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Decision-Support Framework for Linking Regional-Scale Management Actions to Continental-Scale Conservation of Wide-Ranging Species

Open-File Report 2020–1084

U.S. Department of the Interior
U.S. Geological Survey

Cover. Northern pintail (*Anas acuta*) standing in water. Photo from the U.S. Fish and Wildlife Service, National Digital Library.

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Decision-Support Framework for Linking Regional-Scale Management Actions to Continental-Scale Conservation of Wide-Ranging Species

By Erik E. Osnas[1], G. Scott Boomer[1], James H. Devries[2], and Michael C. Runge[3]

Abstract

Anas acuta (Northern pintail; hereafter pintail) was selected as a model species on which to base a decision-support framework linking regional actions to continental-scale population and harvest objectives. This framework was then used to engage stakeholders, such as Landscape Conservation Cooperatives' (LCCs') habitat management partners within areas of importance to pintails, while maximizing cross-taxa effects from the framework. The mathematical framework for the model had been previously developed for pintails. A key assumption incorporated into the model is that density dependence in survival occurs during the post-hunting (winter) period, where resources are hypothesized to be limiting. Because few data are available to directly inform this process, the approach used was to build a hierarchical Bayesian integrated population model (IPM) that simultaneously uses data from bird-band recoveries, breeding population counts, and harvest surveys to estimate values of parameters of an annual population projection model, including population size, survival rate, reproductive rate, and process and observation error variances, that are logically consistent with each other, given the mathematical structure imposed through the IPM.

The main accomplishments of this study are (1) development of an IPM for pintail to guide harvest and habitat management, (2) development of a Prairie Parkland Region breeding submodel to predict pintail productivity, (3) development of statistical methodology to estimate pintail productivity (as measured by the ratio of juvenile to adults in hunter-collected wing samples) and winter survival and to relate these estimates to covariates, and (4) illustration of how to use a model and estimated parameter values to predict pintail population size and sustainable harvest as a function of habitat.

Estimation of pintail survival from bird-banding data shows that there has been relatively little variation in survival over the period 1960–2013. A productivity model showed strong effects of breeding ground conditions, wintering-ground precipitation, and density dependence on pintail productivity. Thus, most temporal variation in pintail demographic rates has been due to effects on reproduction and not survival, including effects of breeding or wintering-ground habitat. These results indicate that habitat conservation efforts may be most effective if they focus on maintaining or increasing breeding and wintering-ground habitat to increase pintail productivity rather than pintail survival. Environmental perturbations in excess of historical experience, such as what could occur under climate change, might have meaningful effects on survival but cannot be estimated with current data. Direct effects of climate, land use, or management are likely to be greater on productivity than survival, but substantial uncertainty remains about predictions of equilibrium population size and sustainable yield.

Introduction

Conserving migratory or wide-ranging species presents considerable challenges because these populations move across disparate jurisdictions, often crossing international borders during crucial stages of their annual cycle (Crooks and Sanjayan, 2006). Within North America, Migratory Bird Joint Ventures (JVs) have established successful partnerships to coordinate the planning and delivery of conservation actions within key regions to benefit migratory bird populations (NAWMP Assessment Steering Committee, 2007). However, the extent to which local conservation actions affect regional demographics and in turn affect continental population dynamics remains poorly understood. Maximizing efficient use of limited resources to conserve habitats for wide-ranging species has motivated a critical need to develop mathematical modeling frameworks to evaluate effects of local-scale conservation decisions on population demographics in the face of stressors such as climate and landscape change (Martin and others, 2007). This is especially relevant to the network of Landscape Conservation Cooperatives (LCCs) in North America with its focus on cross-taxa conservation among multiple LCCs.

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Migratory waterfowl species are excellent subjects for a mathematical model with which to develop this framework because they are not only highly valued by the public, but annual datasets on population demographics throughout their ranges are available (Nichols and others, 1995; U.S. Fish and Wildlife Service [USFWS], 2013a, b). Mattsson and others (2012) developed a mathematical modeling framework to link the consequences of regional-scale changes in habitat or harvest to continental demographics of *Anas acuta* (Northern pintail; hereafter pintail) across core nonbreeding and breeding regions that span nine LCCs (fig. 1). This model incorporates density-dependent relations but lacks an empirical estimation of density and habitat effects on demographic processes. Values of model parameters, like survival and reproductive rates, that are estimated from available data are necessary to predict the effect of alternative conservation actions or climatic scenarios on demographic rates. Therefore, we developed a framework consisting of a continental model similar to that of Mattsson and others (2012) but with parameter values directly estimated from data. We also developed frameworks for mechanistic models of wintering and breeding grounds to provide information on conservation of species that depend upon multiple and potentially geographically distinct landscapes. Our models use pintail as a surrogate for wide-ranging species. With appropriate modification, however, the models could be used for other species and management decisions similar to those in this study.

In total, there are nine LCCs that support core populations of pintails in North America as defined by Mattsson and others (2012) (fig. 1). Three LCCs in Alaska and Canada (Arctic, Northwest Boreal, Western Alaska) and one that spans the central United States and Canada (Plains and Prairie Potholes) support core breeding populations. Five LCCs in the United States and Mexico (California, Great Basin, Great Plains, Gulf Coast Prairie, and Gulf Coastal Plains and Ozarks) support core nonbreeding populations. Many studies on pintails and pintail habitat have been published for each of these LCCs (for example, radio telemetry, nest and duckling survival, bioenergetics), and many surveys span multiple LCCs (for example, May flyover surveys, annual mark-recovery, satellite telemetry, and the harvest surveys administered by the USFWS to estimate species and age composition in hunter bags). This study used a combination of available data and input from experts to build the models and submodels described in Mattsson and others (2012).

This study was conducted by the U.S. Geological Survey (USGS), in cooperation with the Gulf Coast Prairie Landscape Conservation Cooperative, Ducks Unlimited Canada, Environment and Climate Change Canada, and the USFWS. The purpose of this study was to develop mathematical models to support decisions for harvest and habitat management of pintail, a highly migratory species. To do so, we first developed an integrated population model (IPM) of the annual life cycle that uses multiple datasets to simultaneously estimate population size, survival, per capita reproductive rates (recruitment or productivity, defined here as the ratio of juvenile to adult ducks after the breeding season), and other demographic parameters. We refined the spatial resolution of the model to allow flyway-specific decision support. A mechanistic model was constructed to predict per capita reproductive rates from small-scale landscape data in the Prairie Parkland Region (PPR, roughly equivalent to the Plains and Prairie Potholes LCC, fig. 1), with the hope that these local-scale predictions could improve estimates of PPR-scale reproductive rates in a spatial life cycle model. This report presents the structure of the IPM; the methods used to estimate the parameters; the methods used to investigate spatial structure in the dynamics of pintails; the resulting estimates of survival rate, harvest rate, reproductive rate, and population size over time; inferences about environmental drivers of pintail dynamics; and a discussion of the implication of these results for other projects that attempt to link regional management approaches to continental dynamics of a migratory bird.

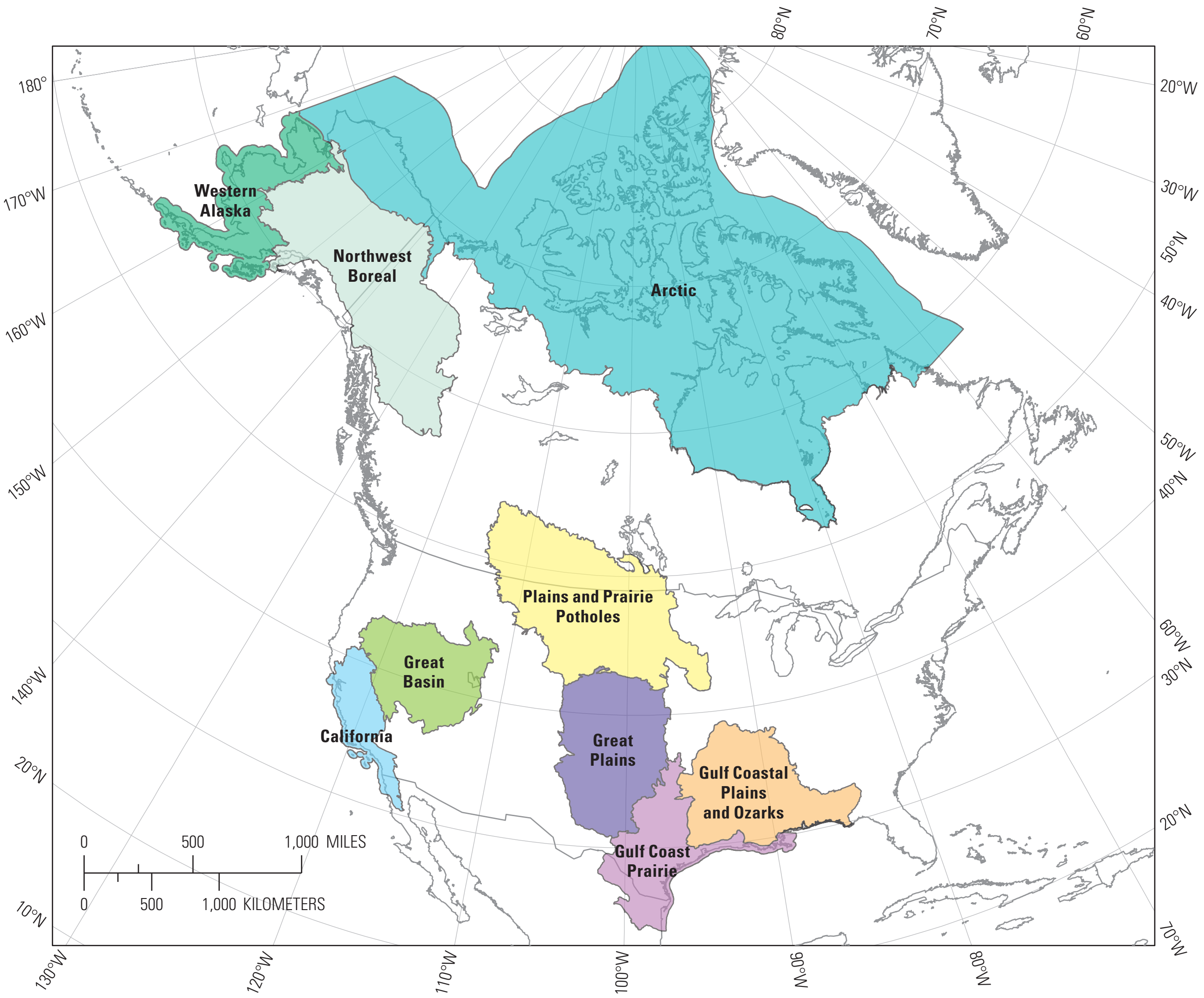
Objectives

There were three objectives for this study.

- Objective 1—Develop a decision-support framework linking regional-scale management actions to continental-scale conservation of wide-ranging species. Regional-scale actions may include harvest management decisions (harvest rate or season and bag limits) or habitat manipulations through climate, agricultural policy, or direct habitat management. The desired conservation outcomes include pintail population size and harvest. As part of this objective, a range of possible future scenarios involving alternative management strategies, policies, and climate effects (for example, Matchett and Fleskes, 2017) was developed to evaluate how these drivers affect sustainable pintail harvest and population size at the continental level. The mathematical model that was developed for this study can be used with cost estimates of alternate management strategies to identify actions that achieve the greatest pintail population and sustained harvest for the least conservation investment. The model also can be used to predict the effect of climate change on pintail sustainable harvest and population size. Finally, the model can be used to estimate the value of new information about parameter values to improve specific management decisions; the value of information can then be used to guide research funding decisions or research priorities.

- Objective 2—Engage stakeholders involved in habitat management within areas of importance to pintails.

- Objective 3—Maximize cross-taxa relevance of the decision-support framework.



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North Pole Lambert Azimuthal Equal Area Projection

EXPLANATION

Landscape Conservation Cooperatives which support core populations of Northern pintail

- 🟦 Arctic
- 🟦 California
- 🟩 Great Basin
- 🟪 Great Plains
- 🟪 Gulf Coast Prairie
- 🟧 Gulf Coastal Plains and Ozarks
- ⬜ Northwest Boreal
- 🟨 Plains and Prairie Potholes
- 🟩 Western Alaska

Figure 1. Landscape Conservation Cooperative areas supporting core breeding and core nonbreeding populations of *Anas acuta* (Northern pintail) in North America. Landscape Conservation Cooperatives (LCCs) are partnerships of Federal, Tribal, State, local, and non-governmental organizations with an interest in natural and cultural resource management in shared landscapes. The individual LCCs span major ecological regions within North America.

Methods

We developed a pintail annual cycle model as an IPM (Besbeas and others, 2002; Kéry and Schaub, 2012). This approach simultaneously uses data from bird-band recoveries to estimate survival, hunter-collected wings to estimate reproductive rates, and annual population counts to estimate rates of population change and observation error. Because the model simultaneously estimates survival and productivity and predicts population size through the annual cycle, these estimates are jointly consistent with all the datasets and can sometimes make an inference that is not possible from any one dataset. Thus, information on one parameter can potentially inform the values of other parameters. For example, with information on population size and survival, productivity can be predicted even when data are not available for a particular year. The original motivation for using an IPM approach for pintail was that information on directly observed processes like survival, productivity, and population size might help inform processes that are not directly observed, such as density dependence during the winter period. Because of the shared dependence between different data sources, correct specification of the submodels is especially important. Therefore, we spent significant time developing the survival and productivity submodels. It was necessary to develop these submodels so that environmental covariates could be added (Objective 1).

Development of the pintail annual cycle model began with the building of a simple model with no explicit spatial structure, a model similar to that used in pintail Adaptive Harvest Management (USFWS, 2010). During this process, it became evident that development of survival and productivity submodels was necessary. These became stand-alone products that could be easily inserted into the annual cycle model once developed. During this process, we explored region-specific patterns in survival and productivity that could be inserted into the annual cycle model, similar to the model of Mattsson and others (2012). Adding spatial structure to the model was partially successful, although we could not get the exact model as specified in Mattsson and others (2012) to work.

In all efforts, a Bayesian approach was taken. This approach was chosen because the long history of waterfowl research gives substantial prior information on processes, such as annual survival, movements, and reproductive performance. The Bayesian approach also was used because it makes the estimation of parameters in complex models relatively straightforward. The Bayesian approach provides a major advantage when the model is being used as a decision-support tool because it allows for a full accounting of parametric uncertainty (that is, sampling error); this approach also provides estimates of true process variation in demographic rates or population counts (that is, environmental stochasticity), given the model structure. The sampling error can be reduced by increased data collection, but environmental stochasticity is not directly under control. Both types of uncertainty can become important for conservation decisions. Thus, the Bayesian approach allows the use of estimates in a decision process governed by these two major sources of uncertainty.

As part of the development of the population model, submodels for productivity and survival were created (these are described in the section “Population Model”). The submodels include environmental (winter habitat) covariates so that the effect of winter habitat could be estimated. For productivity, the effect of winter habitat is a “cross-seasonal effect,” but for survival, it is a direct effect. Because there were no direct historical data on winter habitat quantity, National Oceanic and Atmospheric Administration (NOAA) precipitation data (https://www.ncdc.noaa.gov/cdo-web/) were used; precipitation data were important for predicting waterfowl productivity in previous studies (Heitmeyer and Fredrickson, 1981; Kaminski and Gluesing, 1987; Raveling and Heitmeyer, 1989; Osnas and others, 2016). For productivity, there is no single breeding habitat covariate available, but the mean latitude of the observed population in spring served as a direct proxy for prairie habitat conditions because this has long been known to correlate strongly with pintail productivity (Sheaffer and others, 1999; USFWS, 2010). Finally, we constructed a more mechanistic model of pintail productivity across the PPR that used fine-scale habitat data and models developed by Ducks Unlimited Canada (as described in Devries, 2014) to predict nest site selection and nest success. From these spatially explicit predictions, we predicted the total productivity across the entire PPR and compared this to continental measures of productivity (female wing age ratios).

Data Sources

We used four data sources in the IPM to estimate demographic parameters: (1) population survey estimates from the Waterfowl Breeding Population and Habitat Survey (WBPHS) database for 1960–2013 from the traditional strata 1–18, 20–50, and 75–77 (Division of Migratory Bird Management, USFWS); (2) banding and recovery data for 1961–2014 from the USGS Bird Banding Lab, Patuxent Wildlife Research Center; (3) age, sex, and harvest data for pintails from the USFWS Harvest Surveys branch, Parts Collection Survey (PCS) and migratory bird harvest survey (mail questionnaire or harvest information program; Raftovich and others, 2012); and (4) monthly total precipitation data from October 1960 through February 2013 from the U.S. Department of Commerce, National Climate Data Center (https://www.ncdc.noaa.gov/cdo-web/).

A full description of datasets and processing is given in Osnas and others (2016), and the code used to manipulate data is available from the lead author. For banding data, we selected records of normal, wild-caught pintails that were banded during preseason banding operations (June 1–September 30 with Bird Banding Lab status code 3). Records from all banding locations in the United States and Canada were used. Recoveries were restricted to birds found dead or shot by hunters and reported to the Bird Banding Lab in fall and winter immediately following banding (that is, direct recoveries). The PCS is conducted annually (since 1961) and is based on duck wings that are submitted by hunters. Trained biologists identify species, sex, and age of the wings, and these data can be used to determine the species, age, and sex composition of the waterfowl harvest each year. A separate survey of migratory bird harvest is conducted each year (that is, mail questionnaire survey, 1959–2001, and harvest information program, 1999–2014) that provides an estimate of the total waterfowl harvest. Because both the PCS and the harvest surveys acquire spatially referenced data, the harvest surveys are used to assign weights to each duck wing collected in a particular location to reflect the relative contribution of the area to total harvest. We restricted all analyses to female wings only.

Data used to predict PPR pintail production came from agricultural census data in the United States and Canada, small scale landscape data on wetlands, and Ducks Unlimited Canada pintail nesting studies (as described in Devries, 2014).

Population Model

A mathematical model incorporating the sex of pintails was used as the basis for the expected population dynamics. The model is essentially that used by the USFWS to set annual hunting regulations (USFWS, 2010). In matrix form, the number of pintails on May 1 in calendar year t+1 is found as $N_{t+1} = \mathbf{A}_t N_t + \varepsilon_t$ or

$$\begin{bmatrix} N_{f,t+1} \\ N_{m,t+1} \end{bmatrix} = \begin{bmatrix} S_{f,t} + R_t S'_{f,t} & 0 \\ R_t S'_{m,t} & S_{m,t} \end{bmatrix} \begin{bmatrix} N_{f,t} \\ N_{m,t} \end{bmatrix} + \begin{bmatrix} \varepsilon_{f,t} \\ \varepsilon_{m,t} \end{bmatrix} \tag{1}$$

where

$N_{sex,t}$ is the number of adult pintails of each sex (f = female, m = male) on May 1 of year t,

$S_{sex,\,t}$ is the annual survival of adult pintails from May 1 of year t to May 1 of year $t+1$,

R_t is one-half the number of young per adult female at the end of the breeding season (the beginning of the fall migration season), and

$S'_{sex,t}$ is a compound parameter that is the product of female adult survival through the breeding season of year t ($S^{b}_{f,t}$), sex-specific juvenile hunting-season survival in year t ($S^{h}_{juv,sex,t}$), and juvenile winter survival in year $t+1$ ($S^{w}_{juv,sex,t+1}$).

Thus, age structure for survival is implicit in the S' term. Finally, $\varepsilon_{f,t}$ and $\varepsilon_{m,t}$ are random effects from environmental stochasticity (“process” variation) that are not accounted for in the temporal random effects in the survival ($S_{sex,\,t}$, $S'_{sex,t}$) and reproduction parameters (R_t). The random effects $\varepsilon_{f,t}$ and $\varepsilon_{m,t}$ are distributed as

$$\varepsilon_{sex,t} \sim Normal\left(0, \sigma^{process}_{sex,t}\right). \tag{2}$$

Demographic stochasticity was modeled such that survival components of equation 1, $S_{sex,t}N_{sex,t}$, arose from a binomial random variable, and the reproduction components of equation 1, $R_t S'_{sex,t} N_{sex,t}$, came from a Poisson random variable. We used the normal approximations to the binomial and Poisson distributions because the population size was large ($N > 10^6$). The total variation from demographic stochasticity is the sum of the variance of the survival component and the reproduction component under the assumption of no covariance between these demographic parameters. Therefore, we added another term that scales the variance to population size (ϕ) and allows for departures from the binomial-Poisson expectation of the variance that might be due to extra-binomial or -Poisson variance, environmental stochasticity, or other effects that might reduce the variance (covariance). Thus, the deviation owing to all sources of process stochasticity for females is

$$\sigma^{process}_{f,t} = \sqrt{\left(S_{f,t}\left(1 - S_{f,t}\right) + R_t S'_{f,t}\right)\left(1 + \phi_1\right) N_{f,t}} \tag{3}$$

and for males is

$$\sigma^{process}_{m,t} = \sqrt{S_{m,t}\left(1 - S_{m,t}\right)\left(1 + \phi_1\right) N_{m,t} + R_t S'_{m,t}\left(1 + \phi_1\right) N_{f,t}}\,. \tag{4}$$

In equations 3 and 4, it was assumed that process variation (σ) scales with population size at the same rate for both reproduction and survival. Note that at the population sizes modeled here, the proportional contribution of these terms to the variance in population size is small.

Population observations, Y_t, are made only on a proportion of the total population

$$Y_t = E\left[y_t\right] + \gamma_t = \psi_t N_t + \gamma_t \tag{5}$$

where $E\left[y_t\right]$ is the expected number of observed pintails, which is the product of the proportion of the population observed during surveys, ψ_t, and the total population size, $N_t = N_{f,t} + N_{m,t}$. The proportion of the population surveyed was modeled as a function of mean latitude of the observed pintail population (M.C. Runge, U.S. Geological Survey, and G.S. Boomer, U.S. Fish and Wildlife Service, written commun., 2005; U.S. Fish and Wildlife Service, 2010), $\psi_t = \exp\left[\beta_{lat}\left(l_t - l_{69}\right)\right]$. Thus,

$$\log\left(E\left[Y_t\right]\right) = \log\left(N_t\right) + \beta_{lat}\left(l_t - l_{69}\right) \tag{6}$$

where

β_{lat} is a regression parameter,

l_t is the mean latitude of the observed population in year t, and

l_{69} is the mean latitude of the population in 1969.

Finally, the observation error was distributed as $\gamma_t \sim Normal\left(0, \sigma_t^{obs}\right)$, where

$$\sigma_t^{obs} = \sqrt{\left(\sigma_t^{design}\right)^2 + \phi_2 E\left[Y_t\right]}. \tag{7}$$

The observation standard deviation consists of two parts. The first part is the standard deviation from the stratified random survey design, σ_t^{design}, and is calculated each year on the basis of methods in Smith (1995). The second part, $\phi_2 E\left[Y_t\right]$, allows for additional observation variance that increases or decreases with the expected number of observed pintails where ϕ_2 is a parameter that is estimated. The distribution in equation 7 together with equations 5 and 6 defines the likelihood of an observation in year *t*.

Productivity Submodel

The estimates for productivity, as measured by the ratio of juvenile to adult wings in the sample of hunter bags, R_t, are described below. We modified the methods of Zimmerman and others (2010) to allow for environmental covariates (see Osnas and others, 2016, for a full description of the methods). This method uses samples of hunter-shot wings to estimate age ratios of pintail taken by hunters and uses pre-season band recoveries to correct for age- and sex-related harvest bias. Habitat covariates and temporal random effects are then added to a linear predictor just as in a generalized linear mixed model (Osnas and others, 2016). Hunter-shot wing samples probably provide good estimates of productivity for pintails because pintails are common in hunter bags and are early migrants. For rarer species of ducks, sample size in the PCS would be small, leading to imprecise estimates of age ratio. For later migrant species, PCS samples might be biased because some hunters run out of sample envelopes; thus, later samples might not be included in the survey. The extent of this problem is not known. Therefore, using hunter-collected samples in our model might reduce the usefulness of our modeling approach. However, our approach can easily accommodate other data and, in fact, does not require productivity data because productivity data can be inferred as a latent variable in the integrated population model.

Direct recovery rates for adults and juveniles from banding samples are estimated by defining the likelihood function using the binomial distribution

$$m_{a,t} \sim Binomial\left(p_{a,t}, B_{a,t}\right) \tag{8}$$

where

$m_{a,t}$	is the number of direct recoveries of age *a* in year *t*,
$p_{a,t}$	is the probability of a recovery, and
$B_{a,t}$	is the total number of females that were banded.

The probability of recovery was modeled as

$$logit\left(p_{a,t}\right) = \alpha_0 + \gamma_{a,t} \tag{9}$$

with intercept α_0, and $\gamma_{a,t} \sim Normal\left(0, \sigma_a\right)$ is a temporal random effect with an age-specific standard deviation, σ_a. The relative vulnerability of juveniles is then defined as $v_t = p_{1,t} / p_{2,t}$ with *a* = 1 for juveniles and *a* = 2 for adults. Second, we modeled the linear predictor for true (fall flight) age ratio as

$$log\left(R_t\right) = \beta_0 + \beta_1 N_t + \beta_2 l_t + \beta_3 x_t + \beta_4 x_t N_t + \varepsilon_t \tag{10}$$

where

β_i	are regression parameters,
x_t	is a habitat covariate (here cumulative rainfall in wintering areas of California [see Osnas and others, 2016, for a full description]),
N_t	is the total pintail population in year *t* as described above in section “Population Model,” and
ε_t	is a temporal random effect with standard deviation τ, $\varepsilon_t \sim Normal\left(0, \tau\right)$.

Cumulative winter rainfall was centered at its average, but mean latitude and population size where not centered. Finally, the likelihood of the observed number of juvenile wings is

$$w_t \sim Binomial\left(q_t, W_t\right) \tag{11}$$

where

w_t	is the number of juvenile wings collected in year *t*,
q_t	is the probability of sampling a juvenile female wing, and
W_t	is the total number of female wings collected.

The observed proportion of juvenile wings is calculated from the true age ratio and the vulnerability as

$$q_t = \frac{R_t v_t}{1 + R_t v_t}. \tag{12}$$

See Zimmerman and others (2010) for justification of the above model and Osnas and others (2016) for a complete description.

In order to improve convergence, we used informative prior distributions for the regression parameters β_i and for the direct recovery probabilities $p_{a,t}$. For regression parameters, we used priors that included only negative effects of population size and mean latitude and a positive effect for the interaction between population size and rainfall, and allowed the effect for rainfall to take both positive and negative values. Details are given in the model code in a companion data release (Osnas and others, 2021).

Survival Submodel

The estimates for survival, $S_{sex,t}$ (equation 1), are described here. We used a band recovery model to estimate sex-, age-, and year-specific components of annual survival and harvest probabilities from two-season banding operations (before and after the hunting season). Our method was based on model "H_7" of Brownie and others (1985). This method allows annual survival to be partitioned into two components of semi-annual survival corresponding to the hunting and non-hunting seasons, where the information to estimate season-specific values comes from the difference in recoveries between pre-hunting and post-hunting season banded samples. If all else is equal, post-season banded samples will have lower recovery probabilities due to the additional period of the year that post-season banded individuals need to survive before the first hunting season after banding. Under the original model of Brownie and others (1985), this difference in recovery probability is modeled by including an additional parameter for non-hunting season survival for individuals banded post-season, and all other parameters are shared (that is, identical) between pre- and post-hunting season banded samples, thus implying that these samples come from the same population. Importantly, we found that recovery rate estimates were nearly identical, on average, between pre- and post-hunting season banded samples but that the variance across years could be quite large. This indicated that either (1) no mortality occurred after hunting and the harvest rates for the two banded samples were similar or (2) that the fall survival rates or harvest rates were different between pre- and post-hunting season banded birds and post-hunting season survival was less than 1.0. We found that on average across years, survival estimates for males banded pre-hunting season were slightly higher than for males banded post-hunting season. Therefore, the assumption that these two banding samples represent identical populations is violated, and we modified the model to incorporate a population difference in survival and harvest rate parameters.

Our inference about the partition of "semi-annual" survival depends on the difference between parameter estimates of pre- and post-hunting samples. First, if we assume a model where no parameters are shared, then we are left with two independent estimates of each parameter, and there is no information, other than our prior belief, to partition annual survival into hunting and non-hunting season components. Next, there is a whole range of models where parameters are increasingly constrained until we reach model "H_7" of Brownie and others (1985). These models might include fixing survival across years and banding samples but not recovery rates, fixing recovery but not survival across banding samples or years, and other approaches. One possible solution is to fit a range of models that share an increasing number of parameters between pre- and post-season samples, up to and including model "H_7" of Brownie and others (1985) and then compare or average parameter estimates across models based on an information criterion. We used this approach in the context of a Bayesian hierarchical model and "continuous model expansion" where different models are represented by the values of continuous-valued "random effect" parameters.

Bayesian random effect models can be thought of as a form of model selection, where the random effect variance parameter determines the degree of "shrinkage" or model complexity (Efron and Morris, 1977; Gelman and others, 2013; Kéry and Schaub, 2012). Under this perspective, a model with random effect variance equal to zero is equivalent to a model specifying a grand (constant) mean effect across all years, and a model with infinite random effect variance is equivalent to a model specifying a different, independent, estimate for each year (a "fixed effect"). A Bayesian hierarchical formulation allows for continuous variation between these two extremes, and inspection of the posterior distribution of the random effect variance determines the dimensionality of the model. Under this formulation, individual year effect estimates are also improved (that is, more likely to be closer to truth and with lower variance) compared to independent "fixed effect" estimates (Efron and Morris, 1977). In this context, the random effect parameterization allows for a continuous model set between "H_7" of Brownie and others (1985) and a minimally constrained model where only non-hunting season survival is shared between banding samples.

A random effects parameterization was used for hunting and non-hunting season survival; recovery (parameterized as harvest); and solicitation probability, a nuisance parameter describing the probability that the band was actively solicited for reporting to the USGS Bird Banding Laboratory. For each probability parameter except solicitation and non-hunting season survival, we used a log-odds scale parameter describing the grand mean across all years for each age and sex cohort (hereafter, cohort) and a year-, cohort-, and banding sample-specific random effect. Importantly, each cohort received a cohort-specific effect for the average temporal effect and for adults a sex- and time-specific effect for the banding sample effect (pre- or post-season). All individuals were considered adult in post-season bandings. Variance parameters for the effects were cohort specific. Solicitation probability was defined as a temporal random effect but was not cohort or banding sample specific. Non-hunting season survival was defined as a cohort-specific temporal random effect. However, for this parameter, there were only adult cohorts, and the parameter is not banding sample specific. Thus, we assumed that banding samples fully share winter through summer survival estimates and that all variation across banding samples was due to fall survival and recovery (harvest). If non-hunting survival is allowed to vary across banding samples, the semi-annual survival parameters become non-identifiable. We also explored a spatial model that included the above structure and analogous spatial random effects.

The likelihood function was constructed by formatting recoveries for each age, sex, and banding season cohort (pre- or post-hunting) into an "m-array" matrix, where each row is a banding cohort, the columns are the number of recoveries during subsequent years from each banding cohort, and the last column is the number of bands never recovered. We distinguished between unsolicited recoveries, where the band was reported by the person that first encountered it (typically a hunter), and solicited recoveries that were reported by another person (typically a government employee). Solicited recoveries were determined by USGS Bird Banding Laboratory encounter codes ("why" = 2 and "who" = 22–29). We assumed that the reporting rate was 1.0 for solicited bands but less than 1.0 for unsolicited bands. Therefore, solicited and unsolicited bands had different recovery probabilities, and the m-array was organized to allow this difference. Ignoring sex and age cohort for now, the m-array is a three-dimensional array with cells m_{ijk}, with indexes i for banding year, j for banding season (pre-hunting season or post-hunting season), and k for the "m-array" column (here the combination of recovery year and solicitation type plus one column for unrecovered bands). If there are n recovery years (hunting seasons), then k goes from 1 to $2n + 1$ to index solicited ($k = 1 \ldots n$) recoveries, followed by unsolicited ($k = n+1 \ldots 2n$) recoveries during the hunting season, and finally those bands never recovered ($k = 2n + 1$). If we let t index calendar year of recovery ($t = 1 \ldots n$), then the row vectors $\boldsymbol{m}_{ij}$ are modeled as realizations of a multinomial process

$$\left[m_{ij1}, \ldots, m_{ijt}, m_{ij(t+1)}, \ldots, m_{ij(2n+1)}\right] \sim \mathit{Multinomial}\left(\boldsymbol{P}_{ij}, B_{ij}\right) \tag{13}$$

with parameters $\boldsymbol{P}_{ij} = [P_{ij1}, \ldots, P_{ijk}, \ldots, P_{ij, 2n+1}]$ being the probability vector, and B_{ij} is the number of birds banded in banding season j of calendar year i. $\boldsymbol{P}_{ij}$ is then parameterized in terms of cohort- and banding season specific survival from the mid-point of pre-season banding (approximately August) in year t to year $t+1$ ($S_{age,sex,j,t}$), cohort- and banding season specific harvest during the hunting (that is, recovery) season that begins in year t ($h_{age,sex,j,t}$), and year-specific probabilities of solicitation (s_t) and reporting (r_t). We define the vector $\boldsymbol{p}_{ij} = [p_{ij1}, \ldots p_{ijn}]$ with elements

$$p_{ijt} = 0 \text{ for } t < i,$$

$$p_{ijt} = h_{age,sex,j,t} \text{ for } t = i,$$

$$p_{ijt} = h_{adult,sex,j,t} \prod_{k=i}^{t-1} S_{adult,sex,j,k}$$

for individuals banded as adults and $i < t < n+1$,

$$p_{i,j,i+1} = h_{adult,sex,j,i+1} S_{juv,sex,j,i}$$

for individuals banded as juveniles in i and recovered in $i+1$, and

$$p_{i,j,t} = h_{adult,sex,j,t} S_{juv,sex,j,i} \prod_{k=i+1}^{t-1} S_{adult,sex,j,k}$$

for individuals banded as juveniles in i and recovered after $i+1$. Let $\boldsymbol{s} = [s_1, \ldots s_n]$ and $\boldsymbol{r} = [r_1, \ldots, r_n]$, then for pre-hunting season banded birds ($j = 1$)

$$\boldsymbol{P}_{i,1} = [\boldsymbol{s} * \boldsymbol{p}_{i1}, (1-\boldsymbol{s}) * \boldsymbol{r} * \boldsymbol{p}_{i}, P_{i,1,2n+1}],$$

where * indicates element-by-element multiplication and

$$P_{i,1,2n+1} = 1 - \sum_{k=i}^{2n} P_{i1k}.$$

To be recovered, birds banded post-season in calendar year i must survive the post-hunting period (winter, spring migration, and summer) to the pre-season banding period in year i. We designated this additional survival as $S^{n}_{sex,i}$ for the non-hunting period. There is no age structure to this term because all individuals cannot be reliably aged after their first hunting season. Traditionally, these birds are considered to be adult even though they are a mixture of individuals in their first year of life and older individuals. The probability vector for post-season banded recoveries then is $\boldsymbol{P}_{i,2} = S^{n}_{sex,i}\ \boldsymbol{P}_{i,1}$. The total likelihood function for the dataset is the product of the above multinomial likelihood across all banding years, seasons, and cohorts.

Survival was modeled by breaking annual survival into "semi-annual" components of fall or hunting season survival ($S^{h}_{age,sex,j,t}$), winter to summer survival (hereafter, winter survival, $S^{w}_{sex,t+1}$), and summer (breeding-season) survival ($S^{b}_{sex,t+1}$). Annual survival is then $S_{age,sex,j,t} = S^{h}_{age,sex,j,t} S^{w}_{sex,t+1} S^{b}_{sex,t+1}$. Thus, we have assumed that all variation in annual survival across age classes within a year is due to differences in fall survival.

The model for hunting season survival is

$$\mathit{logit}\left(S^{h}_{age,sex,t,j}\right) = \beta^{h}_{age,sex} + \beta^{post}_{sex,j} + \alpha^{h}_{age,sex,t,j} \tag{14}$$

where $\beta^{post}_{sex,j}$ estimates the average effect of banding season on survival for post-hunting season banding samples relative to pre-season samples as an intercept (that is, $\beta^{post}_{sex,j} = 0$ for pre-season bandings), and $\alpha^{h}_{sex,t,j}$ is a random effect defined as

$$\alpha^{h}_{age,sex,t,j} \sim \mathit{Normal}\left(0, \sigma^{h}_{age,sex}\right). \tag{15}$$

Thus, $\alpha^{h}_{age,sex,t,j}$ is cohort, time, and banding-sample specific. Note that the time-specific banding-season effect comes from the same distribution across all times and banding samples; thus, the variance of this effect includes temporal variance and the variance owing to the difference between samples. Because these sources of variance (temporal and banding sample) come from the same distribution, there is some dependency among them.

For winter survival, the model is

$$\begin{gathered} \mathit{logit}\left(S^{w}_{sex,t}\right) = \beta^{w}_{0,sex} + \beta^{w}_{1} N_t + \beta^{w}_{2} x_t + \beta^{w}_{3} x_t N_t + \alpha^{w}_{sex,t} \\ \alpha^{w}_{sex,t} \sim \mathit{Normal}\left(0, \sigma^{w}_{sex}\right) \end{gathered} \tag{16}$$

with regression parameters β_i^w common across sexes except for the intercept, the covariates as defined in the "Productivity Submodel" section, and a sex-specific random year effect, $\alpha_{sex,t}^w$. For breeding-season survival, the model is

$$\begin{gathered} logit\left(S_{sex,t}^b\right) = \beta_{sex}^b + \alpha_{sex,t}^b \\ \alpha_{sex,t}^b \sim Normal\left(0, \sigma_{sex}^b\right). \end{gathered} \tag{17}$$

Harvest probability was modeled as

$$logit\left(h_{age,sex,t,j}\right) = \beta_{age,sex}^{harvest} + \beta_{age,sex,j}^{harvest,\,post} + \alpha_{age,sex,t,j}^{harvest} \tag{18}$$

where $\beta_{age,sex,j}^{harvest,\,post}$ estimates the average effect on harvest for post-hunting season banding samples, and the random effect is defined as

$$\alpha_{age,sex,t}^{harvest} \sim Normal\left(0, \sigma_{age,sex}^{harvest}\right). \tag{19}$$

Note that in equations 15, 16, 17, and 19, the random effect variance is cohort specific. Thus, the degree of shrinkage across years is cohort specific. For solicitation probability, the model is

$$\begin{gathered} logit\left(s_t\right) = \beta^s + \alpha_t^s \\ \alpha_t^s \sim Normal\left(0, \sigma^s\right). \end{gathered} \tag{20}$$

We used informative priors on all survival and harvest parameters. Band reporting rates were derived from reward-band studies in *Anas platyrhynchos* (mallard) (table 5 in Boomer and others, 2013) because no reward band studies have been done for pintail and there is no evidence that band reporting rates vary significantly by species or sex (Garrettson and others, 2014). For the years 1960–80, we used the mean estimates from Henny and Burnham (1976; as corrected by Nichols and others, 1991). Standard deviation of the estimate during 1960–80 was not reported, but we assumed it to be 0.06. For the years 1981–88, we used the mean and standard error estimates given in Nichols and others (1991). For the years 1989–91, we used the average reporting rate and standard error in reporting rate across flyways and latitude as given by Nichols and others (1995). For the years 1992–97, we used linear interpolation of the mean and variance in reporting rates based on the estimated values for 1991 and 1998. For 1998–2001 we used estimates reported in Royle and Garrettson (2005), and for 2002 to 2013, we used the estimates reported in Boomer and others (2013). We used the reported mean estimates and their variance (the standard error of the mean) to derive a method-of-moments estimate of the parameters of the Beta distribution. Then these year-specific Beta distributions were used as priors for reporting rates.

For the intercepts of harvest probability on the log-odds scale ($\beta_{age,sex}^{harvest}$), we used a Normal(−3, 0.5) prior. For the parameter that controls the mean difference between pre- and post-season banded samples ($\beta_{age,sex,j}^{harvest,\,post}$), we used an Exponential(1) prior to allow only positive values (post-season banded samples have higher harvest rates than pre-season banded samples). For the standard deviation of the harvest random effects, we used a Uniform(0, 1) prior.

For the intercepts of hunting season survival ($S_{age,sex,t,j}^h$) on the log odds scale, $\beta_{age,sex}^h$, we used informative Uniform(0.5, 2) priors for each age and sex. This gave a range of mean survival during the hunting season of 0.62–0.92. For solicitation, a Normal(−2, 1) prior was used for the log-odds scale intercept parameter. For all the standard deviations of the random effects, we used a Uniform(0, 1) prior, which is relatively informative on the variance scale in the sense that very high random-effect variance is less likely than a variance nearer to zero. In terms of model selection, this represents a penalty for very high-dimensional models, founded on a belief that such models are unlikely.

For winter survival, we used informative priors based on the values currently in use for pintail adaptive harvest management (USFWS, 2010). For the log-odds scale intercept parameter of winter survival, $\beta_{0,sex}^w$, we used a Uniform(1, 3) prior that gave a range of mean survival of 0.73–0.95. For covariate effects on winter survival, we used a half-Normal(0, 1) prior restricted to negative real values for the population effect; a standard normal, Normal(0, 1), for the cumulative rainfall effect; and half-Normal(0, 1) restricted to positive real values for the interaction between cumulative rainfall and population size. The restriction to positive real values was necessary for biological realism because cumulative rainfall was centered to a mean of zero. For other details of priors, see the model code (Osnas and others, 2021).

Addition of Spatial Structure

In order to progress toward the model of Mattsson and others (2012), spatial structure was added to productivity and then to survival. For productivity, we partitioned direct bird-band recoveries and PCS results by flyway. The two spatial areas were the Pacific Flyway (the States of Alaska, California, Oregon, Washington, Idaho, Utah, Nevada, and Arizona), and the combined Central (Montana, Wyoming, Colorado, New Mexico, Texas, Oklahoma, Kansas, Nebraska, South Dakota, and North Dakota) and Mississippi (Alabama, Arkansas, Indiana, Illinois, Iowa, Kentucky, Louisiana, Michigan, Minnesota, Mississippi, Missouri, Ohio, Tennessee, and Wisconsin) Flyways (hereafter, Mid-Continent Flyway). Pintail samples from other locations (Atlantic Flyway, Canada, Alaska, and all other areas) were ignored. For direct recoveries, the recovery probability was partitioned into a migration parameter and year-specific harvest recovery parameters. The migration parameter defines the proportion of pintails that migrate to the Pacific Flyway, and the recovery parameters define the probability of a banded pintail being recovered, given that it migrated to the flyway region. We then were able to estimate separate age ratios and regression parameters for each flyway region (Pacific or Mid-Continent Flyway). We also attempted to model age ratios from each breeding source population, as originally modeled in Mattsson and others (2012), but we were not able to run this model successfully owing to a coding error, a directed cycle in the model graph, or incompatible initial values. In any case, the model specified by Mattsson and others (2012) is not identifiable with respect to spatial structure in age ratio; therefore, any spatial partition will be determined solely by prior specification without additional data sources. We attempted to address this by creating a separate model to predict age ratio from the PPR (see section, “Prairie Parkland Submodel”). Spatial models of survival were developed but could not be compiled without error or would not converge even after a very long run time. See model code in a companion data release by Osnas and others (2021).

Climate Change and Habitat Management Scenarios

The regression parameters estimated by the statistical models described in the section “Population Model” are not in units directly meaningful to managers of waterfowl habitat or populations; the units for the regression parameters for productivity are the changes in the log of fall flight age ratio per unit change in covariate. Measures more meaningful to managers and for the integration of harvest and habitat management decisions (Runge and others, 2006; Osnas and others, 2014, 2016) are the expected increase in population or sustainable harvest (both in units of numbers of individuals) owing to a unit change in covariate. Such a change in covariate might come from management intervention, such as increased flooding of crop lands in fall or late winter that mimics large rainfall events, or from climate change that might increase or decrease average rainfall (for example, Matchett and Fleskes, 2017; Neelin and others, 2013).

We used a population dynamic model to explore the effects of habitat management actions or climate change on equilibrium population size and sustainable harvest. We simplified the population model in equation (1) to include only the female population,

$$N_{t+1} = N_t\left[S_t + S_t^{'}R_t\right] \tag{21}$$

where N_t is the size of the female population at the start of the breeding season; R_t is the age ratio in the fall flight; and $S_t^{'}$ is the product of adult female survival during the breeding season, juvenile female survival during the hunting season, and adult survival during the post-hunting (winter) season, as defined above for equation (1). Age ratio (R_t) and winter survival (S_t^w) were modeled as functions described in the “Productivity Submodel” and “Survival Submodel” sections, respectively. For this equilibrium analysis, a 1:1 sex ratio was assumed; therefore, the female population was multiplied by two to predict a total breeding population.

With the addition of stochastic effects on all parameters, equation 21 describes changes in the female population through time, and using constant mean values for the parameters, the model will describe a stationary distribution of N_t. Therefore, we worked with expected values through time (geometric means) for the parameters above and solved the model for positive equilibria of N defined by the solution of $N_{t+1} - N_t = 0$. All parameters were set at their geometric mean through time, and the covariates for precipitation and mean latitude were set to the arithmetic mean without management intervention. The precipitation covariate was modified from zero to reflect a management action or long-term change in precipitation (climate change). For a range of harvest rates $h = \{0, h_{max}\}$, we found the equilibrium population size N numerically.

We first set the winter precipitation covariate to the long-term average ($x = 0$) and found the set of equilibrium N over the range of h at each sample of the joint posterior distribution of the parameters. We sampled only values of the posterior distribution that gave negative density dependence for all covariate values that were used ($\beta_3 + \beta_4 x < 0$). This additional constraint on the posterior distribution assures that there is a finite population in the absence of harvest. From the resulting yield curve, we found the maximum sustained harvest and equilibrium population size at this maximum sustained harvest for each sample of the posterior distribution. The precipitation covariate was increased or decreased, and we again found the equilibrium N over the range of h for the same sample of the posterior distribution. Then for each individual posterior sample, the following were calculated: (1) the change in maximum sustained yield (ΔMSY) as the difference in maximum sustained harvest between the mean covariate value for precipitation (that is, no management intervention, $x = 0$) and intervention/precipitation increase ($x = 1$) or climate change/precipitation loss ($x = -1$), (2) ΔN at MSY as the difference in equilibrium population size obtained at maximum sustained yield (MSY) found in step 1, (3) ΔN as the change in population size with a change in covariate value but where total harvest remains as in the reference condition ($x = 0$), and (4) ΔH as the change in harvest that would be necessary to maintain the population size found at the MSY of the reference condition ($x = 0$). ΔN reflects a policy decision to fix harvest at the historical MSY level. Thus, a positive value achieves the maximum gain in population size with a change in habitat, and a negative value reflects a decline in population, including population extinction if the harvest is greater than can be sustained. ΔH reflects a policy decision to change harvest so that population size remains constant under a change in habitat. We then summarized the posterior of the yield curves by finding the median and 95-percent Bayesian credible interval (BCI) harvest at each level of population size. For precipitation gain, the posterior median yield curve was extremely variable owing to simulation variance; therefore, a polynomial regression of the posterior median harvest as a function of population size was used to smooth the posterior yield curve. For details, see the model code in the data release by Osnas and others (2021).

Prairie Parkland Submodel

We focused on modeling the spatial and temporal variation of breeding productivity in the PPR. For this study, breeding productivity was defined as the expected number of female offspring alive at the end of the breeding season per female at the end of the breeding season (R_t). However, the focus was on the fall flight age ratio from the PPR. In order to calculate the expected number, we needed to integrate several probability distributions that determine the distribution of hatching times: hen survival, nest initiation, clutch size, incubation, nest failure time, re-nesting interval, and nest habitat distribution. Once the distribution of hatching times was found, we integrated hatching time to find the expected number of ducklings alive at the end of the breeding season. Letting the subscripts *t* and *s* represent year and spatial location of hatching, respectively, and defining the continuous variable $t = a$ as the start of the breeding season (approximately April 1) and $t = b$ as the end of the breeding season (approximately September 1), the expected number of young alive at the end of the breeding season produced from a female alive at the beginning of the breeding season is

$$R'_{t,s} = f\int_a^b H(t)C(t)S^d(t,b)\,dt \tag{22}$$

where

the prime indicates that this is in reference to the number of females at the start of the breeding season (in contrast to the fall age ratio at the end of the breeding season),

$f = 1/2$ is the fraction of ducklings that are female,

$H(t)$ is the hatching time distribution,

$C(t)$ is the expected clutch size for nests that hatch at *t*, and

$S^d(t,b) = e^{-\int_0^{b-t} m(t+v,v)dv}$ is the survival of ducklings from hatching at *t* to the end of the season at *b* and where $m(t,v)$ is the time and age-specific duckling mortality hazard.

Equal primary sex ratio and survivorship across the sexes for ducklings were assumed. Note that the probability that a hen hatches a nest at any time between *a* and *b* (“hen success”) is

$$H = \int_a^b H(t)\,dt\,,$$

and the average time of hatching is

$$\bar{t} = \int_a^b tH(t)/H\,dt\,.$$

Next, we focused on the model of the hatching distribution, *H(t)*. Instead of explicitly modeling this complex process as a system of partial differential equations or as a stochastic simulation, a discrete approximation of *H* as proposed by Cowardin and Johnson (1979) and Hoekman and others (2002) was used, but nest success was allowed to vary with attempt, time within the nesting season, and habitat. If *i* is an index of nesting attempt ($i = 1, \ldots, M$); *n,* an index of the period in the nesting season ($n = \{1,2,3\}$ with 1 = early, 2 = mid, 3 = late); *u,* an index of habitat type ($u = 1, \ldots, U$); *t*, an index of year; and *s*, an index of areal political unit within a subregion of the species range (counties in the United States and rural municipalities in Canada), then the proportion of hens that hatch a nest during the nesting season in year *t* in area *s* is approximately

$$H_{t,s} \cong p_{t,s,1}\left[h_{t,s,1} + \sum_{j=2}^{M}\left(h_{t,s,j}\prod_{i=2}^{j}\left(1-h_{t,s,i-1}\right)p_{t,s,i}\right)\right] \tag{23}$$

where

$p_{t,s,i}$ is the probability of nesting during attempt *i*, and

$h_{t,s,i}$ is the average probability of a nest successfully hatching in year *t* in area *s* during nest attempt *i*, where the average is taken over the distribution of nests across habitats (indexed by *u*) and seasons (indexed by *n*),

$$h_{t,s,i} = \sum_n\sum_u r_{n,u}q_{i,n}h_{t,s,n,u,i}\,. \tag{24}$$

The probability of hatching a nest (nest success), $h_{t,s,n,u,i}$, was estimated using standard methods and field data (Devries, 2014), and the probability of nesting in habitat *u* during nesting season *n* ($r_{n,u}$) was estimated from a resource utilization model and regional distribution model described in Devries (2014). Finally, $q_{i,n}$ is the proportion of hens that initiate a nest in season *n* given that this is their *i*th attempt. This quantity was unknown for pintail, so values estimated for mallard were used (Devries and others, 2008; Devries, 2014).

The predicted breeding productivity for year *t* in area *s*, based on equations 22, 23, and 24, becomes

$$R'_{t,s} = fH_{t,s}C_{t,s}\left(\bar{t}\right)S^{d}_{t,s}\left(\bar{t},b\right) \tag{25}$$

where the bar indicates the mean over the hatching time distribution. This approximation introduces some bias owing to evaluating the convex functions *C* and S^d at the mean hatching time; however, results of the simulations have shown that duckling mortality or clutch size decline needs to be extreme for this bias to be large enough for concern. In what follows, it was assumed that clutch size was constant across locations and time but that duckling survival was only constant across time,

$$C_{t,s}\left(\bar{t}\right) = \overline{C_{t,s}\left(t\right)} = 8 \text{ and}$$

$$S^{d}_{t,s}\left(t,s\right) = S^{d}_{t,s}\left(\bar{t},b\right) = S^{d}_{s}\,.$$

To find the ratio of young to adult females at the end of the breeding season, we divided by the expected survival of adult females through the breeding season, $S^{b}_{t,s}$,

$$R^{PPR}_{t,s} = \frac{R'_{t,s}}{S^{b}_{t,s}}\,. \tag{26}$$

To translate the location-specific age ratio to the fall age ratio for an entire region, a weighted sum across all locations was calculated, with the weights determined by the contribution of a local area to the regional fall flight

$$R^{PPR}_{t} = \sum_{s} w_{t,s}R_{t,s} \tag{27}$$

with

$$w_{t,s} = \frac{N_{t,s}S^{b}_{t,s}\left(1+R_{t,s}\right)}{\sum_{s} N_{t,s}S^{b}_{t,s}\left(1+R_{t,s}\right)}\,. \tag{28}$$

Year- and location-specific breeding season survival ($S^{b}_{t,s}$) could potentially come from a statistical model, as does population size or hen success, but these data are not available other than for one location studied over 3 years (Richkus and others, 2005). Thus, there are no data to estimate spatial variation in breeding survival; therefore, we assumed breeding survival to be a function of landscape wetness.

Models for age ratio with spatially constant duckling survival, adult survival, and breeding propensity severely underpredicted the fall age ratio. Therefore, we forced these parameters to covary with an index of local wetland conditions. This was largely an exercise in expert judgement because few data are available to inform these parameters or their spatial covariance. Simulations showed that the spatial covariance was especially important for determining the region-wide fall age ratio (E.E. Osnas, U.S. Geological Survey, written commun., 2014). Working with PPR waterfowl experts Robert G. Clark (Environment and Climate Change Canada) and James H. Devries (Ducks Unlimited Canada), we developed functions that allowed local wetland conditions to affect duckling survival, adult breeding propensity, and adult survival,

$$logit\left(D_s\right) = b_0 + b_1 w_s \tag{29}$$

where

D_s	is the demographic parameter (duckling survival, breeding propensity, or adult survival),
b_0 and b_1	are parameter-specific regression coefficients, and w_s is the location-specific wetland condition index.

Data layers, a hatching success model, and a habitat selection model were obtained from Devries (2014). Briefly, the hatching success model estimates daily nest loss as a function of land cover at the nest-site scale and larger scales, initiation date, pintail density, and wetland conditions. The habitat selection model predicts the proportion of pintail settling into each habitat as a function of local habitat type, region-level habitat, and pintail density. An important property of this model is that pintail settle into habitats with lower nest success in years of high pintail density (Devries, 2014).

We studied the performance of the model by comparing predictions of the PPR age ratio, R^{PPR}_{t}, to age ratios, R_t, estimated directly from PCS (USFWS) data as described in the section “Population Model,” subsection “Productivity Submodel,” For details, see the model code in Osnas and others (2021).

Decision-Support Framework Results

Population Model

The estimated population size followed very closely the observed survey counts with generally high populations in the 1960s and 1970s, followed by a decrease (fig. 2). The proportion of the population observed during surveys decreased as mean latitude of the observed population increased (β_{lat} = –0.09; –0.12, –0.07, all quantities are reported as 95-percent BCI in the format: parameter = posterior median; posterior 2.5-percent quantile, 97.5-percent quantile). The posterior distribution of the observation standard error indicates that there was very little additional observation error over that expected from the stratified random sampling design (ϕ_2 = 0.009; –0.007, 0.027). The posterior distribution for the excess process error indicates less process variance than expected from the binomial-Poisson expectation (ϕ_1 = –0.75; –0.85, –0.58), perhaps owing to negative covariance between demographic parameters.

Annual survival was relatively constant across years but differed among ages and sexes (fig. 3). On average, adult males had the highest annual survival (BCI for mean across years = 0.75; 0.74, 0.75) followed by adult females (0.65; 0.63, 0.67), juvenile males (0.65; 0.65, 0.66), and juvenile females (0.58; 0.56, 0.61; fig. 3). There appears to be some trend in juvenile survival where both sexes experienced increasing survival through the 1960s and 1970s. In contrast, estimated harvest rates (using mallard reporting rates from Boomer and others, 2013) varied substantially across years with relatively high harvest rates in the 1960s, 1970s, and since the mid-2000s, and relatively lower harvest rates from the late-1980s through the mid-1990s (fig. 4).

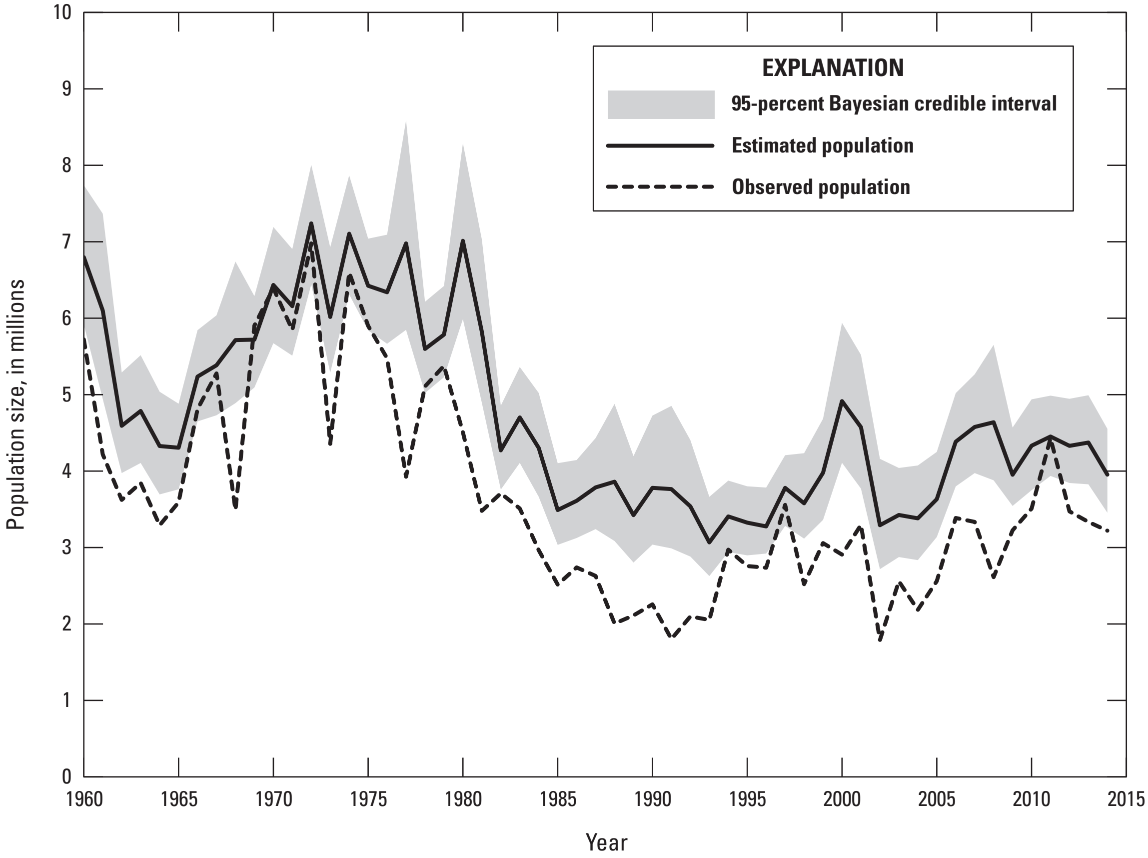

Figure 2. The observed Northern pintail population estimate from the Waterfowl Breeding Population and Habitat Survey of the U.S. Fish and Wildlife Service and estimated population size from an integrated population model, 1960–2014.

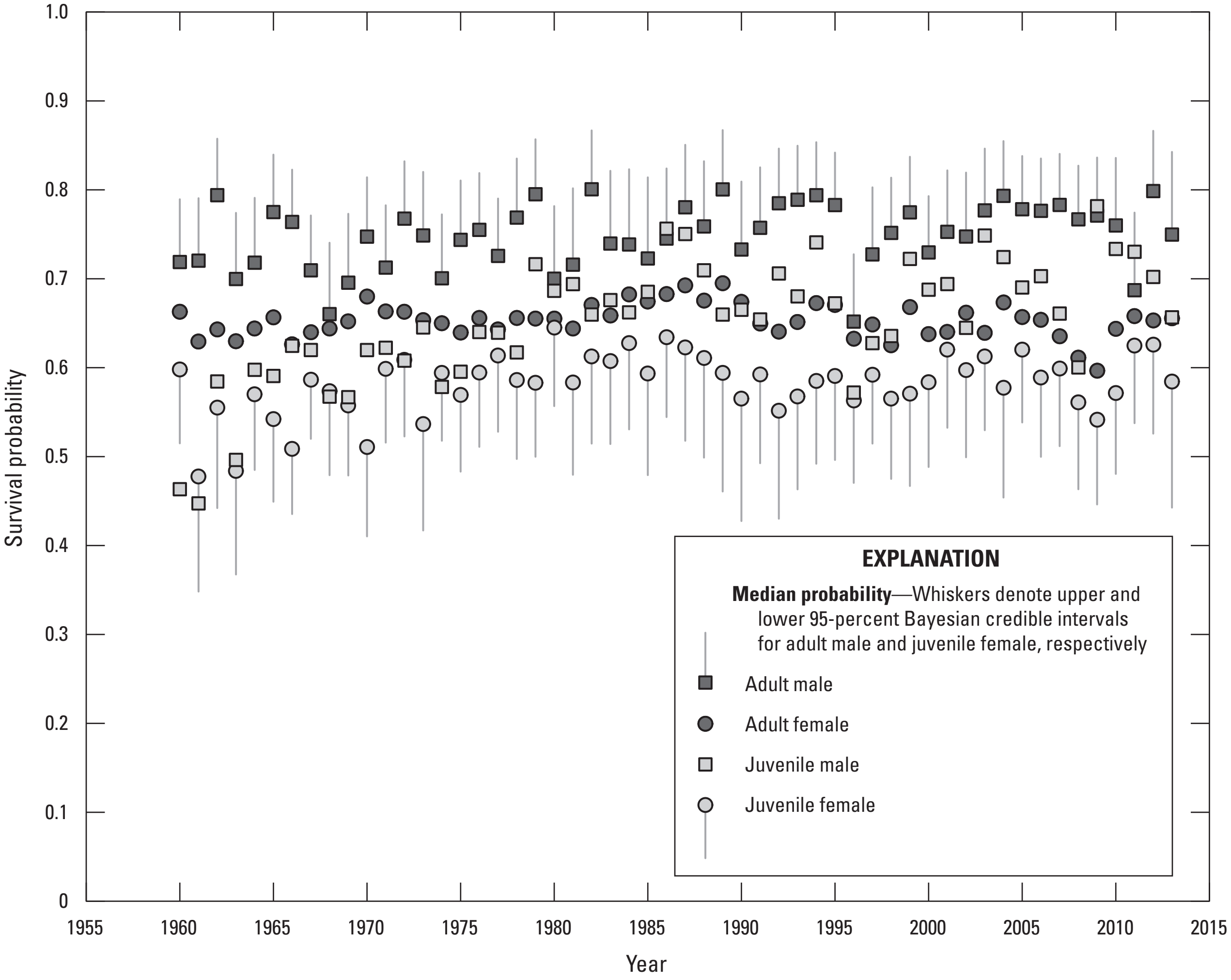

Figure 3. Annual survival estimates from bird-band recoveries of Northern pintail in North America, 1960–2013. Median with 95-percent Bayesian credible interval (BCI) is presented. Only the upper and lower BCIs are given for adult males and juvenile females, respectively, to reduce clutter.

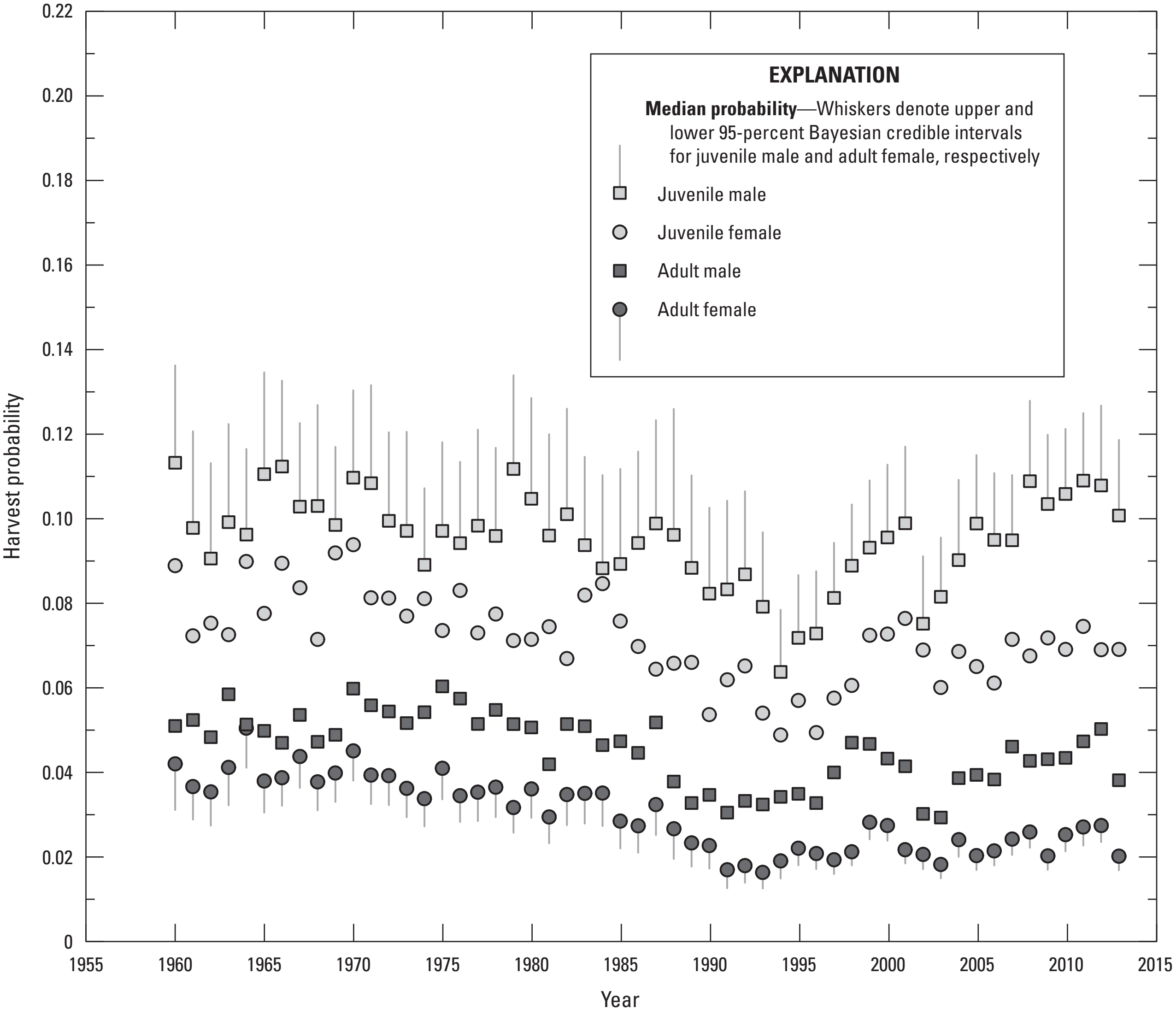

Figure 4. Harvest probability estimates from bird-band recoveries of Northern pintail in North America, 1960–2013.

Estimated fall flight age ratios in pintail are shown in figure 5. Age ratio fluctuated from 0.5 to approximately 2.0, or potentially higher (fig. 5). Pintail age ratio is related to the estimated population size from the population model (fig. 6). Posterior distributions for covariate effects on age ratio show large differences from the specified prior distributions (fig. 7). Age ratio decreased with population size ($\beta_1 = -0.06$; −0.14, −0.01; fig. 7A) and decreased with mean latitude of the breeding population ($\beta_2 = -0.08$; −0.10, −0.05; fig. 7B). Cumulative rainfall interacted with population size ($\beta_4 = 0.01$; 0.001, 0.02) so that higher winter-season rainfall reduced the negative effects of population size (fig. 7D). The average effect of cumulative rainfall was not clear ($\beta_3 = -0.04$; −0.10, 0.01), but much of the posterior density was negative (fig. 7C). Given that this result seems biologically implausible, a more informative prior restricted to positive values might be used in future implementations. The magnitude of estimated effects indicates that mean latitude, a surrogate for prairie wetland conditions, and population size (density-dependence) are the most important drivers of pintail age ratio (figs. 7A, B).

Estimated covariate effects on winter (post-hunting) survival are shown in figure 8. Posterior distributions were centered more strongly toward zero compared to the prior distributions (fig. 8). The population size effect shows the

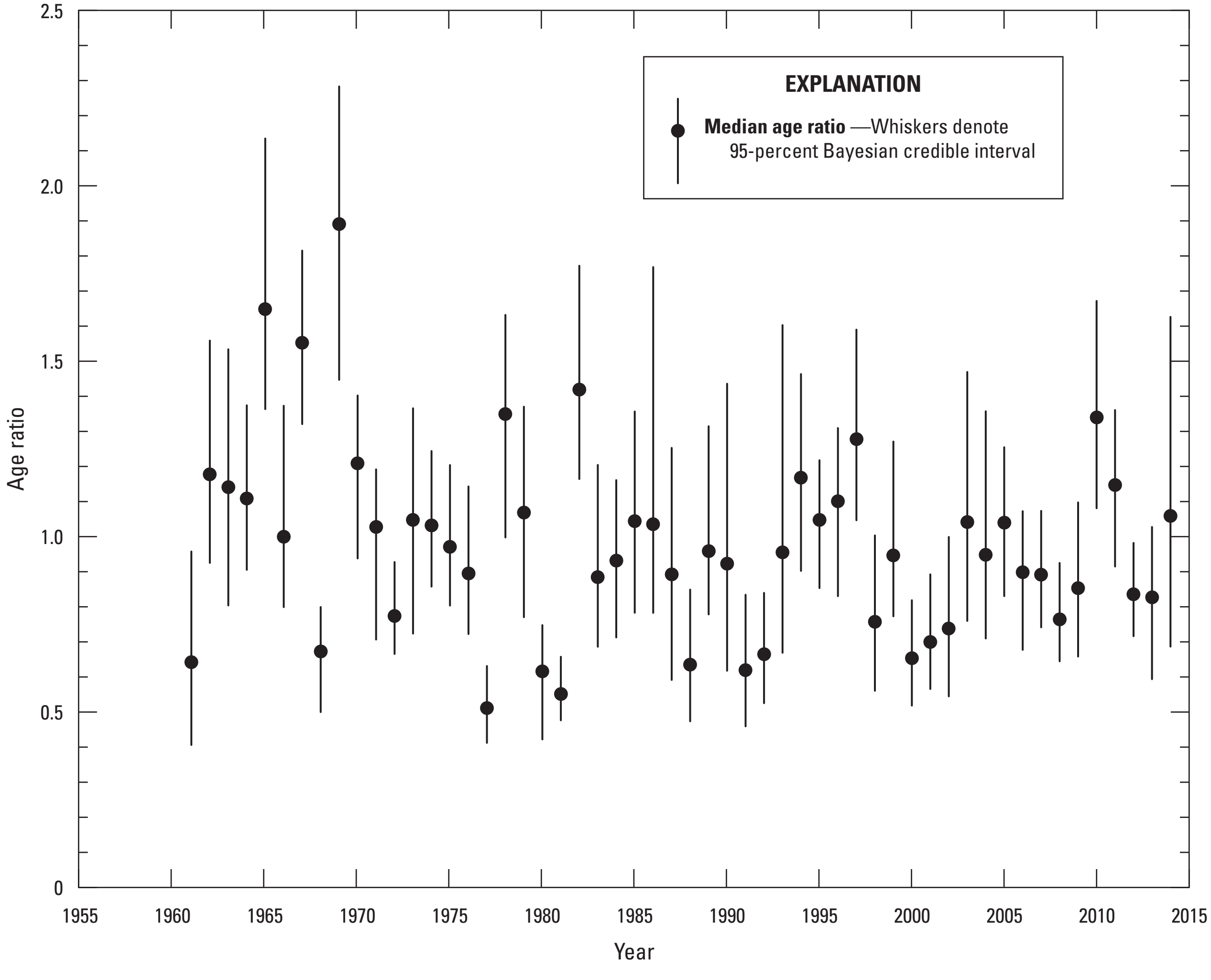

Figure 5. Estimated productivity (age ratio) of Northern pintail measured as the ratio of juvenile females to adult females in the fall flight, 1961–2014. Median with 95-percent Bayesian credible interval is presented.

potential for moderate density dependence ($\beta_1 = -0.09$; −0.25, −0.01; fig. 8A), and the interaction between population size and rainfall shows that cumulative rainfall on the wintering grounds might ameliorate the effect of density on the breeding grounds ($\beta_3 = 0.02$; 0.001, 0.057; fig. 8C). The posterior density for the average rainfall effect was mostly negative, which seems implausible, but overlapped zero ($\beta_3 = -0.13$; −0.35, 0.001; fig. 8B).

The posterior distributions of age ratio and winter survival as a function of population size and cumulative rainfall are shown in figure 9. At mean rainfall, age ratio and survival decreased with population size (fig. 9). When rainfall decreased, the effect of population size became more negative; in contrast, with an increase in rainfall, the effect of population size became less negative (fig. 9). Note that these estimated effects (figs. 8 and 9) include prior and posterior distributions that gave large negative effects for rainfall and a large positive interaction between rainfall and populations size for both age ratio and survival; therefore, compared with a model that only allowed for positive rainfall effects, the magnitude of the total rainfall effect may be overestimated.

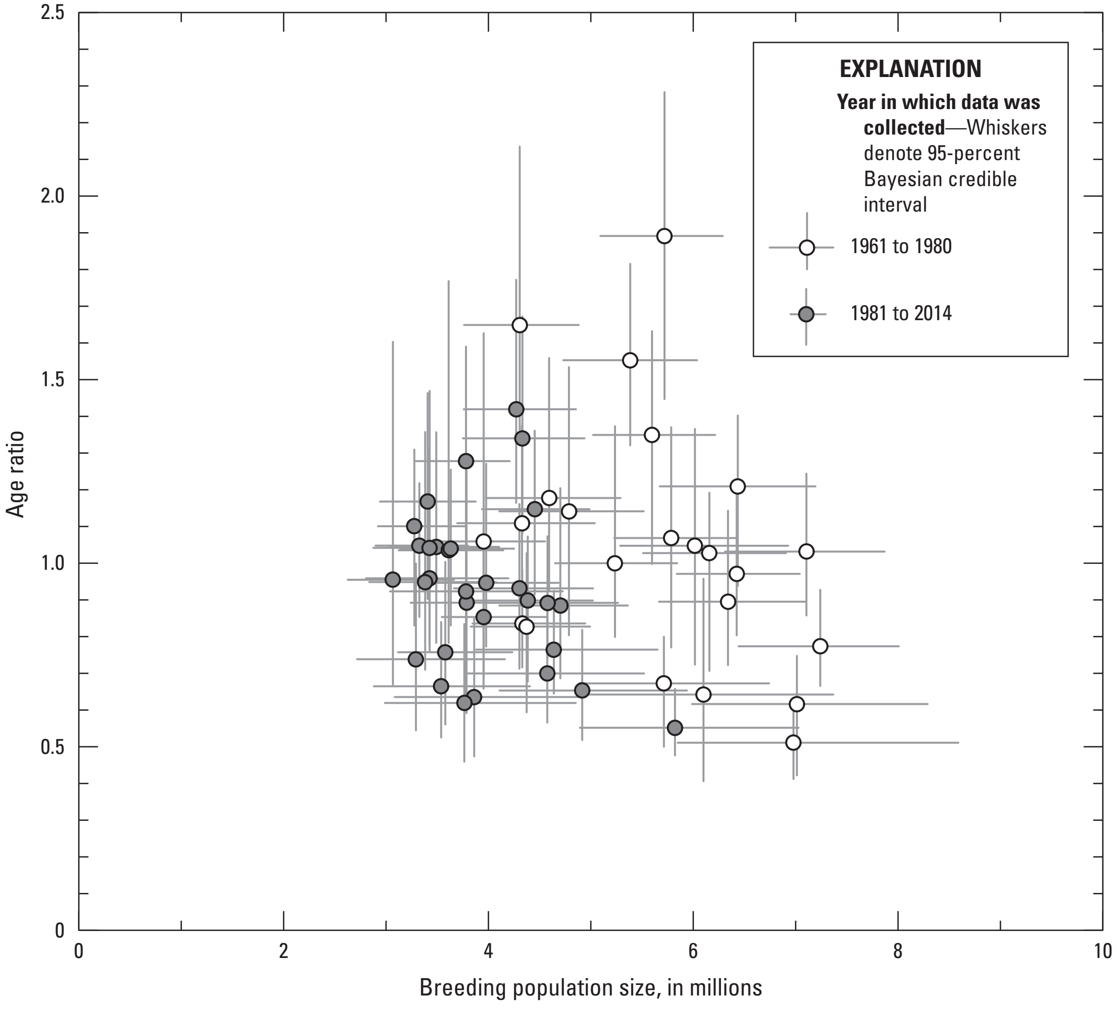

Figure 6. The age ratio in relation to the estimated breeding population size of Northern pintail in North America, 1961–2014. The gray crosses show the 95-percent Bayesian credible intervals along both dimensions.

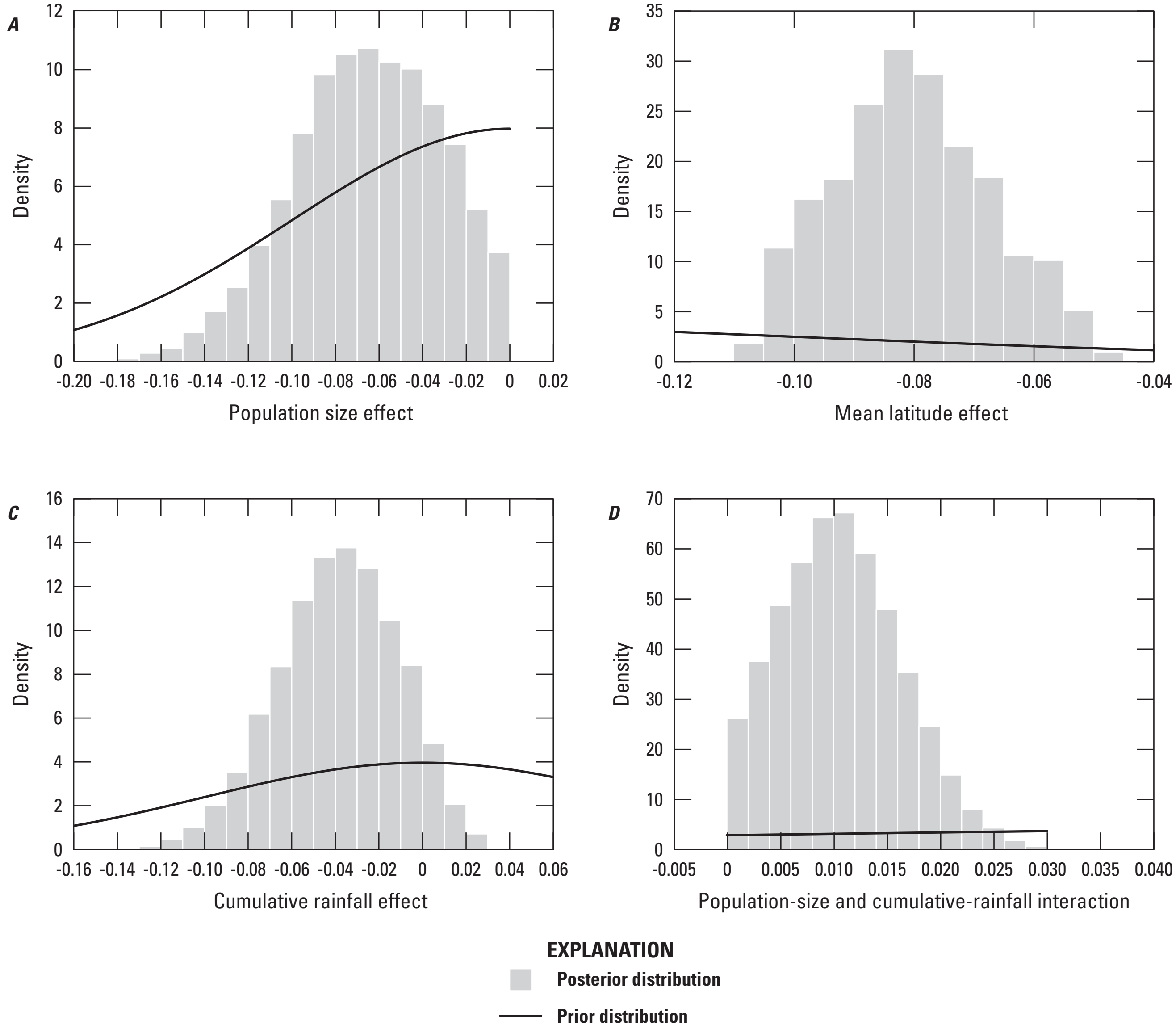

Figure 7. Prior and posterior probability densities for the estimated regression parameters relating the natural logarithm of Northern pintail age ratio in North America to *A*, post-hunting population size, *B*, mean latitude of the observed breeding population, *C*, cumulative rainfall on the California wintering area, and *D*, the interaction between post-hunting population size and cumulative rainfall, 1960–2014.

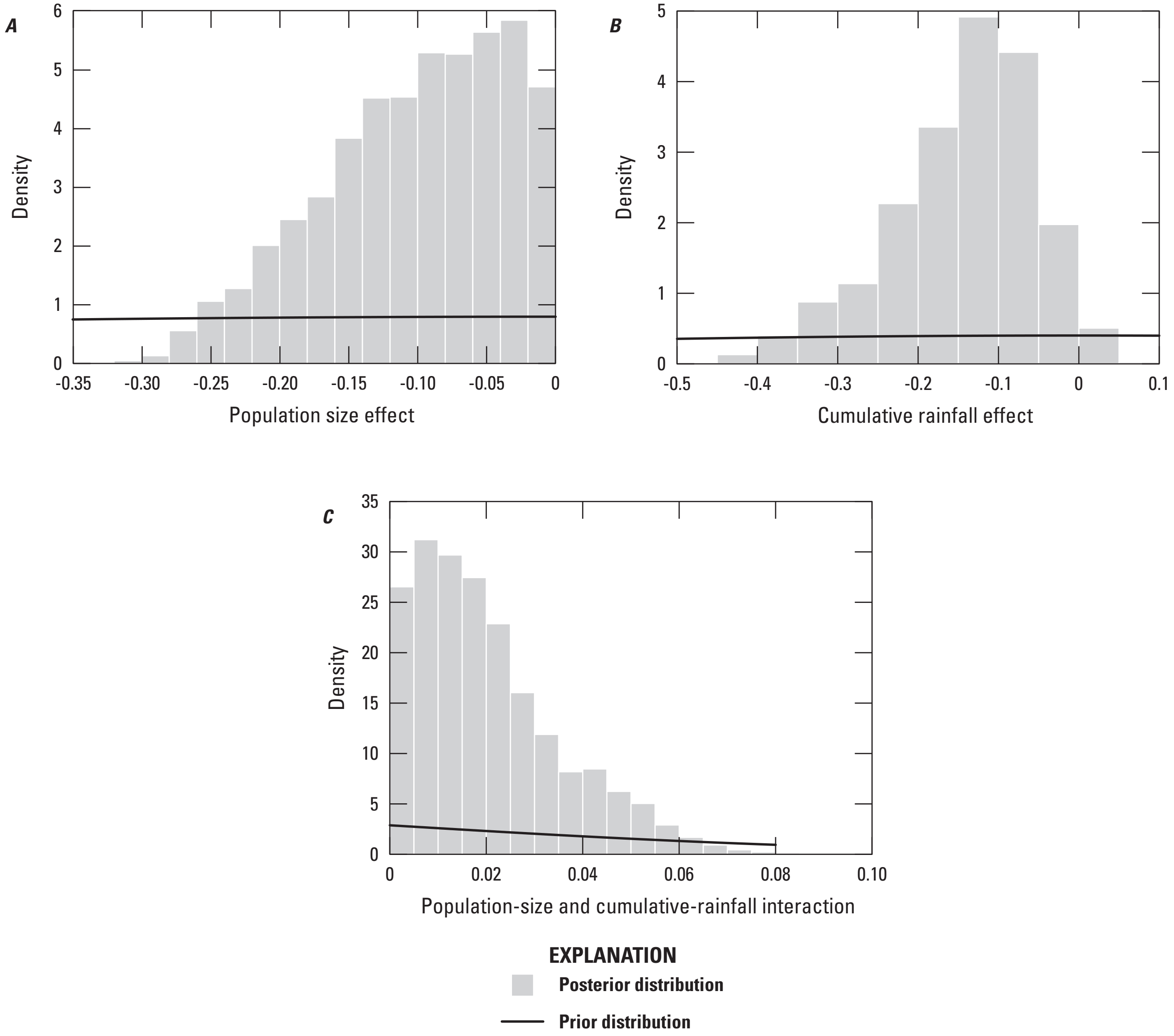

Figure 8. Prior and posterior probability densities for the estimated regression parameters relating the log odds ratio of Northern pintail winter survival to *A*, post-hunting population size, *B*, cumulative rainfall, and *C*, the interaction between post-hunting population size and cumulative rainfall, 1960–2014.

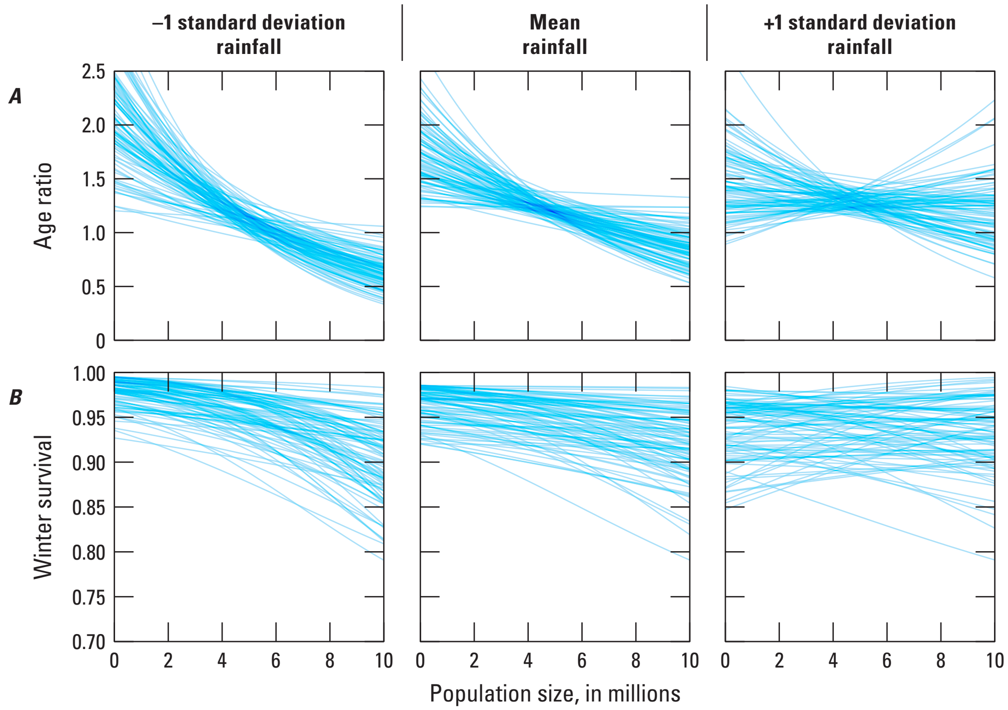

Figure 9. The combined effect of Northern pintail population size and California wintering-ground cumulative rainfall on *A*, age ratio and *B*, winter survival, demonstrating a reduction in density dependence with increased rainfall in California. (Columns are different levels of historical rainfall.)

Spatial Patterns in Survival and Reproduction

The model that allowed for a spatial age ratio (Pacific and Mid-Continent Flyways [Mid-Continent is Central and Mississippi Flyways combined]) did not converge (R-hat > 1.5 for all parameters); however, we summarized results because posterior distributions gave reasonable estimates and were similar to posterior distributions fit in other exploratory models that did converge, including spatial models of age ratio fit outside of the IPM context. The main results from the spatial model are differences in the temporal patterns of age ratio across regions (fig. 10) and in the covariate effects on age ratio (fig. 11). Age ratio in each region appeared to fluctuate around a similar mean from the 1960s until the mid-1980s and was often similar across regions (fig. 10). In the mid-1980s, the average age ratio in the Mid-Continent Flyway increased and became more variable, whereas in the Pacific Flyway, the age ratio became less variable and fluctuated around a lower mean slightly greater than 0.5 (fig. 10).

The estimated covariate effects also differed across regions (fig. 11). The posterior distribution for the post-hunting population size parameter (β_N) was much closer to zero for the Pacific Flyway than for the Mid-Continent Flyway (fig. 11A). To explore this pattern, we relaxed the prior distribution (made it less informative) to allow for positive parameter estimates and re-fit the model (data not shown). This gave largely positive estimates for the population size parameter in the Pacific Flyway, but the values for the Mid-Continent Flyway parameter were largely unchanged. Thus, when the North American breeding population was large, productivity in the Pacific Flyway was high. Similar patterns were found when age ratio was estimated using only banding and PCS data outside of the IPM; this pattern needs further investigation as it might be an artifact of long-term shifts in pintail demographics, spatial banding patterns, or other processes. Latitude and rainfall effects were similar between regions (figs. 11B and C), although the latitude effect did not fully converge in the results presented here (this parameter converged in previous model runs not presented). The large and negative effects of rainfall (figs. 11C and D) need to be examined and more appropriate priors applied.

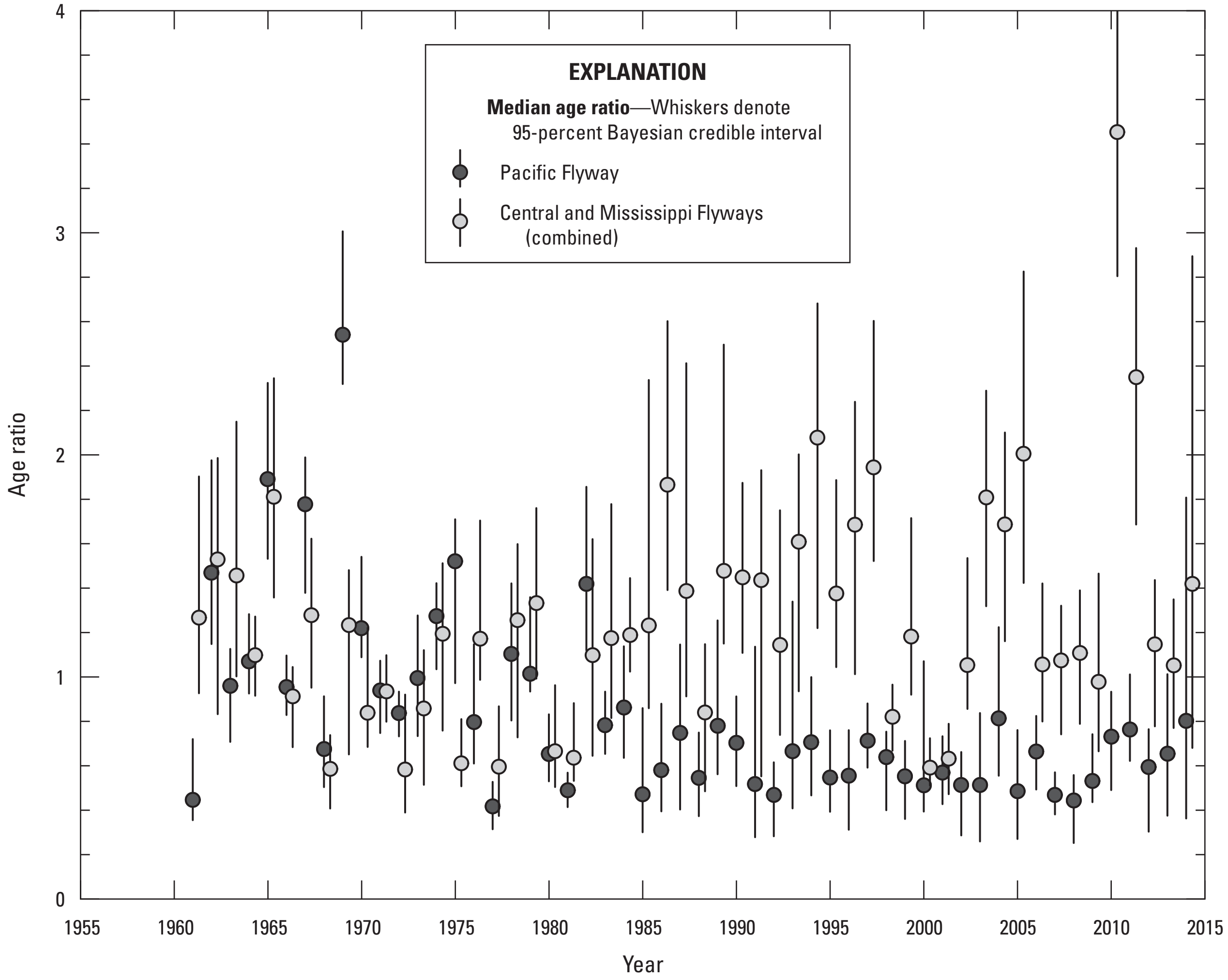

Figure 10. Northern pintail age ratio in the Pacific Flyway and the combined Central and Mississippi Flyways in North America, 1961–2014. Median with 95-percent Bayesian credible interval is presented.

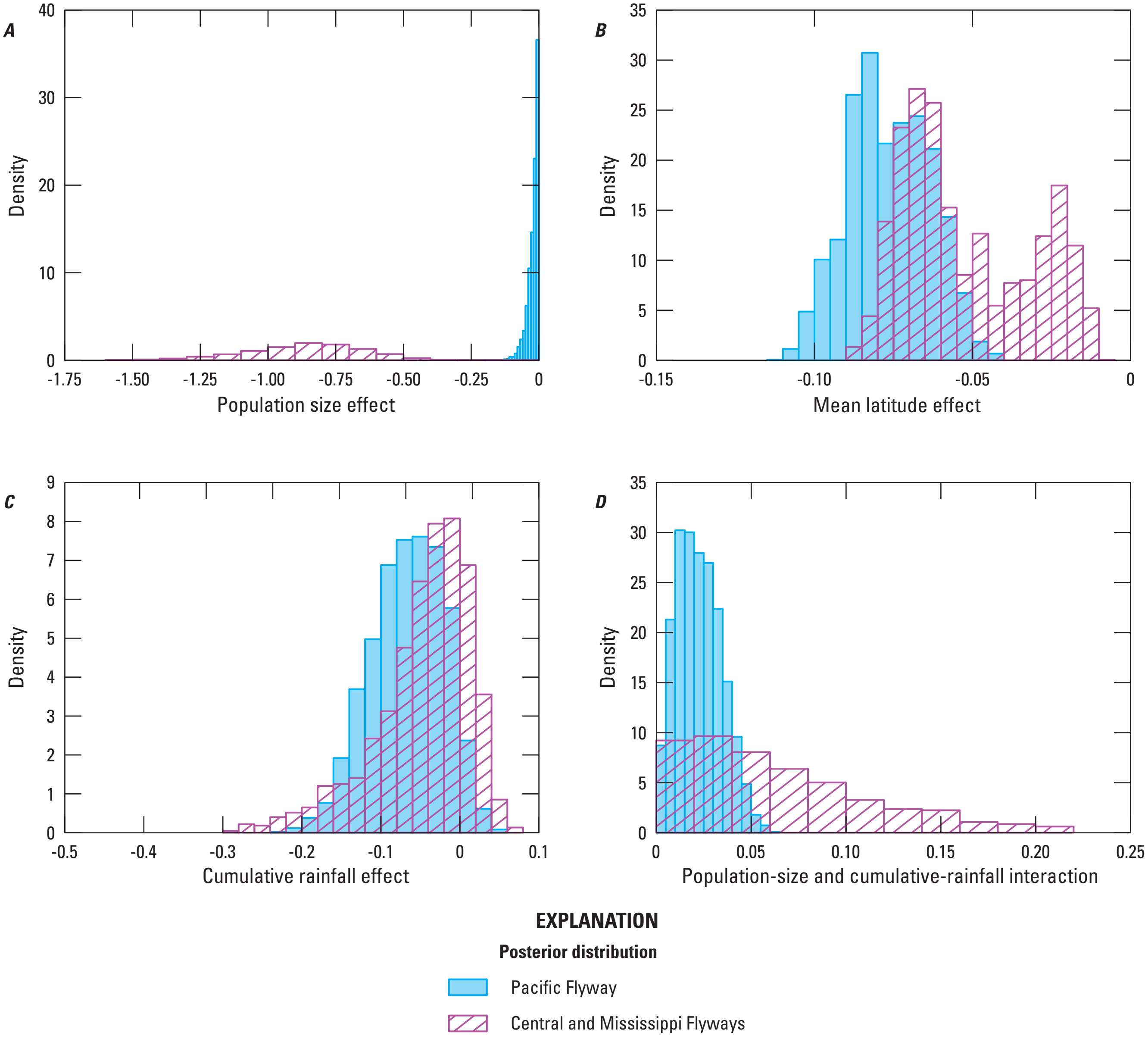

Figure 11. Posterior probability density for the estimated regression parameters relating the natural logarithm of Northern pintail age ratio in two flyways to *A*, post-hunting population size, *B*, mean latitude of the observed breeding population, *C*, cumulative rainfall on wintering areas, and *D*, the interaction between post-hunting population size and cumulative rainfall, 1960–2014.

Climate Change and Habitat Management Scenarios

Changes in the yield curve resulting from rainfall gain or loss due to climate change or habitat management are illustrated in figure 12. Rainfall gain shows a large expansion of the yield curve (increased equilibrium harvest for a given equilibrium breeding population size) compared to the yield curve at the long-term average condition (fig. 12). In contrast, a decrease in precipitation gave a small decline in maximum sustained harvest but a relatively large decline in population size under no harvest (that is, carrying capacity), as shown at the non-zero population size where harvest is also zero (fig. 12). Metrics describing the posterior change in yield curve are shown in table 1. Note that under reduced precipitation (−1 standard deviation in fig. 12), the posterior median yield curve is larger (more harvest) compared to average conditions as population and harvest approach zero; this implies that the intrinsic growth rate of the population under reduced rainfall was greater than under average rainfall conditions. This pattern is a consequence of the estimated posterior rainfall effects on age ratio (figs. 7C and D) and survival (figs. 8B and C). To the extent that this pattern is implausible, the prior might be adjusted to prevent implausible estimates and give more realistic yield curves in response to habitat change.

Table 1. Metrics summarizing the change in equilibrium harvest and population size with increased or decreased wintering-ground rainfall compared to the yield curve estimated under long-term average conditions.

[Metrics are the difference in maximum sustained harvest (ΔMSY), the difference in equilibrium population size obtained at maximum sustained yield (Δ*N* at MSY), the change in population size when total harvest remains as in the reference condition (Δ*N*), and the change in harvest that would be necessary to maintain the population size found at the MSY of the reference condition (Δ*H*). SD, standard deviation]

Metric (in millions)	–1 SD Precipitation[1]	+1 SD Precipitation[1]
ΔMSY	−0.05 (−0.38, 0.62)	1.33 (−2.12, 4.97)
Δ*N* at MSY	−1.35 (−5.45, −0.05)	13.81 (−10.16, 22.31)
Δ*N*	−3.09 (−10.95, 2.83)	18.47 (−11.38, 22.46)
Δ*H*	−0.09 (−0.47, 0.31)	0.44 (−1.38, 3.15)

[1] Values within parentheses are the upper and lower bounds of the 95-percent Bayesian credible interval.

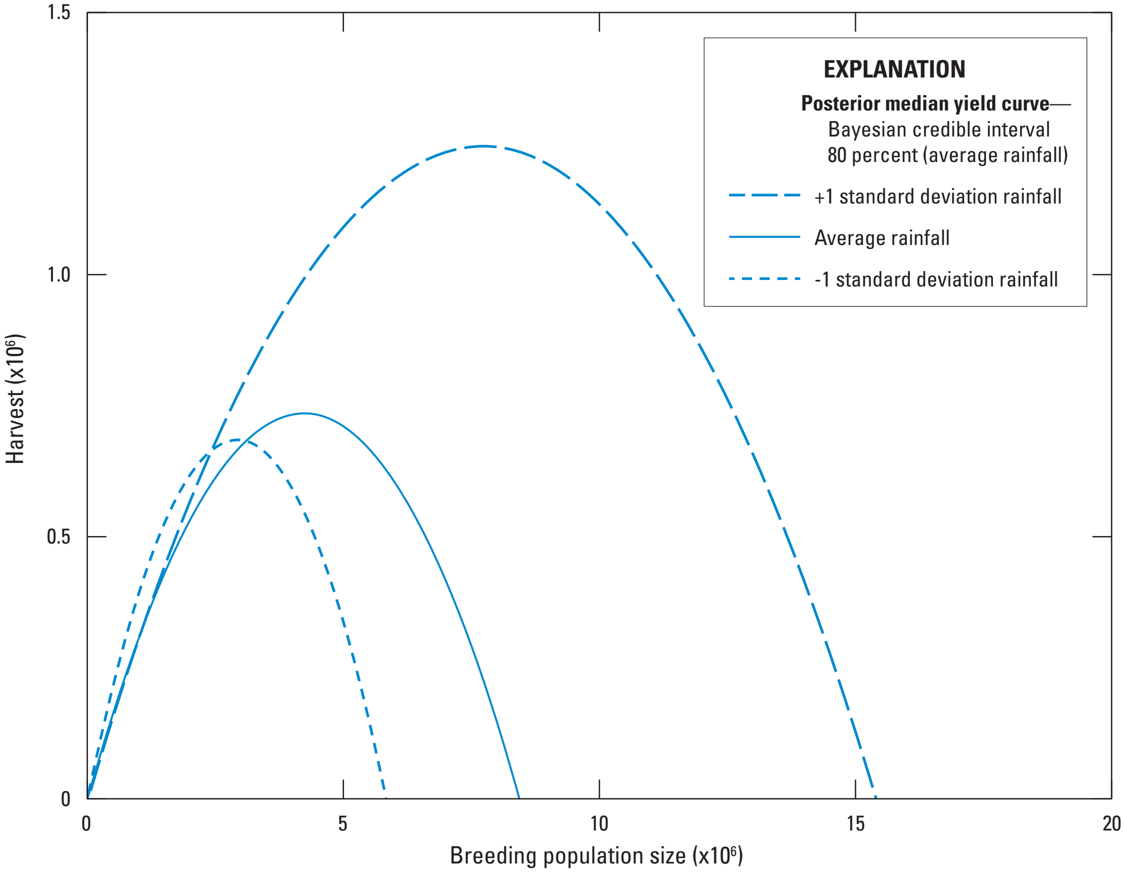

Figure 12. Posterior distributions of equilibrium harvest as a function of equilibrium breeding population size (the "yield curve") of Northern pintail under three climate scenarios.

Prairie Parkland Region Submodel

The predicted PPR age ratio is not closely related to the continental age ratio estimated from bird-band recoveries and the PCS when all years are considered together (fig. 13). During the recent past (1985–2009), however, the PPR age ratio increased faster than the continental age ratio. For the earlier years (before 1985), there was good agreement between continental and PPR age ratios when both were low, but the estimated PPR age ratio did not capture large spikes in continental age ratio during this period (fig. 13). These predictions do not include long-term changes in landscape cover other than changes in an index to PPR wetland conditions; therefore, the difference in pattern between early (before 1985) and late (after 1985) periods might be due to a large-scale shift in prairie landscapes, such as reduction in summer fallow (for example, Podruzny and others, 2002), predator communities, climate, or other mechanisms. Alternatively, better fit during the later period may be because the mechanistic model was based on nest survival and habitat selection data gathered during this period (Devries, 2014). In any case, it appears that the model gives plausible prairie age ratio (productivity) estimates for years after the mid-1980s.

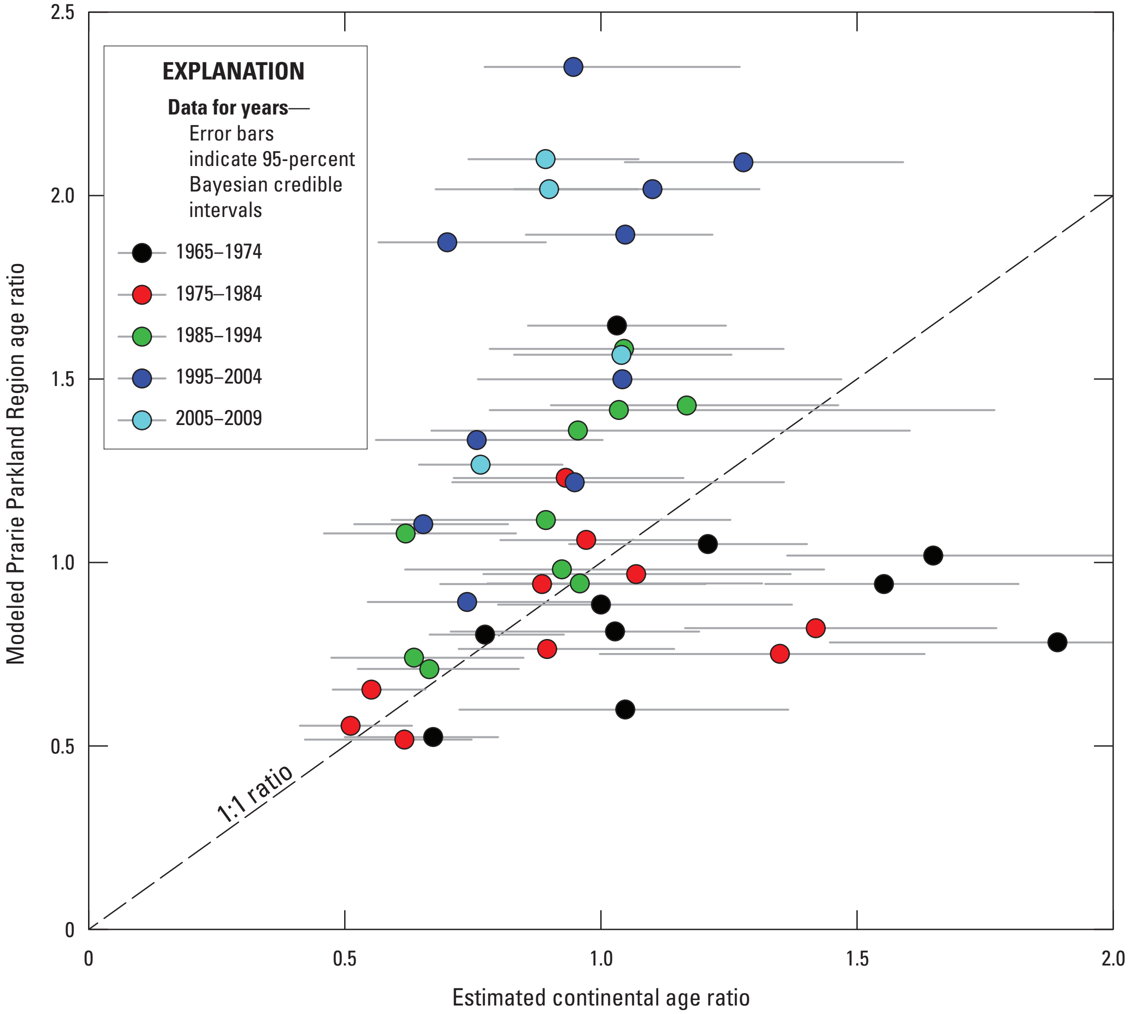

Figure 13. The Prairie Parkland Region age ratio of Northern pintail estimated from the Prairie Parkland Region model in relation to the continental age ratio estimated from Parts Collection Survey data, 1965–2009. Error bars indicate 95-percent Bayesian credible intervals.

Discussion

General Insights

Four major insights for management of wide-ranging species and integration of habitat and harvest management emerged from work on modeling pintail population dynamics. (1) Use of an IPM is highly valuable for building an annual cycle model that is consistent with all available data, but an IPM does not solve all inferential problems. (2) Essentially, no useful habitat data are available at the same spatial and temporal scale as the waterfowl demographic data, and given temporal changes in pintail demographics that occurred in the mid-1980s, the usefulness of the full time series of demographic data for inference is compromised. If a model is constructed to guide current management decisions, model development might be based on data sources available after the 1980s. (3) Little evidence is available for large variation in survival, which has been the basis for many hypotheses of waterfowl harvest and habitat management; instead, age ratio (recruitment) is variable across time and regions. This does not mean that survival does not respond to variation in harvest or habitat, just that the relative variation in survival is low, especially in adult cohorts, compared to variation in harvest and presumably, habitat. (4) The model of Mattsson and others (2012) is probably too complex to be estimated from available data and to make operational in a management context.

Use of an annual cycle model integrating data on population counts, bird-band recoveries, and age ratio is highly valuable with respect to understanding pintail population dynamics, but the model is no panacea for relating habitat to demographics. The main advantage of the model is estimation of all processes (for example, latitude correction of population estimates from the WBPHS, seasonal survival components, productivity, and habitat effects on survival and productivity) simultaneously. This ensures that estimates are logically consistent with each other and the underlying mathematical model. In addition, process variance (true stochastic fluctuations) and observation (sampling) variance of demographic rates and population size can be estimated, and this allows for a full accounting of uncertainty in a straightforward way.

A consequence of the linked structure of IPMs is that various components of the life cycle are not independent. Thus, assumptions imposed on one part of the life cycle can be carried through to affect estimates in other parts of the life cycle, especially parts for which there is little information. This property can help identify model-formulation errors in a component of the life cycle when the errors are large enough to become obvious by producing unbelievable patterns in other components. For example, the estimated harvest rates were far too high in an initial version of the model, and this caused winter survival estimates to be positively related to population size (positive density dependence)—a biologically unreasonable result. We therefore revised the harvest rate model by incorporating solicitation of bird bands and found more reasonable harvest estimates, and the positive relation between population size and survival disappeared. Thus, the linked nature of IPMs serves to evaluate the consequence of hypotheses and estimated parameters from one component of the life cycle through all other components.

A major issue with our effort was the uncertainty in the measure of habitat. There are essentially no relevant annual winter or breeding habitat datasets to form the basis of relating habitat to survival or productivity on an annual basis. Some data on annual breeding habitat are available from annual USFWS surveys and agricultural census efforts in the United States and Canada, at least in the PPR. Unfortunately, surveys of breeding habitat (May ponds in the WBPHS) do not increase the ability to predict pintail productivity (Sheaffer and others 1999; M.C. Runge, U.S. Geological Survey, and G.S. Boomer, U.S. Fish and Wildlife Service, written commun., 2005). For wintering areas, only NOAA weather data (https://www.ncdc.noaa.gov/cdo-web/) and U.S. Department of Agriculture crop acreage data (https://www.nass.usda.gov/Data_and_Statistics) are available on an annual basis for the same time frame and spatial scale as the pintail data. These data are rough proxies for the habitat conditions that directly affect pintail survival; thus, only a "framework" can be established now. The functional relation between habitat and demography might be determined if habitat data that reflected the winter conditions that matter to pintail were collected annually and made available. Similar concerns occur for breeding ground habitat data, especially outside of the agriculturally important PPR. Even in this region, however, land use, agriculture, and climate datasets were difficult to assemble, and many variables could be produced only from extensive geographic-information-system-based modeling efforts (Devries, 2014). If information on habitat is important for decision making, then a major effort of JVs and LCCs might be either to directly collect, synthesize, and freely distribute region-wide data on habitat conditions or foster others to do so (much as is done with bird-band recovery, the WBPHS, and PCS data). Perhaps an annual simple random sample in mid winter to late winter within a JV or LCC would suffice, including the use of remote sensing technology. When such information is available, a simple substitution of covariates into our model could take place.

Even if suitable habitat data were available, however, there is very little evidence for variation in survival using bird-band recovery data for 1960–2014, especially in adult cohorts (fig. 3). Therefore, regressions between a putative habitat covariate and survival for these years are not likely to be highly informative. Moreover, the steady survival rates indicate that the range of historical environmental variation is not sufficient to produce a response in pintail survival. Our analysis of pre-and post-season bird banding, as well as most radio-telemetry studies, indicates that survival after the hunting season is invariably high and that mortality occurs instead during the fall hunting season in greater rates than predicted by estimated harvest rates. Thus, hypotheses that include significant non-harvest mortality during the fall need to be considered and potentially included in pintail (and perhaps other waterfowl species) harvest management decisions. Hypotheses that form the basis of pintail or other species habitat management need to be reconsidered.

We were not successful in fully implementing the spatial annual cycle model as described in Mattsson and others (2012). The original model of Mattsson and others (2012), although highly informed by experts with extensive knowledge of pintail biology, is probably too detailed to be operational with the data collected on an annual basis (WBPHS population counts, wing samples from the PCS, and bird-band recoveries). The main drawback is a lack of spatially explicit annual estimates of the seasonal components of survival (fall, post-hunting, and breeding season survival), as well as annual estimates of breeding-area specific age ratios. To acquire such data would probably require massive investments in effort and new technologies, and such efforts may not be justified by an improvement in management outcomes. To complicate matters, there appears to have been long-term monotonic system changes that limit the utility of these time series for inferring causation. The first limitation introduces structural uncertainties in the model because processes are not well identified, and the second limitation, at worst, causes questionable inferences or, at best, restricts inferences to a subset of the time series, which increases parametric uncertainty. Thus, in the absence of new data, probably the best alternative is a simplification in model structure that still captures the major processes of habitat and harvest effects, such as is used for pintail or mallard adaptive harvest management (USFWS, 2013b), potentially including simple spatial structure in harvest, survival, or fall age ratio. Given the evidence for system change that occurred in the mid-1980s, limiting data for model development and prediction to those data after the 1980s needs to be considered. With any approach, considerable uncertainties will remain, and these need to be incorporated into the decision process. Then the effects of manipulations in an adaptive management framework can be monitored.

Although we believe our approach is reasonable and that the use of integrated population models and Bayesian methods are an improvement upon previous efforts, there are serious limitations in data sources to inform developed models and hypotheses. If similar approaches are to be applied to other species, especially taxa that lack the data common in hunted species, data limitations will become more severe. The approach used here, however, can still be applied, but the inference will be more reliant on the prior distributions supplied rather than any data. If the goal is transparency and a full accounting of uncertainties, then this is an advantage of our framework and likely very important to most taxa.

Specific Insights

Survival and Harvest

Remarkably, little variation in survival was found, especially for adult female pintail, across more than 5 decades (fig. 3), even though harvest rates changed nearly twofold (fig. 4) and population size underwent large fluctuations (fig. 2). This is consistent with other studies on pintail (Hestbeck, 1993; Franklin and others, 2002; Nicolai and others, 2005; Rice and others, 2010) and other avian species, including several waterfowl species (Gould and Nichols, 1998; Franklin and others, 2002). Unlike these past studies, we attempted to partition annual survival into components of the hunting and non-hunting seasons by comparing recovery probabilities between bird-banding samples from two periods of the year. Because these recovery probabilities were similar between the bird-banding samples, the results indicate that survival through the non-hunting period (late winter to fall) is very high. Such high survival rates challenge hypothesized mechanisms of density dependence for survival. Instead, these patterns indicate that survival during fall migration and the hunting season might be the limitation. Therefore, efforts to increase productivity might be most amenable to manipulation and respond most quickly to environmental change.

Density-dependent mortality during the post-hunting season has been assumed to be the underlying mechanism of harvest compensation (Boyce and others, 1999; Mattsson and others, 2012), including in the original articulation of the hypothesis for waterfowl (Anderson and Burnham, 1976). Instead we found very high survival during the post-hunting season and nearly constant but lower survival during the fall hunting period. Thus, fall survival seems to be largely independent of harvest rates, especially for adult females but also for most other cohorts in most years. High survival during the post-hunting period is consistent with some other studies that were based on radio telemetry in California (Miller and others, 1995; Fleskes and others, 2002, 2007), and Miller and others (1995) indicate that, on the basis of their data, survival during fall migration or breeding is the only component of annual survival that could be improved. Miller and others (1995) also report little difference in radio-marked female pintail survival between liberal and restrictive hunting regulations, as did Rice and others (2010) using band-recovery data from North America. These results are consistent with the analysis presented in this report. Fleskes and others (2007), who report on a larger range of study years (1987–2000) and regions within California than Miller and others (1995), found that fall and winter survival of adult females before, during, and after the hunting season had increased relative to the study years 1987–90 of Miller and others (1995). Fleskes and others (2007) attributed this to restrictive hunting regulations and increased habitat area. In this study, similar trends in continental patterns of adult survival were not seen, indicating that survival may have decreased outside California, although neither our investigation of spatial models nor the results of Rice and others (2010) show spatial variation in survival trends that would cancel out when pooled continentally. Moreover, radio telemetry estimates of winter survival in central North America (northern Texas and the Louisiana Gulf Coast) also indicate high survival after the hunting season (Cox and others, 1998; Moon and Haukos, 2006), and no mortalities were recorded during the spring migration for 71 radio-marked pintail in Nebraska (Pearse and others, 2011). Taken together, our analysis of long-term bird-banding data, as well as various studies in specific years and locations, indicates nothing other than high and constant survival after the hunting season.

The stationary nature of continental survival over five decades, especially for adult pintail, indicates that survival does not easily respond to variations in habitat, harvest, or population size. Instead, historical fluctuations of habitat, harvest, or population seem to have been within a zone of relative tolerance where pintail might compensate for any environmental perturbations. In life-history theory, such invariance of a phenotype to environmental perturbation is described as a “flat reaction norm” or demographic buffering (Stearns, 1992; Koons and others, 2014), and it has long been hypothesized that traits that contribute most to population growth should exhibit the most demographic buffering (Stearns, 1992; Caswell, 2001). For a life history like that of pintail, population growth will be most sensitive to adult survival (Flint and others, 1998; Koons and others, 2014); therefore, we expect pintail and other similar migratory species to have evolved life-history behavior in order to modulate environmental fluctuations and maintain survival. When considering habitat or harvest manipulation, such demographic buffering might be considered in the decision process.

There are at least two important implications of survival invariance. First, pintail survival is not expected to change in response to perturbations in habitat, harvest, or population size of the historical magnitude seen over the last 50 years (1961–2014), including wetland habitat gains or losses and changes in agricultural practices on the breeding and wintering grounds. Thus, environmental changes resulting from either management actions or climate change will need to be larger than historical perturbations before a large response in survival will be observed. Second, the invariance of survival indicates that using survival to evaluate habitat management actions is unlikely to be useful, as has been proposed recently to assess habitat management actions (NAWMP Assessment Steering Committee, 2007). Therefore, the results presented here indicate future investments to improve pintail survival, especially during the late winter through breeding season, may be misplaced. Instead, investment to improve reproductive success might be more effective for increasing population size or harvest yield, as well as easier to measure in order to evaluate habitat management. This includes investments in the wintering grounds (such as habitat that is designed to increase body mass upon spring departure) that might increase reproductive output (that is, “cross-seasonal effects”), although the marginal benefits of these indirect effects on reproduction seem unlikely to be more important than the direct effects of breeding habitat improvements and likely would be very difficult to measure. Alternatively, investments might be made with the intent to maintain current pintail survival (such as providing sanctuary habitat). However, in this case, no change in population size or harvest yield is expected, and this begs the question as to whether investments for survival of pintail or similar organisms are the best use of limited conservation resources. These considerations deserve greater analysis that is beyond the scope of this study, including a multi-species and ecosystem-wide evaluation. Results of this study are consistent with a recent analysis of a pintail population model, based on expert judgement (Mattsson and others, 2012), that showed proportional improvements on breeding grounds had a much larger population-level effect than proportional habitat improvements on wintering habitats. Because the model of Mattsson and others (2012) incorporated the assumption that survival varied after the hunting season owing to negative density dependence, the results reported here indicate that the relative difference in realized gains between breeding and wintering-ground improvement might be larger than that predicted by the model of Mattson and others (2012) and would more highly favor habitat investment in breeding areas.

One exception to the constant survival rates of pintail is the upward trend in juvenile male fall survival through the 1960s and 1970s (fig. 3). During this period, our estimates of harvest rates were relatively constant at the historical maximum (fig. 4). One possible explanation is that some environmental condition was improving that affected juvenile males disproportionately. We have difficulty imagining what age- and sex-specific effect this might be that could account for a 10- to 20-percent increase in survival over these two decades, perhaps a reduction in disease occurrence. A more likely mechanism is that the estimates of harvest rates in 1960s and 1970s are biased low. We extrapolated the reporting rates from Henny and Burnham (1976; also reported in Nichols and others, 1991) backwards to 1960 because there are no direct estimates for this period. If reporting rates were lower than those we used, harvest estimates would be higher, and a relation between survival and harvest might be found in juvenile males. In any case, the lack of annual reporting rate estimates reduces the value of these historical datasets.

Many of the investigations of annual variation in survival have used classical “fixed effect” estimates of annual survival (in pintail see Hestbeck, 1993; Rice and others, 2010), even though it has long been known that these lead to an “inadmissible” estimator, meaning that an equal or better estimator is known to exist (Efron and Morris, 1977). In our context, the better estimator is one that is shrunk toward a grand mean, as we have done in this hierarchical Bayesian analysis or others have employed in a non-Bayesian context (Gould and Nichols, 1998; Franklin and others, 2002). An important implication of past work that used a “fixed effect” specification in survival models is that the annual variation in survival estimates (as estimated by the sample variance across all year estimates) is too high. This is not just an academic point based on theoretical statistics. At a minimum, this causes researchers and managers to conclude more variation than is justified (for example see the plots in Rice and others, 2010). In important applications, such as modeling stochastic population processes that form the basis of harvest management decisions, this will lead to overestimation of the true demographic process variation.

Productivity

Unlike survival, pintail age ratio responds strongly to habitat conditions (breeding wetland conditions as indexed by mean latitude of the observed breeding population in the WBPHS) and population density (fig. 7), as has been found previously (Sheaffer and others, 1999; M.C. Runge, U.S. Geological Survey, and G.S. Boomer, U.S. Fish and Wildlife Service, written commun., 2005). Evidence of a direct effect (main effect) of winter habitat conditions (cumulative rainfall) on productivity (cross-seasonal effects) is weak and might be negative at average conditions (fig. 7). Instead there is evidence for an interaction between winter habitat conditions and population size on age ratio so that when rainfall is increased, the effect of density is reduced (fig. 7D).

When productivity patterns are examined spatially, the Pacific Flyway had high and variable productivity in the 1960s and 1970s, followed by relatively low and constant productivity through current years (1985–2013) (fig. 10). In the Mid-Continent Flyway, however, the mean and variance of productivity increased after the mid-1980s (fig. 10). This indicates substantial demographic differences between these flyways, as is reflected in differences in estimates of regression parameters (fig. 11), and may warrant different harvest or habitat management approaches. However, simulation chains of this spatial model did not converge on the same posterior distribution; therefore, inferences are suspect. In any case, demographic differences between regions deserve more investigation and if present would affect harvest yield potential across regions.

Prairie Parkland Region Submodel

The submodel to predict PPR age ratio (breeding productivity) of pintail showed some promise. Except for the early decades of the 1960s and 1970s, the relation between estimates of continental productivity and PPR age ratio was as expected (fig. 13); as continental age ratio increased, PPR age ratio increased at a greater rate to reflect the higher productivity of this area in good (wet) years compared to more northern areas. However, the relation left much unexplained variation. Much of this unexplained variation is due to the proportion of pintail that breed in the PPR. Although this was estimated with the IPM, it was not incorporated into the submodel. An important source of unexplained variation is due to landscape change not captured in our land-use dataset. Because we were still attempting to build a land-use dataset that extended over the history of the age ratio data, we could not fully evaluate this option. In addition, no data on spatial covariance between important demographic processes (hen survival, nest success, duckling survival, and others) were available, and early simulations showed these to be important in predicting a region-wide age ratio. Therefore, we assumed that these demographic processes covaried with local wetland conditions. Thus, any departure from our assumptions about these processes would have an effect on predictions. Nevertheless, there was a positive relation between continental and PPR age ratio for 1980–2009. The difference in dynamics during the 1960s through 1970s remains to be explained, as it was not captured by preliminary landscape-change data.

Summary

This study was conducted by the U.S. Geological Survey, in cooperation with the Gulf Coast Prairie Landscape Conservation Cooperative, Ducks Unlimited Canada, Environment and Climate Change Canada, and the U.S. Fish and Wildlife Service, to build a framework to integrate habitat and harvest management of *Anas acuta* (Northern pintail, hereafter pintail).

We developed an integrated population model (IPM) of the annual life cycle of pintail using available datasets to provide a decision support framework for habitat and harvest management. An IPM uses multiple datasets to simultaneously estimate population size, survival, per capita reproductive rates, or other demographic parameters. We attempted to expand the model to a spatially specific framework to allow flyway-specific decision support. We also built a mechanistic model to predict per capita reproductive rates from small-scale landscape data in the Prairie Parkland Region, with the intent to allow these predictions to inform prairie-parkland-specific reproductive rates in a spatial life cycle model.

The main accomplishments of this study are (1) development of an IPM for pintail to guide harvest and habitat management, (2) development of a Prairie Parkland Region (PPR) breeding submodel to predict pintail productivity, (3) development of statistical methodology to estimate pintail productivity (as measured by the ratio of juvenile to adult ducks in hunter-collected wing samples) and winter survival and relate these estimates to covariates, and (4) an illustration of how to use a model and estimated parameters to predict pintail population size and sustainable harvest as a function of changes in habitat. Estimation of pintail survival from bird-banding data shows that there has been relatively little variation in survival. A productivity model showed strong effects of breeding ground conditions, wintering-ground habitat cumulative precipitation, and population size on pintail productivity. Thus, most temporal variation in pintail demographic rates is due to effects on reproduction and not survival, including effects of breeding or wintering-ground habitat. These results indicate that habitat conservation efforts may be more successful if they focus on maintaining or increasing breeding and wintering-ground habitat to protect or increase pintail productivity, as opposed to managing habitat to change survival rates.

An IPM that allowed for different demographic patterns between the Pacific Flyway and the combined Central and Mississippi Flyways (Mid-Continent Flyway) showed striking differences in productivity across years between these regions. Until the mid-1980s, pintail productivity was similar between these regions. After the mid-1980s, pintail productivity became low and stable in the Pacific Flyway, whereas in the Mid-Continent Flyway, productivity remained high and variable. Covariate effects on productivity also differed between regions. There was a much larger negative effect of population size in the Mid-Continent Flyway, indicating optimal habitat and harvest management strategies differ between regions.

Predictions from a mechanistic model of PPR productivity also differed across time periods. The model used contemporary landscape cover data, year- and location-specific data on pintail population size, and landscape wetness to predict local pintail breeding effort, nest site selection, nest success, and duckling survival, which were combined and summed across the entire region. Predictions were highly variable across years, but patterns of variation differed between early and later periods. For the years after the mid-1980s, model predictions for pintail productivity in the PPR were, on average, greater than those for the continental region, and as the continental age ratio increased, the model predictions for the PPR increased by a greater amount, as is expected if the PPR is highly productive for pintail compared to more northern areas. In contrast, model predictions for productivity in the PPR before the mid-1980s were, on average, lower than those for the continental region and did not increase with continental productivity. This difference in patterns indicates that fundamental changes in pintail productivity occurred between periods owing to landscape change not associated with wetness, which is known to have occurred, and possible changes in the reproductive response (hen effort, nest site selection, nest success, or duckling survival) of pintail to landscapes.

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