologically plausible for ducks (e.g. a hunting mortality probability of ~ 0.4 with no effect on survival probability). Fully additive models are based on the assumption that individual heterogeneity in susceptibility to natural or hunting mortality is non-existent, despite substantial evidence to the contrary (Arnold, 2021; Gimenez et al., 2018), and also fail to consider concepts such as annual variation in natural mortality, which is substantial (Figure 3). Given that the average natural mortality hazard rate was thirty times greater than the average hunting mortality hazard rate, we believe that the strength of density-dependent relationships obscures any effect of hunting on survival for adult female blue-winged teal. We urge development of novel, biologically plausible model structures (e.g. Cubaynes et al., 2012; Gimenez et al., 2012; Riecke, Sedinger, et al., 2022; van de Pol & Brouwer, 2021) to inform waterfowl harvest management in North America, and elsewhere.

We do not believe a complete understanding of the drivers of demographic components or any ecological mechanism is possible in the absence of experimentation (Burnham & Anderson, 2002) given potential confounding among ecological processes. This study does not seek to resolve the decades-long debate (Anderson & Burnham, 1976; Arnold et al., 2016; Péron, 2013) about the impacts of hunting on wildlife populations. Rather, we seek to demonstrate that models missing key environmental processes will inevitably fail to fully and accurately explain the impacts of hunting. In fact, recent research (Koons et al., 2022) has demonstrated that existing adaptive harvest management models for mallards in North America produce more biased predictions than a simple persistence (i.e. $N_{t+1} = N_t + \epsilon_t$) model, where the inclusion of hypotheses about relationships between survival and hunting mortality has actually diminished the performance of existing models relative to a simple null model. As research progresses, the incorporation of life-history trade-offs and biotic and abiotic processes will be critical as we seek to enhance our understanding of the impacts of anthropogenic actions on wildlife populations (e.g. Riecke, Sedinger, et al., 2022; Sandercock et al., 2011). Recent research indicates that managers can most efficiently and effectively gather information regarding wildlife population dynamics by using active adaptive management techniques, where managers seek to accomplish management objectives while developing knowledge about ecological systems by experimentally manipulating management actions (Williams & Brown, 2014, 2016).

We believe that more biologically plausible, mechanistic models exploring the potential for compensatory natality and or density-dependent mortality (Boyce et al., 1999) might benefit wildlife managers and the populations they manage (Walters, 2007), as well as current and future opportunities of user groups that often contribute to conservation actions (Anderson et al., 2018). While risk-averse management strategies can be highly beneficial in the face of minimal information, this benefit is gained at the cost of reduced or even misguided learning, as well as a potential reduction in the development of improved management strategies (Walters, 1986). Sans learning, managers are ill-equipped to deal with crises once environmental conditions change. We show that a strong negative relationship between survival and hunting mortality indicating depensatory hunting mortality is clearly spurious, and is instead driven by density-associated increases in natural mortality (Figures 3–5). We suggest that relationships among hunting, mortality, and abundance of hunted populations be examined in more detail across taxa. Critically, while this case study demonstrates a case where the effects of harvest are overestimated, overly simplistic models might also disguise the negative effects of harvest in other systems. Thus, our overarching goal is to develop a better understanding of the underlying processes driving observed relationships among survival and hunting mortality to better conserve waterfowl populations and other taxa, while providing maximum sustainable opportunities for the user groups that fund conservation efforts.

AUTHOR CONTRIBUTIONS

Thomas V. Riecke led the writing of the manuscript, with critical input from all authors. Thomas V. Riecke, Madeleine G. Lohman, Benjamin S. Sedinger, Todd W. Arnold, Michael Schaub, Perry J. Williams and James S. Sedinger designed and conducted the analysis. All authors contributed critically to manuscript drafts and gave final approval for publication.

ACKNOWLEDGEMENTS

The authors thank the tens of thousands of waterfowl banders, as well as the millions of citizen scientists (i.e. waterfowl hunters), who contributed to the development of this dataset. The authors also thank the biologists and pilots that collected the aerial survey data, and the USGS Bird Banding Lab for compiling and maintaining the banding data. Thomas V. Riecke was supported by the Bonnycastle Fellowship

in Wetland and Waterfowl Biology from the Institute for Wetland and Waterfowl Research, Ducks Unlimited Canada, Thomas V. Riecke and BSS were supported by Delta Waterfowl and the California Department of Water Resources, and Thomas V. Riecke and James S. Sedinger were supported by the National Science Foundation (DEB 1252656). David N. Koons was supported by Delta Waterfowl and the James C. Kennedy Endowed Chair of Wetland & Waterfowl Conservation at Colorado State University. Todd W. Arnold was supported by Delta Waterfowl. The authors thank Jean-Michel Gaillard, Ray Alisauskas, Guillaume Souchay, and three anonymous reviewers for their constructive and extremely helpful critiques. Open access funding provided by Schweizerische Vogelwarte.

CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Blue-winged teal banding and band-recovery data are publicly accessible through the Bird Banding Lab https://doi.org/10.5066/P9R1L6Q7 (Celis-Murillo et al., 2020). Data on pond and teal 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 & Wildlife Service, 2018). R script for analysing the data in JAGS and an input file are available from the Dryad Digital Repository https://doi.org/10.5061/dryad.zpc866tbz (Riecke, Lohman, et al., 2022).

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How to cite this article: Riecke, T. V., Lohman, M. G., Sedinger, B. S., Arnold, T. W., Feldheim, C. L., Koons, D. N., Rohwer, F. C., Schaub, M., Williams, P. J., & Sedinger, J. S. (2022). Density-dependence produces spurious relationships among demographic parameters in a harvested species. *Journal of Animal Ecology*, *91*, 2261–2272. https://doi.org/10.1111/1365-2656.13807