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# Potential economic consequences along migratory flyways from reductions in breeding habitat of migratory waterbirds

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#### ABSTRACT

The migration of species, often across continents, makes it difficult to quantify the cumulative effects of localand regional-scale conservation actions. Further, variation in stakeholder interests, differing jurisdictional governance processes, priorities, and monitoring abilities across the migratory range shapes place-specific differences in management actions. These differences may lead management of migratory species to benefit both species and stakeholders in some places more than others. In the case of North American waterfowl, possible reduction of wetland protection in breeding areas may lead to substantive shifts in benefits among stakeholders across their range by adversely affecting recreational viewing and hunting opportunities for these species. To understand possible consequences of wetland loss in the U.S. Prairie Pothole Region, the breeding region for 12 focal species of waterfowl, on the recreation economics for these species, we modeled a causal pathway linking wetland loss in the breeding grounds to changes in duck abundance and then assessed the consequences of that change in abundance on recreational hunting and viewing within migratory flyways. Under a scenario where wetland protections cease, we find annual economic activity associated with recreation may decrease as much as \$489 million at the highest levels of predicted wetland loss, the majority of it coming from impacts to viewing behavior in the Mississippi Flyway. The number of hunters may decline by as much as 18,000, leading to \$32 million less in annual economic activity. At highest levels of wetland loss, viewing value is expected to decline by more than one-quarter. Lost economic value associated with reductions in recreation in the Mississippi and Central Flyway states is not likely to be overcome by increases in agricultural economic output in drained wetlands of the Prairie Pothole Region. Our analyses indicate local effects of national water policies likely have far-reaching consequences because of the multi-dimensional connections arising from place-specific differences in management action, global and national agricultural economic drivers of crop expansion, and the biotic phenomena of transcontinental avian migration. Reductions in habitat in one location could ramify to economic consequences throughout the continent through connections fostered by migrating waterfowl.

#### 1. Introduction

The movement of migratory species, often across continents, makes it difficult to quantify the cumulative effects of local- and regional-scale conservation actions (Martin et al., 2007; Dunn et al., 2019). The limited

availability of range-wide demographic information for groups or guilds of species adds to this challenge (Marra et al., 2015). These limitations lead to single-species approaches in full-annual-cycle investigations, inhibiting inferences about how communities of migratory species respond to habitat loss or conservation actions implemented in any

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given part of their range. Added complexity arises from migratory species management programs needing to account for diverse stakeholder interests, differing jurisdictional and governance processes, priorities, and monitoring abilities. Furthermore, the diverse viewpoints among stakeholders often entail a varied list of desired ecological, social, and economic returns on conservation investments that shape place-specific differences in management actions. These differences may lead management and conservation of migratory species to benefit both species and stakeholders in some places more than others (Semmens et al., 2011; Schröter et al., 2020). Such mismatches are particularly stark for migratory waterfowl in North America, which provide hunting and viewing opportunities across the continent. In this example, investments in habitat conservation within breeding areas (Mattsson et al., 2020) generate hunting and bird viewing benefits throughout their range (Bagstad et al., 2019). Breeding habitat for northern pintail ducks (Anas acuta), for instance, has been shown to support about one-third (\$5.6 M) of the \$17.3 M in benefits provided by the species in their winter range along the Gulf of Mexico each year (Bagstad et al., 2019). An important question is how the loss of breeding habitat affects services provided by waterfowl to places they visit across their annual cycle. Understanding and quantifying these impacts is essential for developing widely supported, equitable, and comprehensive management strategies for migratory species (Chester et al., 2022). Increased clarity regarding the consequences of wildlife policy and management for the full set of stakeholders, including those distant from where policy actions may take place, provides crucial insight for properly considering stakeholder concerns (Song et al., 2021).

Waterfowl in North America provide both use and non-use values for people (Goldstein et al., 2014; Loomis et al., 2018; Haefele et al., 2019; Thogmartin et al., 2022). Use values include those tied to recreation (i.e., hunting and viewing; Brown and Hammack, 1972, 1973; van Kooten et al., 2011) and subsistence harvest (Goldstein et al., 2014). Non-use values are associated with immaterial benefits derived from the mere knowledge a population exists or is viable. Although little is known regarding trends in non-use and recreation values, the number of recreational duck hunters declined by one-third from 1995 to 2021 (Vrtiska et al., 2013; Raftovich et al., 2022). Despite this decline in hunting participation, investments in waterfowl habitat conservation increased by 86 % from ca. 2009 to ca. 2014 within the U.S. portion of the Prairie Pothole Region, primarily due to inputs other than those by waterfowl hunters (e.g., duties on imports of arms and ammunition; Mattsson et al., 2020).

Investment in waterfowl habitat conservation in the Prairie Pothole Region (hereafter PPR) occurs to ensure that this "duck factory," responsible for 50-80 % of North America's ducks (Batt et al., 1989) and the "single most productive habitat for waterfowl in the world" (Johnson et al., 2005), continues to provide abundant numbers of ducks for waterfowl harvest throughout North America. However, despite the importance of this region for duck production and the associated investments in waterfowl habitat conservation, wetland area in the PPR has been declining, largely from conversion to agriculture (Dahl, 1990, 2014; Johnston, 2013). Over the last century, the PPR has become an important agricultural area for cereal grain, oil seed, and row crop production. Today, the PPR is an intensively cultivated landscape with high levels of privately owned, highly productive cropland (Foley et al., 2005; Hoekstra et al., 2005). For a host of economic, social, and political reasons, remnant prairie wetlands are often viewed as impediments to further agricultural development (Leitch, 1989; Johnson et al., 2008; Wachenheim et al., 2019). Drainage and degradation of wetlands, and conversion of grassland to annual cropland, have substantially altered the capacity of the region to attract and support breeding ducks (e.g., Stephens et al., 2005). Since settlement by Europeans in the 1800s, up to 89 % of wetlands have been lost to agricultural drainage in some parts of the PPR (Dahl, 1990; Watmough et al., 2017). These effects represent a primary concern for international waterfowl conservation under the North American Waterfowl Management Plan (NAWMP; U.S. Fish and Wildlife Service and Canadian Wildlife Service, 1986).

Prairie Pothole Region wetlands are afforded less protection in Canada (Scarth, 1998; Lloyd-Smith et al., 2020) whereas mechanisms to forestall wetland loss in the United States include passage of the 1985 Food Security Act and subsequent farm bills implementing a provision known as "Swampbuster" (Gleason et al., 2011), which disincentivized draining of wetlands. However, lax enforcement has allowed erosion of wetland capacity to continue (GAO, 2021). Currently, substantial political and legal concerns surround the Waters of the United States (WOTUS) rule (Sullivan et al., 2019; Keiser et al., 2022), which determines waterways and wetlands falling under federal oversight (U.S. Department of the Army Corps of Engineers and Environmental Protection Agency, 2023). Those concerns center in large part around geographically isolated wetlands such as the small depressional wetlands known as prairie potholes; these wetlands are "wetlands with no apparent surface water connection to perennial rivers and streams, estuaries, or the ocean" (Tiner et al., 2002). Because past legal rulings resulted, albeit temporarily, in 95 % of prairie pothole wetlands being stripped of legal protection under the Clean Water Act (e.g., Solid Waste Agency of Northern Cook County v. U.S. Army Corps of Engineers, 531 U.S. 159 [2001] and Rapanos v. United States, 547 U.S. 715 [2006]), rejecting current protections for geographically isolated wetlands has the potential to increase on-going loss of prairie potholes and, in turn, affect the number of ducks produced. Recently, the U.S. Supreme Court determined wetland protections extended only to those having a continuous surface connection with a larger water body (Sackett et ux. vs. Environmental Protection Agency et al., 2023).

Our aim here is to understand potential consequences to the recreation economics associated with 12 duck species from continuing and possible changes in wetland loss to agriculture in the U.S. portion of the Prairie Pothole Region. We do this by modeling a causal pathway linking wetland loss in the PPR to changes in duck abundance and then assessing the consequences of that change in duck abundance on recreational hunting and viewing in states located within the Central and Mississippi Flyways. We develop a series of predictive models according to the causal pathway and parameterize these using data from the literature. Although we focus on wetland loss to drainage associated with agricultural expansion, we acknowledge the effects of climate change on waterfowl in the region. However, given the high levels of uncertainty and the complexity required to link climate change, wetland loss caused by agricultural land use, and waterfowl population dynamics, we opted to focus only on wetland loss driven by agricultural expansion. Furthermore, we expect this wetland loss to have a subtractive effect on the capacity of the PPR to support waterfowl populations relative to climate change. Our findings allow inferences about the potential economic consequences of important policy and law currently in debate today, including the ongoing debate surrounding the WOTUS rule (U.S. Department of the Army Corps of Engineers and Environmental Protection Agency, 2023).

#### 2. Methods

#### 2.1. Study area

The most important breeding habitat for North American waterfowl exists in the formerly glaciated region of the North American Great Plains, also known as the Prairie Pothole Region (Stewart and Kantrud, 1973). This 770,000 km² region straddling three Canadian provinces and five U.S. states (Fig. 1) represents one of Earth's largest wetland complexes (Mushet, 2016). The region is composed of millions of small depressional wetlands that formed as subterranean masses of ice melted following the last continental glaciation event (Doherty et al., 2018). Most PPR wetlands are small (<1 ha in size), geographically isolated, depressional wetlands with no surface water connection to perennial rivers and streams, receiving inflows only from rain and snowmelt within the capture zone of each depression and in some instances groundwater (Tiner et al., 2002; Anteau et al., 2016). As a result, prairie



Fig. 1. Changes in the amount of geographically isolated wetlands in the Prairie Pothole Region of the United States (hatched) is expected to alter number of breeding duck pairs, which in turn affects hunting and viewing activity in the states of the Central (green) and Mississippi (yellow) Flyways. Note: we used the flyway boundary for attributing hunting activity to the appropriate flyway, but state boundaries to attribute viewing activity to the appropriate flyway, because viewing activity was only known to the state level. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

potholes are particularly sensitive to the high interannual variation in precipitation characteristic of the PPR, which greatly affects the number of wetland basins in the region containing water each year (Doherty et al., 2018). Temporary, seasonal, and semi-permanent basins (Stewart and Kantrud, 1973; Cowardin, 1979) comprise 13, 24, and 24 % of U.S. PPR wetland area respectively (Doherty et al., 2018). These dynamic characteristics enhance their productivity for aquatic invertebrates, the primary source of food for most breeding female ducks (e.g., Swanson et al., 1979). Historically, diverse wetlands and extensive grasslands provided ideal habitats for successful waterfowl reproduction in this region (Stephens et al., 2005). Given the high wetland density, this region can host over two-thirds of the North American breeding ducks and be responsible for up to 80 % of their annual production (Batt et al., 1989; Doherty et al., 2018).

#### 2.2. Overview of modeling approach

We modeled the effects of wetland loss on the economics of duck-based recreation in four steps. Assuming continuing loss of wetlands, specifically geographically isolated wetlands, we estimated amounts of wetlands lost under several plausible land-change scenarios in the U.S. portion of the PPR. Next, we estimated the change in number of duck pairs that would be supported under these scenarios of wetland loss. Third, we used expected changes in duck pairs to estimate changes in duck hunting and viewing and, fourth, their associated change in recreation expenditures and consumer surplus. The causal chain is as follows:

 $\Delta Wetland\ Area \stackrel{yields}{
ightarrow} \Delta Duck\ Abundance \stackrel{yields}{
ightarrow} \Delta Recreation\ Behavior \stackrel{yields}{
ightarrow} \Delta Recreation\ Economics$ 

#### 2.3. Wetland area: empirical estimation of loss

We first characterized recent wetland loss based on published information in the PPR of Canada and the United States. Compared to the U.S. portion of the PPR, prairie pothole wetlands in Canada have no federal, and relatively limited provincial, legislative protection, but generally exist in a landscape with similar agricultural pressures (Scarth, 1998; Lane and D'Amico, 2016). Recent PPR wetland loss rates in the United States are approximately 0.096 % annually with a mean size of lost basins equal to ca. 0.3 ha (Dahl, 2014). These annual losses are

similar in magnitude to longer-term losses for the PPR (0.16 % per year, Oslund et al., 2010; 0.05–0.57 % per year, Doherty et al., 2013). From 2001 to 2011 in the Canadian PPR, annual wetland loss rates were two-and-a-half times higher (~0.26 %) compared to those in the United States, with mean, median, and maximum size of lost basins being 0.39, 0.14, and 20.9 ha, respectively (Watmough et al., 2017). Hence, wetland loss rates experienced in prairie Canada are assumed as a worst-case scenario should existing protections of geographically isolated wetlands be removed in the United States.

#### 2.4. Wetland area: loss scenarios

To estimate the impact of wetland loss in the U.S. PPR, we first estimated the total wetland area as defined by the National Wetland Inventory (NWI; U.S. Fish and Wildlife Service, 2016a) within the PPR boundary of Montana, North Dakota, South Dakota, Minnesota, and Iowa, using ArcGIS (ESRI, Redlands, California; Fig. 1). Relative to this baseline, we created four wetland loss scenarios, one based on the historical (1997–2009; Dahl, 2014) loss rate in the United States (0.096 %/yr), and three based on the historical (2001-2011; Watmough et al., 2017) loss rate in Canada (0.260 %/yr). Wetland loss scenarios were calculated in SAS (SAS Institute, Cary, North Carolina) using all NWI-PPR basin polygon areas (with 'geographically isolated' basins identified by Lane and D'Amico, 2016; provided by C. Lane, March 23, 2020) exported as an attribute database from ArcGIS (Environmental Systems Research Institute, Redlands, CA). We implemented wetland loss scenarios by first generating size-class bins matching the log-normal size class distribution (mean, median, maximum) of lost basins observed in the Canadian PPR (Watmough et al., 2017). We then binned all NWI-PPR wetland polygon areas less than or equal to the maximum size lost and defined as 'geographically isolated' by Lane and D'Amico (2016) into the 20 log-normal size-class bins. We used PROC SURVEYSELECT in SAS to randomly select basins from the binned subsample, while matching the mean and median wetland sizes, until a target percent area loss (relative to baseline area) had been achieved. Sampling was conducted without replacement, basins were assumed to be completely lost to drainage, and loss scenarios represent complete basin losses over specified time horizons (i.e., not annual). A low-loss scenario was defined by losses observed historically in the U.S., comprising (0.096  $\%/yr \times 20 \ yr = )1.9 \%$  less area in wetlands over 20 years; this baseline scenario (labeled low) describes status quo levels of protection for U.S. wetlands.

**Table 1**Description of scenarios of geographically isolated wetland loss in the U.S. portion of the Prairie Pothole Region.

Loss scenario	Δ PPR wetland (ha)	$\Delta$ Number of wetland basins	$\% \Delta \text{ in}$ wetland area	$\Delta$ PPR duck pairs	% Δ PPR ducks
Low Medium-	-58,633 -161,151	-107,400 -293,940	-1.91 -5.26	-146,622 -401.688	-2.58 -7.07
Low	-101,131	-255,540	-3.20	-401,000	-7.07
Medium- High	-297,556	-482,195	-9.72	-717,306	-12.62
High	-368,423	-596,540	-12.03	-887,696	-15.63

In the event WOTUS protections for geographically isolated wetlands are removed (McLaughlin et al., 2014; Cohen et al., 2016), as the recent Supreme Court ruling indicates (Sackett et ux. v. Environmental Protection Agency et al., 2023), we defined wetland loss scenario endpoints based on historical losses in Canada, representing medium-low (-5.26 %), medium-high (-9.72 %), and high (-12.03 %) wetland area loss, respectively (Table 1). These wetland area loss percentages were defined by applying a 0.26 % observed annual loss over 20-, 40- and 50-year time horizons. Relative to the NWI baseline wetland area, these scenarios resulted in the loss of geographically isolated wetland areas totaling 58,633 ha (low), 161,151 ha (medium-low), 297,556 ha (medium-high), and 368,423 ha (high), respectively. Although we calculated for each scenario the magnitude of habitat loss as a function of time elapsed (i.e., loss per year times number of years elapsed), the scenarios we examined hereafter are treated as instantaneous measures of effects at each level of habitat loss.

#### 2.5. Duck abundance: estimating lost duck breeding pairs

We simulated the potential effects of these wetland loss scenarios on the duck breeding population by estimating the current capacity of wetlands in the U.S. PPR to attract breeding pairs using, to our knowledge, the only model available for this purpose. Cowardin et al. (1995, Table 3) related breeding duck pairs to wetland area by the equation

$$Pairs = A \times wetland \ area + B \times \sqrt{wetland \ area},$$

based on image analysis of aerial photographs of waterfowl in Prairie Pothole wetlands. We used these wetland area-based regression equations to estimate the baseline number of pairs of 12 species of breeding ducks supported by baseline NWI wetlands. The 12 species were mallard (*Anas platyrhynchos*), American green-winged teal (*An. crecca*), northern pintail, blue-winged teal (*Spatula discors*), northern shoveler (*S. clypeata*), canvasback (*Aythya valisineria*), scaup spp. <sup>2</sup> (*Ay. affinis* and

same regression equations to the samples of selected 'lost' basins in each of the four loss scenarios described above. Our modeling approach assumes a lost wetland basin results in permanent loss of a landscape's ability to attract and support breeding waterfowl pairs.

## 2.6. Recreation behavior: modeling duck hunter days afield and number of active duck hunters

To ensure our inferences about economic effects applied only to birds originating from the U.S. PPR, we examined the distribution of hunter recoveries from birds banded in that region. We summarized recovery records from the U.S. Geological Survey Bird Banding Laboratory (Smith, 2013) for the 12 species banded during the preseason period (July, August, September) for the years 1970-2018 and encountered during any hunting season in subsequent years. We assumed almost 5 decades of recovery data would sufficiently account for variations in annual duck recovery distributions driven by environmental factors. We summed the number of recoveries for each species within each major area of North America (i.e., Alaska, Canada, the continental United States, Mexico), the Caribbean, and South America. We then calculated the proportion of total duck recoveries occurring in each of the four administrative flyways in the continental United States (Atlantic, Mississippi, Central, and Pacific; Fig. 1). Results indicated that 91.47 % of the duck recoveries from the U.S. PPR occurred in the Central (22.67 %) and Mississippi (68.80 %) flyways. Because the vast majority of recoveries occurred in these two flyways, we limited subsequent analyses of economic impacts to these areas.

To calculate predicted effects of wetland loss in the United States portion of the PPR on the consumer surplus and expenditures of hunters in the Mississippi and Central Flyways, we estimated both the reduction in duck hunter days afield and reduction in the number of active duck hunters from U.S. Fish and Wildlife Service survey data available for 1961 to 2018 (U.S. Fish and Wildlife Service, 2022). We regressed annual total duck hunter days afield against annual total breeding duck abundance (BPOP; U.S. Fish and Wildlife Service, 2022) with linear mixed-effect and generalized additive regressions. Methodological differences (see Appendix A) between data collected through 1999 (Mail Questionnaire Survey; MQS) and after 1999 (Harvest Information Program; HIP) required us to include a covariate effect of method in the model. Because of the time-series nature of the data, we examined the effect of year on duck hunter days afield. We expected there may be differences in hunter behavior and duck abundance between the flyways, so we also examined an effect of flyway (i.e., Central vs. Mississippi). The global model we assessed included 2- and 3-way interactions between the explanatory variables:

$$Days \ Afield_{t} = \beta_{0} + \beta_{1} \times BPOP_{t} + \beta_{2} \\ \times Flyway_{t} + \beta_{3} \times Year_{t} + \beta_{4} \times Flyway_{t} \times Year_{t} + \beta_{5} \\ \times Method_{t} \times BPOP_{t} + \beta_{6} \times Method_{t} \times Year_{t} + \beta_{7} \times Flyway_{t} \times BPOP_{t} + \beta_{8} \times Flyway_{t} \times Method_{t} + \beta_{9} \times Year_{t} \times BPOP_{t} + \beta_{10} \times Method_{t} \\ \times Flyway_{t} \times BPOP_{t} + \varepsilon_{t}$$

Ay. marila combined), redhead (Ay. americana), ring-necked duck (Ay. collaris), American wigeon (Mareca americana), gadwall (M. strepera), and ruddy duck (Oxyura jamaicensis). Populations of these species comprise >90 % of the ducks breeding in the PPR (U.S. Fish and Wildlife Service, 2022). We estimated lost duck breeding pairs by applying the

To assess whether duck abundance affected the number of hunters actively hunting, we used a similar approach in modeling the annual number of *active hunters*. We log-transformed the response to ensure normality of residuals. The global model was simpler, as there was only one method for estimating *active hunters*, and was:

<sup>&</sup>lt;sup>2</sup> Primarily lesser scaup because breeding range of greater scaup is outside of the Prairie Pothole Region (Baldassarre, 2014).

 $log(Active\ Hunters_t) = \beta_0 + \beta_1 \times BPOP_t + \beta_2 \times Flyway_t + \beta_3 \times Year_t + \beta_4 \times Flyway_t \times Year_t + \beta_5 \times Flyway_t \times BPOP_t + \beta_6 \times BPOP_t \times Year_t + \varepsilon_t$ 

### 2.7. Recreation behavior: evaluating models of hunting days afield and of active hunters

We examined a suite of models with increasing complexity by including interactions and combinations of additive effects (Appendix B). One such regression included a generalized additive model with a spline on year to control for non-linear temporal effects on the number of active hunters.

For each model, we examined model fit by plotting residuals against fitted values, Q-Q plotting of standardized residuals, plotting residuals versus leverage, and, using the DHARMa package (Hartig, 2021) in R (R Core Team, 2022), testing for dispersion, zero inflation, outliers, and heteroscedasticity (Appendix C). We calculated explained variance  $(r^2)$  as a measure of model performance and Akaike's Information Criterion corrected for small samples (AICc) as a measure of model parsimony. The model with adequate fit and the lowest AICc was used to derive inference (Appendix C). Models included in the confidence set were those with a  $\Delta$ AICc of  $\leq$ 4. We used scaled slope estimates to compare the influence of predictors on the response variable and used an alpha level of 0.05 for determining statistical significance.

Using the fitted relations between duck abundance from the Waterfowl Breeding Population and Habitat Survey (e.g., U.S. Fish and Wildlife Service, 2022) and duck hunter days afield and active hunter abundance from annual surveys of hunters (e.g., Raftovich et al., 2022), we predicted the effect of reductions in duck abundance resulting from the four scenarios representing losses in wetland habitat. The number of duck pairs lost in each of these four scenarios of wetland habitat loss was multiplied by two to obtain the total number of ducks lost due to wetland habitat loss. The number of ducks lost was subtracted from the number of ducks in 2016, the baseline year.

#### 2.8. Recreation economics: modeling hunting-related effects

The most parsimonious model describing patterns in duck hunter days afield and active number of duck hunters was then used to predict the effect of changes in these variables on hunter expenditures and consumer surplus. Economic activity associated with hunting and viewing can be described in two ways (Mattsson et al., 2018). Expenditures are the amount spent on items associated with hunting and viewing activity, including travel-related costs, such as lodging, fuel, and meals, as well as equipment, such as firearms, ammunition, clothing, decoys, spotting scopes, and binoculars. Consumer surplus is the difference between the price a consumer pays for an item and the price they would be willing to pay rather than do without it. We calculated losses in expenditures and consumer surplus due to changes in the amount of time hunters spent in the field as well as from changes in the number of hunters expected to hunt. The U.S. Fish and Wildlife Service Survey of Hunting, Fishing, and Wildlife Associated Recreation (2016b) indicated that, per capita, duck hunters spent \$546 per year during 7.54 days afield, yielding \$72.44 per day afield; consumer surplus was 38.8 % higher in the Central Flyway (\$58.66/day) compared to the Mississippi Flyway (\$42.26/day) (note: more than four decades ago, Charbonneau and Hay, 1978 estimated a consumer surplus equivalent to an inflation-adjusted value of \$75.53).

#### 2.9. Recreation economics: viewing-related economic impact

Unlike duck hunting, which has been extensively studied and is annually surveyed in the United States, there are comparatively fewer studies and no lengthy surveys of waterfowl viewing. Loomis et al. (2018) reported results of a willingness-to-pay survey of Ducks Unlimited members that described the annual number of trips to view waterfowl (1.99 and 2.40 for Central and Mississippi Flyway respondents, respectively) and the expenses willing to be incurred per trip (\$27.96 and \$120.04, respectively) for viewing waterfowl at current levels of abundance (Appendix D). We assumed Ducks Unlimited members surveyed by Loomis et al. (2018) represented the interests of birders interested in viewing waterfowl. Crucially, the survey also asked respondents how many trips and how much they would be willing to expend per trip if waterfowl abundance was doubled (Appendix D). There were 34 and 12 responses from respondents in the Central and Mississippi Flyway states, respectively. Because of the low number of responses in the Mississippi Flyway, we calculated the geometric mean number of trips per birder and the expenses per trip to guard against outlier responses. We associated the number of birders by state as determined by the U.S. Fish and Wildlife Service (Table 6 of Carver, 2013; Appendix E) to each flyway; we made this attribution even though the Central flyway bisects the westernmost states in the flyway along the Rocky Mountain divide. In R, with the rebird package (Maia and Chamberlain, 2021), we extracted observations for the 12 focal duck species from the eBird data repository (eBird, 2021) for 2014 (the year coincident with the Ducks Unlimited survey) from each state within the Central and Mississippi Flyways. We calculated the flyway-specific proportion of focal ducks as the proportion of focal duck observations among all birds reported in eBird in the Central and Mississippi Flyways. With these values in hand, we used the following equation to estimate total viewing expenditures for ducks at their current and double current abundance in each flyway:

```
Total viewing expenditures = number of birders (n) × number of trips per birder (\text{trips}/n) × expenses per trip (\$/\text{trip}) × eBird focal duck proportion
```

where number of trips per birder is the only variable changing between viewing expenditures at current and double abundance. The focal duck proportion is the proportion of eBird observations comprised of the 12 waterfowl species included in our study.

For each flyway, we calculated the slope,  $\beta$  (\$/duck), between the current and double abundance level of expenditures to establish how economic value changes with waterfowl abundance for use in estimating the economic loss associated with decreasing abundance:

```
\beta = \text{(Viewing expenses at double current abundance} \\ - \text{Viewing expenses at current abundance)/((2 \times Breeding Population}_{2014})} \\ - (1 \times Breeding Population}_{2014}))
```

where the total duck breeding population (12 focal species plus black duck [An. rubripes], goldeneye [Bucephala clangula], and bufflehead [B. albeola]) in 2014 was 49,152,200. The last step was to then calculate the total loss in viewing expenditures by flyway corresponding with loss in wetlands according to the scenarios using the following equation (2014\$):

```
Change in viewing expenditures = (Duck abundance under scenario i
-Duck abundance at baseline) × flyway – specific \beta
×flyway – specific proportion of ducks × 0.9147.
```

We decremented this change in viewing expenditures by 0.9147 because not all of the ducks originating in the U.S. PPR BPOP migrates to the Central and Mississippi Flyways; band encounter information indicated 91.47 % of the focal ducks banded in the U.S. PPR were recovered in the Central and Mississippi Flyways BPOP (of which 22.67 % were in

Table 2 Parameter estimates (and 95 % confidence intervals) for the most parsimonious model describing variation in duck hunter days afield. To allow better comparison among covariate parameter estimates, estimates for an equivalent model with scaled covariates are provided. BPOP is the breeding population of ducks, in millions of ducks. Method is the type of survey of hunter behavior (MQS = 0, HIP = 1).

Predictor	Estimate	95 % CI	Scaled Estimate	Scaled 95 % CI	t	p
Intercept	-45.06	-69.48 to -20.64	8.13	7.96-8.31	-3.66	< 0.001
BPOP	0.20	0.15-0.26	0.68	0.49-0.86	7.32	< 0.001
Method	184.31	125.53-243.08	-1.29	-1.87 to $-0.70$	6.22	< 0.001
Year	0.03	0.01-0.04	0.47	0.25-0.69	4.17	< 0.001
Flyway [relative to Mississippi Flyway]	-65.58	-87.02 to -44.14	0.82	0.64-1.01	-6.06	< 0.001
$BPOP \times Method$	-0.13	-0.21 to $-0.05$	-0.44	-0.70 to $-0.18$	-3.34	0.001
$Year \times Method$	-0.09	-0.12 to $-0.06$	-1.67	-2.20 to $-1.14$	-6.26	< 0.001
$Year \times Flyway \ [relative \ to \ Mississippi \ Flyway]$	0.03	0.02-0.04	0.60	0.41-0.79	6.15	< 0.001

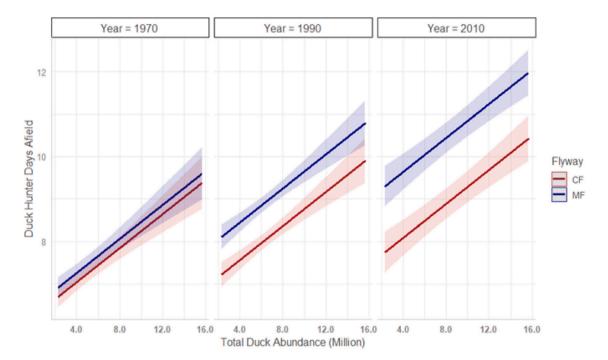


Fig. 2. Estimated duck hunter days afield for three representative years in the Central Flyway (CF) and Mississippi Flyway (MF) as a function of the abundance of 12 duck species breeding in the Prairie Pothole Region of the United States.

the Central Flyway and 68.8 % were in the Mississippi Flyway). All dollar values are ca. 2014, with inflation adjustment as necessary (https://www.bls.gov/data/inflation\_calculator.htm). Data and analysis code are available at Thogmartin et al. (2023).

#### 3. Results

#### 3.1. Reduced number of duck breeding pairs

Based on our scenarios of isolated wetland loss in the U.S. PPR, we estimated this would result in 146,622 (Low), 401,688 (Medium-Low), 717,306 (Medium-High), and 887,696 (High) fewer duck pairs. These losses represent changes of about -2.6 %, -7.1 %, -12.6 %, and -15.6% in the estimated total breeding population of the region (equivalent to

**Table 3**Parameter estimates (and 95 % confidence intervals) for the most parsimonious model describing variation in the annual log number of duck hunters. To allow better comparison among covariate parameter estimates, estimates for an equivalent model with scaled covariates are provided. BPOP is in millions of ducks.

Predictor	Estimate	95 % CI	Scaled estimate	Scaled 95 % CI	t	p
Intercept	12.01	11.91-12.10	12.14	12.05-12.23	246.29	< 0.001
BPOP	0.02	0.01-0.03	0.06	0.03-0.09	3.988	< 0.001
Year (knot 1)	-0.02	-0.13 - 0.09	-0.02	-0.13 - 0.09	-0.38	0.707
Year (knot 2)	0.02	-0.11 - 0.15	0.02	-0.11 - 0.15	0.28	0.783
Year (knot 3)	0.79	0.57-1.02	0.79	0.57 - 1.02	6.93	< 0.001
Year 4 (knot 4)	-0.73	-0.85 to $-0.61$	-0.73	-0.85 to $-0.61$	-12.10	< 0.001
Flyway [relative to Mississippi Flyway]	2.14	-2.64 - 6.92	0.82	0.78-0.86	17.07	0.382
$Year \times Flyway \ [relative \ to \ Mississippi \ Flyway]$	-0.0007	-0.003 – 0.002	-0.01	-0.05 - 0.03	50.99	0.588

a loss of 2.42 breeding pairs per hectare of wetland area lost).

#### 3.2. Duck hunter days afield

Eleven models of increasing complexity were evaluated for understanding patterns in duck hunter days afield (Appendix B). The model minimizing AICc, explaining 83 % of the variation in duck hunter days afield, was a function of duck abundance interacting with method (MQS vs HIP) of data collection (Method  $\times$  BPOP), a year effect interacting with method of data collection (Method  $\times$  Year) plus an interaction of year and flyway (Flyway  $\times$  Year) (Table 2). The interactions of the main effects were as influential as the main effects themselves. The most important effect on duck hunter days afield was duck population size. This model controlled for a temporal difference in duck abundance as reported in the duck hunter surveys (Method) as well as allowed for patterns in duck hunter days afield to differ by year and flyway (Fig. 2).

In our baseline year (2016), duck hunter days afield differed between flyways; hunters in the Central Flyway (8.89 days afield; 95 % Confidence Interval [CI]: 8.47–9.32) spent roughly 19 % fewer days afield than hunters in the Mississippi Flyway (10.64; 95 % CI: 10.22–11.07). The best model indicated duck hunter days afield would decline  $\sim\!2$  % between the baseline and the highest predicted wetland loss ( $\sim\!0.13$  days).

#### 3.3. Number of active duck hunters

The method by which duck hunter participation was measured (Method, HIP or MQS) did not affect annual estimates of the number of duck hunters. This difference in results led to fewer (n=8) and less complex models than the analysis of hunter days afield (Appendix B). The model minimizing AICc, explaining 97 % of the variation in annual number of active duck hunters, was a function of the annual abundance

of the 12 duck species, year, and flyway, with year and flyway interacting (Table 3). Year had the largest effect on the number of duck hunters, followed by the interaction of year and flyway. Duck population size had the smallest effect, but still substantially affected the number of duck hunters (Fig. 3).

At a U.S. PPR total breeding duck population size of 9.2 million ducks (the survey-estimated abundance for 2016), 177,000 (95 % CI: 166000-187,000) and 404,000 (95 % CI: 381000-429,000) active duck hunters were predicted for the Central and Mississippi Flyways, respectively. Under the highest predicted wetland loss, the best model predicted about 12,000 and 6000 fewer duck hunters in the Mississippi and Central Flyways, respectively (Table 4).

#### 3.4. Hunting-related economic impact

Because duck hunters in the Mississippi Flyway were predicted to spend 19.6 % (i.e., 1.75 days) longer hunting than those in the Central Flyway, their expenditures were also expected to be commensurately higher (\$771.05 per Mississippi Flyway hunter trip, 95 % CI: \$740.26–801.85 versus \$644.03 per Central Flyway hunter trip, 95 % CI: \$613.24–674.83). However, because the daily consumer surplus of duck hunters in the Central Flyway was 38.8 % higher than the daily consumer surplus of duck hunters in the Mississippi Flyway, the per-trip consumer surplus overcame the flyway-level difference in duck hunter days afield (\$521.53 per Central Flyway hunter trip, 95 % CI: \$496.59–546.47 versus \$449.83 per Mississippi Flyway hunter trip, 95 % CI: \$431.86–467.79).

Under scenarios of wetland loss, expected reductions in both the time duck hunters spent afield and the number actively participating in hunting led to increasing losses in both consumer surplus and expenditures as wetland area loss increased (Table 4, Fig. 4). Total annual economic impact from changes to hunter numbers and activity ranged

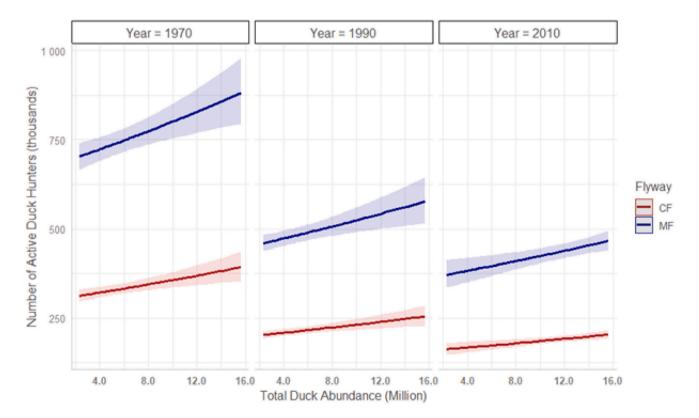


Fig. 3. Estimated number of active duck hunters for three representative years in the Central Flyway (CF) and Mississippi Flyway (MF) as a function of the abundance of 12 duck species breeding in the Prairie Pothole Region of the United States.

Table 4
Scenarios of wetland loss in the U.S. portion of the Prairie Pothole Region and associated change in days afield and number of active hunters, and associated losses in consumer surplus (CS) and expenditures (EX), with 95 % confidence intervals presented parenthetically. Number of active hunters, CS, and EX are expressed in thousands. Dollars (1000\$) are ca. 2016.

Scenario	Days afield			Active hunters	Active hunters					
	Days afield	CS (\$)	EX (\$)	Active hunters	CS (\$)	EX (\$)	Sum (\$)			
Mississippi										
Baseline	7.04	0	0	404	0	0	0			
	(6.02, 8.06)	(0,0)	(0, 0)	(325, 502)	(0, 0)	(0, 0)	(0, 0)			
Low	7.02	344	590	402	929	1592	3454			
	(6.00, 8.04)	(342, 346)	(586, 593)	(323, 500)	(738, 1168)	(1265, 2002)	(2931, 4110)			
Medium-Low	6.98	942	1615	398	2533	4342	9432			
	(5.96, 8.00)	(938, 947)	(1608, 1623)	(321, 495)	(2024, 3169)	(3469, 5433)	(8063, 11,148)			
Medium-High	6.94	1683	2885	394	4498	7710	16,776			
	(5.92, 7.96)	(1652, 1714)	(2832, 2937)	(317, 490)	(3618, 5592)	(6202, 9585)	(14,472, 19,661)			
High	6.91	2082	3570	392	5550	9514	20,716			
	(5.89, 7.94)	(2029, 2136)	(3478, 3661)	(315, 487)	(4481, 6875)	(7680, 11,785)	(17,958, 24,167)			
Central										
Baseline	5.29	0	0	182	0	0	0			
	(4.27, 6.30)	(0, 0)	(0, 0)	(146, 226)	(0, 0)	(0, 0)	(0, 0)			
Low	5.27	240	297	181	484	598	1619			
	(4.25, 6.28)	(239, 242)	(295, 299)	(145, 225)	(385, 609)	(475, 752)	(1394, 1902)			
Medium-Low	5.23	658	813	179	1321	1631	4422			
	(4.21, 6.25)	(655, 661)	(809, 813)	(144, 223)	(1055, 1652)	(1303, 2041)	(3836, 5157)			
Medium-High	5.19	1176	1452	177	2345	2896	7868			
	(4.17, 6.20)	(1154, 1197)	(1425, 1478)	(143, 220)	(1887, 2915)	(2330, 3600)	(6891, 9095)			
High	5.16	1455	1796	176	2894	3573	9718			
	(4.14, 6.18)	(1418, 1492)	(1751, 1842)	(142, 219)	(2336, 3584)	(2885, 4426)	(8555, 11,179)			

from \$3.5 million to \$20.7 million in the Mississippi Flyway and \$1.6 million to \$9.7 million in the Central Flyway, across the range of predicted wetland losses. Total annual losses across both flyways, therefore, ranged from \$5.1 million to \$30.4 million. Losses in both consumer surplus and expenditures due to reductions in active hunters were, in the Mississippi and Central Flyways, respectively,  $\sim\!\!2.7$  and  $\sim\!2.0$  times greater than losses due to reductions in duck hunter days afield. Economic impact was  $\sim\!\!1.4$  to 2.7 times greater in the Mississippi Flyway compared to the Central Flyway, depending on the magnitude of wetland loss.

#### 3.5. Viewing-related economic impact

Duck enthusiasts suggested they will increase the number of trips they take by  $\sim 3-4$  times over their current number if the waterfowl population was doubled (Loomis et al., 2018; Fig. 5; Appendix C). Furthermore, they suggested they will increase the amount they expend by 25–50 % per trip if the waterfowl population was doubled (Loomis et al., 2018). These effects act multiplicatively. For instance, Central Flyway duck enthusiasts claimed to expend \$55.64 per year viewing waterfowl (1.99 trips  $\times$  \$27.96 per trip); if the waterfowl population was doubled, they claimed to be willing to expend \$244.17 (5.63 trips  $\times$  \$43.37 per trip), >4 times as much. For Mississippi Flyway duck enthusiasts, these values go from \$288.10 (2.40 trips  $\times$  \$120.04 per trip) at current waterfowl abundance to \$1600.32 (10.31 trips  $\times$  \$155.22 per trip), >5.5 times as much, when doubling the waterfowl population.

In the Central Flyway in 2014, there were 667,166 observations of the 12 focal duck species out of 11,281,367 total birds reported to eBird (5.9 %), whereas in the Mississippi Flyway, there were 1,105,560 duck observations out of 9,344,824 total birds reported to eBird (11.8 %). These fractions were then used to help apportion the economics of all birding to just the fraction attributable to waterfowl.

Viewing expenditures ranged from  $\sim$ \$21 million to \$529 million between the two flyways and would be expected to increase to \$91 million and \$2.9 billion, respectively, if waterfowl abundance were doubled (Table 5). The large difference between flyways in the estimated viewing expenditures occurred because the Mississippi Flyway had 2.5 times as many birders and 2 times the proportion of waterfowl

reported to eBird.

The total breeding population of waterfowl in 2014 was 49,152,200 (U.S. Fish and Wildlife Service, 2022). Thus, the slopes were \$1.43 per duck in the Central Flyway and \$49.08 per duck in the Mississippi Flyway (the Mississippi Flyway is 34 times greater). Therefore, per habitat loss scenario, losses ranged from \$803,295 in the low habitat loss scenario for the Central Flyway to \$447 million lost in the high habitat loss scenario for the Mississippi Flyway (Table 6). The difference between flyways in the expected lost economics is vast, nearly 2 orders of magnitude greater for Mississippi Flyway losses compared to Central Flyway losses for all loss scenarios.

#### 3.6. Total economic loss

The PPR habitat loss scenarios we examined would be expected to lead to combined annual hunting and viewing economic losses totaling between  $\sim\!\!\$2.5$  million and \$474 million depending on the magnitude of habitat lost and the flyway affected (Table 7, Fig. 4e). Losses in the Mississippi Flyway (\$78.3-473.7 million) were considerably larger than those for the Central Flyway (\$2.5-15.1 million). Viewing losses were 20 times as great as hunting-related losses in the Mississippi Flyway whereas in the Central Flyway, hunting-related losses were 2 times greater than viewing losses. Across all scenarios and both flyways, isolated wetland loss causes an average economic impact of \$1351.29 per hectare per year to recreational hunters and viewers.

#### 4. Discussion

Our simulations revealed large economic effects from forecasted losses of breeding habitat for migratory waterfowl under several plausible land-change scenarios in the U.S. portion of the PPR. Decreases in wetland habitat area in the U.S. PPR, and resultant lowered duck abundances, were predicted to lead to a reduction in the number of waterfowl hunters and birders in the Mississippi and Central Flyways, as well as in the amount of time spent in pursuit of those activities. As expected, based on the models of Cowardin et al. (1995) and the disproportionate contribution of small wetland basins prone to loss, the relative loss of waterfowl carrying capacity was greater than the relative

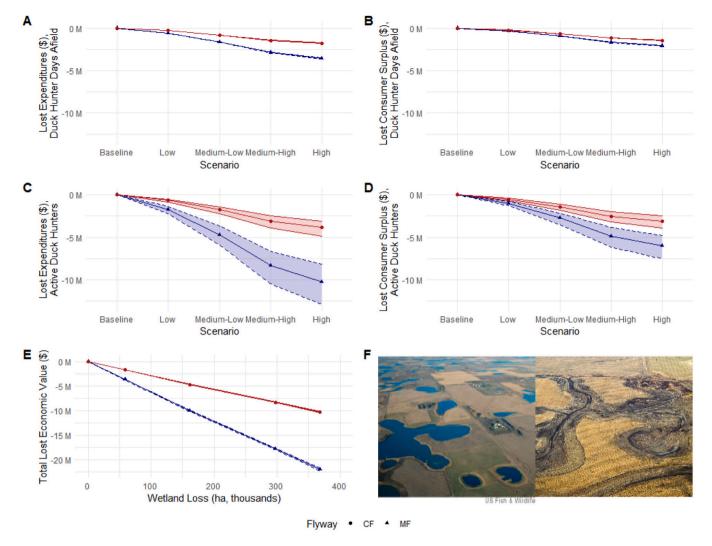


Fig. 4. Predicted effects of wetland loss in the U.S. portion of the Prairie Pothole Region on duck hunter expenditures and consumer surplus, by duck hunter days afield (A and B, respectively) and active number of duck hunters (C and D, respectively), in the Central and Mississippi Flyways. Total lost economic value among these four sources is depicted in panel D, whereas panel F depicts extant (left) and drained (right) wetlands embedded in the agricultural matrix of the Prairie Pothole region. Image sources: https://www.climatehotmap.org/global-warming-locations/prairie-pothole-region-sd-usa.html and https://www.ducks.ca/places/prairie-pothole-region/.

loss of wetland area. The loss of 18,000 hunters was predicted under the highest wetland loss scenario, amounting to 3 % fewer hunters compared to baseline; in turn, fewer hunters and reduced activity by those continuing to hunt would be expected to lead to annual economic losses of as much as \$30 million per year. Similarly, we predicted losses of as much as \$447 million per year in reduced economic activity associated with waterfowl viewing.

Declines in participation and economic activity differed between regions and types of recreation activity. There were substantial differences in the ratio of expected hunting-related losses to viewing-related losses between regions, with the Central Flyway states dominated by hunting-related losses (>20:1) whereas the Mississippi Flyway states were much in favor of viewing-related losses (>2:1). This difference may be related to a rural:urban difference in population distribution between regions insofar as the Mississippi Flyway has more people and is more urbanized than the Central Flyway (e.g., Seager et al., 2018).

Previous research has examined economic consequences of changing waterfowl hunter numbers (Grado et al., 2011; Mattsson et al., 2020). Based on equations describing probability of hunter participation, Miller and Hay (1981) indicated that a reduction in duck hunting resulting from the loss of an equivalent amount of habitat as in our high wetland

loss scenario, but in wintering habitat in the Mississippi flyway, would lead to (inflation-adjusted) losses of \$96 million, which is almost four times as great as we estimated for an equal amount of lost breeding habitat in the U.S. PPR. Vrtiska et al. (2013) reported a weakening of the relationship between the duck breeding population and duck stamp sales, their proxy to hunting participation; we found a similar weakening, with the slope of the relationship declining over time (Fig. 3).

Our analyses expand on this work in two important ways. First, we included overall expenditures and consumer surplus when describing variation in hunter economics caused by changes in hunter participation. These analyses are more granular than Vrtiska et al. (2013) in that, in addition to numbers of duck hunters, we estimated, similar to Miller and Hay (1981), the effort hunters put into hunting. Second, although we provide inference regarding the relationship between stakeholder participation and recreational economics (including duck stamps), importantly, our analyses take this one step further and identify how these elements react to changes in duck abundance as mediated by conversion to agriculture.

Our analyses are premised on the assumption that reductions in duck abundance lead to reductions in duck hunter numbers and participation as well as reduced birding activity. For instance, attributes determining

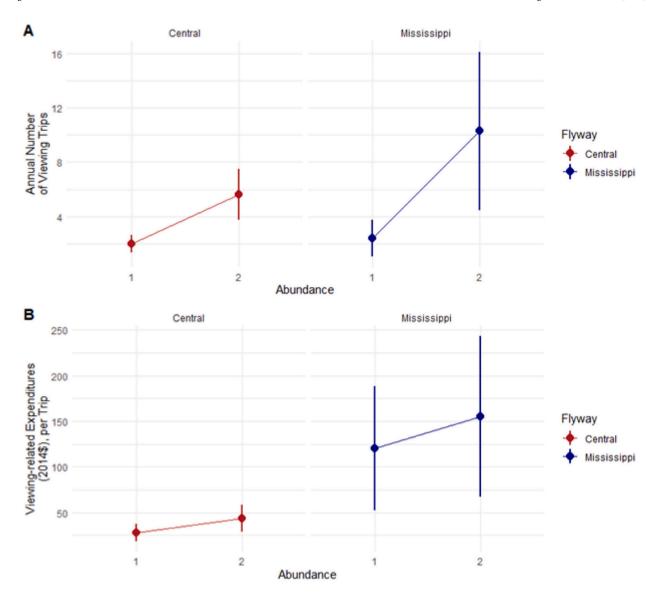


Fig. 5. Annual number of trips and per-trip viewing-related expenditures based on willingness-to-pay surveys of Ducks Unlimited members, by Central and Mississippi Flyways, for current (1) and double (2) abundance of waterfowl (see Appendix D for tabular results).

Table 5

Total number of birders (ca. 2014), number of trips and expenses per trip, proportion of waterfowl among all birds observed as reported to eBird, and estimated total viewing expenditures, by flyway, at current and double levels of waterfowl abundance.

Flyway	Abundance	Number of birders	Number of trips	Expenses per trip (\$)	Proportion waterfowl	Total viewing expenditures (\$)
Central	Current	6,306,000	1.99	27.96	0.0591	20,714,425
Mississippi	Current	15,538,000	2.40	120.04	0.1183	529,300,995
Central	Double	6,306,000	5.63	43.37	0.0591	91,083,692
Mississippi	Double	15,538,000	10.31	155.22	0.1183	2,941,879,418

satisfaction among waterfowl hunters usually include both seeing and successfully harvesting ducks (e.g., Miller and Hay, 1981; Bradshaw et al., 2019; Schroeder et al., 2019; Gruntorad et al., 2020). Empirical support for the relationships we drew between historical patterns in hunting participation and duck abundance is vast, due to annual surveys estimating duck abundance (e.g., May waterfowl surveys), hunter numbers and hunting effort (Martin and Carney, 1977; Elden et al., 2002; U.S. Fish and Wildlife Service, 2016b), and banding programs that provide bird encounters by hunters and other individuals. Thus, the hunting economic inferences drawn from our results are robust.

In contrast, surveys of viewers of waterfowl, their expenditures, and

other aspects of their birding activities are not as extensive and/or have been in place for much fewer years. Therefore, we have less confidence in our inferences regarding economic impacts associated with viewing activity, having inferred the relationship between activity and abundance only from a small survey of waterfowl enthusiasts (Loomis et al., 2018) and over a narrow period of time. Based on this survey, waterfowl viewers would take 3.64 (Central Flyway; 1.99 at baseline versus 5.63 under double duck abundance) to 7.89 (Mississippi Flyway; 2.40 versus 10.31) more trips per year if the number of ducks was doubled (Fig. 5a). These quantities were crucial, because they allowed us to estimate the change in number of trips as a function of duck abundance. This

**Table 6**Annual total lost viewing expenditures and consumer surplus, by flyway, for each habitat loss scenario.

Lost viewing economics (\$)								
Loss scenario	Central Flyway	$\%$ $\Delta$ from Baseline	Mississippi Flyway	$\%$ $\Delta$ from Baseline				
Low	803,295	-3.88	73,815,549	-13.95				
Medium- Low	2,200,719	-10.62	202,226,271	-38.21				
Medium- High	3,929,889	-18.97	361,121,362	-68.23				
High	4,863,401	-23.48	446,902,701	-84.43				

**Table 7**Annual hunting-related and viewing economics lost in the Central and Mississippi Flyways under various Prairie Pothole Region habitat loss scenarios.

Flyway	Loss scenario	Lost hunting- related economics (2014\$)	Lost viewing- related economics (2014 \$)	Grand total losses (2014\$)
Mississippi	Low	3,657,999	74,618,844	78,276,843
	Medium-	9,985,600	204,426,991	214,412,591
	Low			
	Medium-	17,752,790	365,051,252	382,804,042
	High			
	High	21,917,499	451,766,102	473,683,601
Central	Low	1,706,634	803,295	2,509,929
	Medium-	4,660,103	2,200,719	6,860,822
	Low			
	Medium-	8,287,858	3,929,889	12,217,747
	High			
	High	10,234,109	4,863,401	15,097,510

approach however required extrapolation beyond the range of observation to infer the economic impact of reduced duck abundance. Other studies have only asked birders how many trips an individual may take over a specified time period. Eubanks et al. (2004), for instance, characterized differences among birders in their level of engagement and reported considerably higher numbers of annual birding trips (4.5–14.1 trips per year) than Loomis et al. (2018). If the estimated slope between trips and duck abundance from Loomis et al. (2018) held true but at the higher levels of trips reported by Eubanks et al. (2004), the estimated value of viewing-related losses could increase by 2- to 7-fold over what we report here.

We acknowledge that the proportion of focal duck species among eBird records served only as a proxy for the actual allocation of expenditures for viewing focal and non-focal species. Birders vary in the types of species that draw their interests (e.g., Laney et al., 2021), but Scher and Clark (2023) recently found birders submitting their observations to eBird reported species breeding in coastal and wetland habitats more than would be expected. Lee et al. (2010) reported that birders expressed interest in seeing large aggregations of birds, supporting the notion that this interest could wane with declines in waterfowl flocks. Recent surveys of birders in the Central and Mississippi Flyways indicated that in addition to seeing abundant (i.e., thousands of) birds and seeing them in a natural setting, viewing waterfowl and wetland birds had some of the highest utilities when birders were presented with discrete choices in their birding preferences (Slagle and Dietsch, 2018a, 2018b). Results from a mail questionnaire of sandhill crane (Grus canadensis) watchers reported similar results, with viewers reporting less value with declines in crane abundance and, therefore, decreased recreational activity (Stoll et al., 2006). Aside from Loomis et al. (2018), though, we know of no study attempting to quantify the relationship between waterfowl abundance and birder participation/effort. The effect of such bias on recreational viewing economics is not immediately obvious.

There are reasons, however, to believe the estimates of viewing activity and the amount expected to be lost are correct within an order-ofmagnitude. Wildlife-watching expenditures were estimated at \$75.9 billion, approximately three times that expended by hunters (U.S. Fish and Wildlife Service, 2016b). Our viewing expenditures for waterfowl for the Central and Mississippi flyways comprises <1 % of this total. Proportionally, our estimated viewing losses resulting from wetland losses are similar in magnitude for the Central Flyway (e.g., 1.91 % wetland loss versus 3.88 % fewer total expenditures in the lowest habitat loss scenario). The magnitude of predicted losses is proportionally greater for the Mississippi Flyway, with a 12 % loss of PPR wetlands leading to 887,696 fewer ducks, causing an 84 % reduction in waterfowl viewing in the Mississippi Flyway. If we were to presume that losses in the Mississippi Flyway mirrored those in the Central Flyway, expected losses would be \$20 million (low loss scenario) to \$100 million (high loss scenario) less than we reported. The principal cause of uncertainty lies with how birding effort and the resultant economic value of waterfowl viewing relates to duck abundance. On a per-duck basis, waterfowl viewers in the Central Flyway expressed a value of \$1.43 per duck whereas in the Mississippi Flyway it was \$49.08 per duck. This large difference, if true, highlights spatially divergent consequences from losses of breeding habitat for the economics of viewing on the wintering grounds. Clearly, more research to obtain information on birder effort and expenditures relative to bird abundance would be useful to better estimate economic consequences of declining bird abundance.

There is at present considerable controversy relating to the Waters of the United States rule (Sullivan et al., 2019; Keiser et al., 2022). Geographically isolated wetlands such as those we examined in the U.S. PPR could be drained and converted to agriculture because geographically isolated wetlands were determined not to be covered under WOTUS (Sackett et ux. v. Environmental Protection Agency et al., 2023). Our work indicates this change could result in the potential loss of as many as 1.8 million ducks ( $\sim$ 3.7 % of 2014 breeding population, U. S. Fish and Wildlife Service, 2022) and considerable reduction in hunter and birder participation, leading to as much as \$488 million less annual economic activity. This lowered participation would be expected to have large consequences within this coupled human and natural system given the role duck stamps play in supporting wildlife habitat preservation and restoration (Mattsson et al., 2020). The annual loss of \$5.1 million to \$30.4 million associated with reduced participation in waterfowl hunting translates to a cost of \$83 per hectare of wetland lost. Similarly, viewing-related losses translate to a cost of \$1226 per hectare of wetland lost. This loss of economic activity from reduced hunter and birder participation would, however, be offset to some degree by increased agricultural output (Rashford et al., 2011); for example, for the high loss scenario of wetland loss (368,423 ha) we examined, assuming ca. 2014 corn yield of 124 bushels/acre and a 2014 corn price of \$3.34/bushel, could return \$377 million, approximately 3/4 of the recreational loss. The combined per-hectare recreational losses, >\$1326, are approximately 28 % greater than the return expected from corn agriculture. Even if the value of increased agricultural yield was equivalent to that lost from reduced recreation, converting isolated wetlands to agriculture would concentrate economic activity currently distributed across the continent to the footprint of the PPR. Our analyses did not consider additional economic impacts associated with declines in outdoor recreation in the health and tourism sectors (e.g., Winter et al., 2019), economic effects in the Pacific and Atlantic Flyways and in Canada and Mexico, declines in the populations of other species dependent upon wetland habitat, nor the loss of other ecosystem services such as carbon sequestration, groundwater recharge, sediment retention, pollination services, or flood regulation (e.g., Gascoigne et al., 2011). As a result, our estimates of economic impacts are highly conservative. They are also consistent with numerous previous studies; for example, a synthesis of 320 publications on ecosystem valuation found the average value of inland wetlands to be 2014\$29,109/ha, with recreation comprising \$2506 of that value (de

#### Groot et al., 2012).

Our predictions of the consequences of wetland conversion to cropland in the U.S. PPR also does not account for potential effects of climate change (Johnson et al., 2005) or shifts in U.S. agricultural policy (Westcott, 1993). North American duck populations have historically fluctuated with the drought and deluge climate cycle typical of the northern Great Plains. Wetland losses in the region, however, represent a long-term change to the carrying and productive capacities for waterfowl in the region. Loss of wetland habitat essentially creates permanent drought conditions by altering local hydrology. Continued wetland loss is likely to further complicate and increase the predicted effects of climate change in much of the region (Sorenson et al., 1998; Johnson et al., 2010; Sofaer et al., 2016; Zhang et al., 2021). Recent ensembles of global climate change projections indicate the PPR will be  $\sim$ 5 °C warmer and have 10–15 % more mean annual precipitation, with more warming (Bukovsky and Mearns, 2020) and seasonal accumulated precipitation (Zhang et al., 2020) to the east than the west. These climatic changes are likely to affect wetland dynamics (Cressey et al., 2016; Zhang et al., 2021), possibly reducing the number of wetlands (Sofaer et al., 2016; McKenna et al., 2019) and some populations of waterfowl (Zhao et al., 2016, 2019). Bioeconomic modeling and optimization in the PPR of western Canada indicates climate change may reduce the optimal number of wetlands from 5 to 38 % depending on the climate scenario used (Withey and van Kooten, 2011), which would be expected to have important consequences to waterfowl populations. Thus, irrespective of changing land use, climate change may yield similar or even greater consequences to waterfowl recreational economics than we estimated.

In conclusion, our analyses indicate effects of ecoregion-scale policies likely have far-reaching consequences for duck populations and associated economics. These consequences depend on many factors, including national water policies, global and national agricultural economic drivers of crop expansion, and demographics of transcontinental avian migration. Reductions in habitat in one location have economic consequences throughout the continent via connections fostered by

migrating waterfowl. Our work quantifies, for the first time, distant effects of potential habitat modifications on multiple stakeholder groups whose activities center around migratory species. These possible economic effects were heretofore unclear because of the great distance between the stakeholders affected and the modified habitats. Recognizing the distant effects of local action can help inform conservation planning aimed at maximizing satisfaction among all parties involved.

#### CRediT authorship contribution statement

No generative AI or AI-assisted technologies were used in creation of this manuscript. All text was conceived and written by the authors.

#### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

#### Data availability

Code and data are available from ScienceBase.

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#### Appendix A. Explanation of difference between MQS and HIP

Each year, the U.S. Fish and Wildlife Service (Service) conducts surveys of hunters to estimate annual waterfowl harvest and hunter participation in the United States. All waterfowl hunters are required to purchase a federal Migratory Bird Hunting and Conservation Stamp (i.e., "Duck Stamp") to legally hunt waterfowl (i.e., ducks, geese, swans, and coots). Beginning in 1962, the Service used information from contact cards filled out by Duck Stamp purchasers to conduct surveys of hunters wherein they estimated total harvests of waterfowl, total number of waterfowl hunters, the number of days spent afield by hunters, and other harvest and hunter effort metrics. This survey was called the Mail Questionnaire Survey, or MQS (Martin and Carney, 1977). Using information on post office location where hunters purchased the stamps, the Service could obtain finer-grained estimates (e.g., flyway-wide and state-level estimates). However, this process allowed the estimation of metrics only for waterfowl hunters. Many other species of game birds are harvested (e.g., doves, woodcock, cranes), and harvest information is needed for appropriate management of those species as well. Although states often conducted their own harvest surveys for these species, methods varied among states. Therefore, estimates from the states were not always comparable and could not reliably be pooled to generate overall harvest estimates for the country.

In response to this concern, the Service and state wildlife agencies worked collaboratively to develop an alternative survey beginning in 1992 but fully implemented by 1998 that would include information allowing estimation of harvest and hunter effort for all migratory game bird species, the Harvest Information Program (HIP; Elden et al., 2002, Ver Steeg and Elden, 2002). Instead of using Duck Stamps as the basis for sample frames, hunters in each state are required to register in their state's HIP, whereby the hunter includes their contact information as well as the species of migratory birds they intend to hunt during the upcoming hunting season. The states share that information with the Service, which then selects guild-specific (e.g., ducks, doves, sandhill cranes) samples from the universe of migratory bird hunters in each state to survey. The Service generates report each year that provides estimates for metrics essentially the same as under the MQS, but for all species of migratory game birds.

However, due to the differences in methodology between the MQS and the HIP, managers were concerned whether the estimates from each process would be comparable, allowing all estimates in the historic and future time series to be used similarly. To address this concern, the Service decided to conduct the MQS survey for an additional three years once the HIP was fully operational (i.e., 1999, 2000, and 2001) so that waterfowl harvest estimates between the two methods could be compared. Results indicated that at a large scale (i.e., national level), duck harvest estimates from the two methods were not different (Padding and Royle, 2012).

Appendix B. Models, ordered by the small-sample Akaike's Information Criterion (AICc) weight ( $\omega$ ), describing effects of covariates on (A) duck hunter days afield and (B) active number of duck hunters. The explained variation ( $R^2$ ) is adjusted for sample size; when two values are shown, the first represents the total explained variation, and the second represents the marginal effect of the covariates alone (minus the random effect). BPOP is the breeding duck population

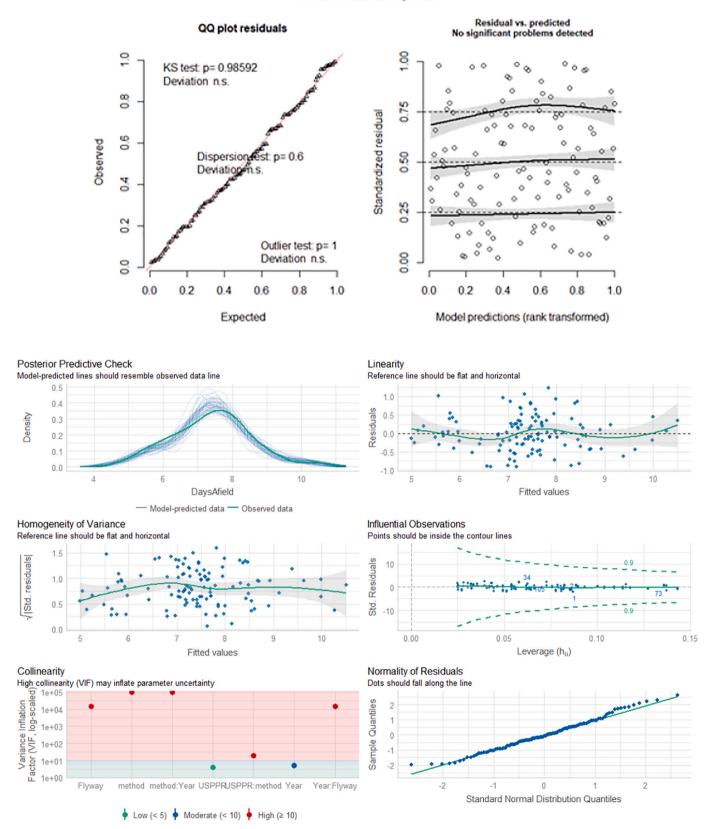
Model	Covariates	df	logLik	AICc	$\Delta \text{AICc}$	ω	$R^2$
A) Duck Hunter Da	nys Afield						
8	Flyway $\times$ Year, Method $\times$ BPOP, Method $\times$ Year	9	-77.71	175.12	0.00	0.708	0.83
9	Flyway $\times$ Year, Method $\times$ BPOP, Method $\times$ Year, Flyway $\times$ Method, Flyway $\times$ Method $\times$ Year	11	-76.18	176.90	1.77	0.292	0.83
11 <sup>(9</sup> with spline on Year)	Year spline, Flyway $\times$ Year, Method $\times$ BPOP, Method $\times$ Year, Flyway $\times$ Method, Flyway $\times$ Method $\times$ Year	8	-105.09	227.66	52.54	0	0.72
10* <sup>(9</sup> with Year random)	Year random, Flyway $\times$ Year, Method $\times$ BPOP, Method $\times$ Year, Flyway $\times$ Method, Flyway $\times$ Method $\times$ Year	12	-116.14	259.31	84.19	0	0.94/ 0.83
6* <sup>(4 with Year</sup> random)	BPOP, Year random, Flyway $\times$ Year	7	-142.80	300.64	125.52	0	0.93/ 0.26
7* <sup>(5 with year</sup> random)	Year random, Flyway $\times$ Year, Flyway $\times$ BPOP	8	-159.34	336.02	160.90	0	0.93/ 0.26
4	BPOP, Flyway $\times$ Year	6	-164.46	341.69	166.57	0	0.25
5	Flyway $\times$ Year, Flyway $\times$ BPOP	7	-164.45	343.94	168.82	0	0.24
3	BPOP, Flyway, Year	5	-168.83	348.21	173.09	0	0.19
2	BPOP, Flyway	4	-173.56	355.48	180.36	0	0.13
1	ВРОР	3	-182.25	370.71	195.59	0	0.00
B) log(Number of A	Active Hunters)						
K	BPOP, Flyway $\times$ Year, Year spline	11	126.84	-227.72	0.00	1	0.97
F	BPOP, Flyway $\times$ Year, Year random	7	38.24	-61.44	166.28	0	0.98/
							0.83
С	BPOP, Flyway, Year	5	26.65	-42.75	184.98	0	0.83
I	BPOP, Flyway $\times$ Year	6	26.69	-40.62	187.11	0	0.83
3	Flyway $\times$ Year, Flyway $\times$ BPOP	7	26.80	-38.56	189.17	0	0.82
3	Flyway $\times$ Year, Flyway $\times$ BPOP, Year random	8	20.99	-24.63	203.09	0	0.98/
							0.83
3	BPOP, Flyway	4	10.52	-12.67	215.05	0	0.77
A	ВРОР	3	-75.62	157.45	385.17	0	0.01

Appendix C. Model diagnostics for best-performing models describing influence of covariates on (A) duck hunter days afield and (B) active number of duck hunters. BPOP is the breeding duck population

A) Duck Hunter Days Afield

 $DaysAfield \sim BPOP \times method + Year \times method + Year \times Flyway$ 

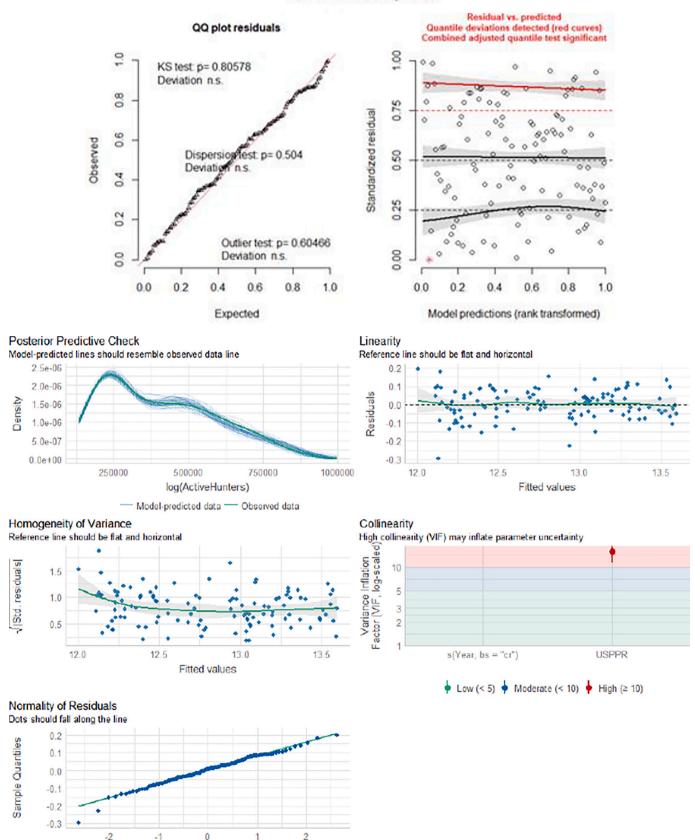
#### DHARMa residual diagnostics



#### B) Number of Active Duck Hunters

 $log(ActiveHunters) \sim BPOP + s(Year, bs = "cr") + Year \times Flyway$ 

#### DHARMa residual diagnostics

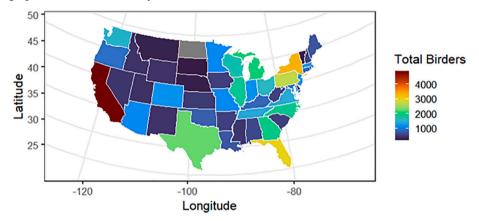


Standard Normal Distribution Quantiles

Appendix D. Number of viewing trips and per-trip expenditures by flyway (from willingness-to-pay survey of Ducks Unlimited members conducted by Loomis et al., 2018), with standard deviation (SD) and lower and upper 95 % confidence intervals (LCL and UCL)

Flyway	Respondents	Abundance	Trips (n)	SD	LCL	UCL	Expenses (\$)	SD	LCL	UCL
Central	34	1	1.99	1.44	1.32	2.65	27.96	4.65	18.56	37.36
Mississippi	12	1	2.40	1.80	1.04	3.76	120.04	2.63	52.12	187.95
Central	34	2	5.63	2.73	3.74	7.53	43.37	4.10	28.79	57.94
Mississippi	12	2	10.31	5.59	4.48	16.14	155.22	2.58	67.40	243.05

Appendix E. Number of birders (in thousands) estimated per state according to the U.S. Fish and Wildlife Service report, Birding in the United States: a demographic and economic analysis (Carver, 2013). Note: No estimate was made for birders in North Dakota



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