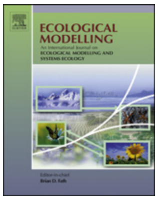
Ecological Modelling 225 (2012) 146–158

Contents lists available at SciVerse ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel



A modeling framework for integrated harvest and habitat management of North American waterfowl: Case-study of northern pintail metapopulation dynamics

B.J. Mattsson[a,*], M.C. Runge[b], J.H. Devries[c], G.S. Boomer[d], J.M. Eadie[e], D.A. Haukos[f], J.P. Fleskes[a], D.N. Koons[g], W.E. Thogmartin[h], R.G. Clark[i]

[a] U.S. Geological Survey, Western Ecological Research Center, United States
[b] U.S. Geological Survey, Patuxent Wildlife Research Center, United States
[c] Ducks Unlimited Canada, Canada
[d] U.S. Fish & Wildlife Service, Division of Migratory Bird Management, United States
[e] University of California, Davis, United States
[f] Kansas State University, Cooperative Fish & Wildlife Research Unit, United States
[g] Utah State University Wildland Resources Department, United States
[h] U.S. Geological Survey, Upper Midwest Environmental Sciences Center, United States
[i] Environment Canada, Prairie and Northern Wildlife Research Center, Canada

ARTICLE INFO

Article history:
Received 14 February 2011
Received in revised form 28 October 2011
Accepted 31 October 2011

Keywords:
Metapopulation model
Integrated management framework
Northern pintail
Anas acuta
Carrying capacity
Sustained yield

ABSTRACT

We developed and evaluated the performance of a metapopulation model enabling managers to examine, for the first time, the consequences of alternative management strategies involving habitat conditions and hunting on both harvest opportunity and carrying capacity (i.e., equilibrium population size in the absence of harvest) for migratory waterfowl at a continental scale. Our focus is on the northern pintail (*Anas acuta*; hereafter, pintail), which serves as a useful model species to examine the potential for integrating waterfowl harvest and habitat management in North America. We developed submodel structure capturing important processes for pintail populations during breeding, fall migration, winter, and spring migration while encompassing spatial structure representing three core breeding areas and two core nonbreeding areas. A number of continental-scale predictions from our baseline parameterization (e.g., carrying capacity of 5.5 million, equilibrium population size of 2.9 million and harvest rate of 12% at maximum sustained yield [MSY]) were within 10% of those from the pintail harvest strategy under current use by the U.S. Fish and Wildlife Service. To begin investigating the interaction of harvest and habitat management, we examined equilibrium population conditions for pintail at the continental scale across a range of harvest rates while perturbing model parameters to represent: (1) a 10% increase in breeding habitat quality in the Prairie Pothole population (PR); and (2) a 10% increase in nonbreeding habitat quantity along in the Gulf Coast (GC). Based on our model and analysis, a greater increase in carrying capacity and sustainable harvest was seen when increasing a proxy for habitat quality in the Prairie Pothole population. This finding and underlying assumptions must be critically evaluated, however, before specific management recommendations can be made. To make such recommendations, we require (1) extended, refined submodels with additional parameters linking influences of habitat management and environmental conditions to key life-history parameters; (2) a formal sensitivity analysis of the revised model; (3) an integrated population model that incorporates empirical data for estimating key vital rates; and (4) cost estimates for changing these additional parameters through habitat management efforts. We foresee great utility in using an integrated modeling approach to predict habitat and harvest management influences on continental-scale population responses while explicitly considering putative effects of climate change. Such a model could be readily adapted for management of many habitat-limited species.

1. Introduction

Achieving broad-scale conservation goals and societal demands for the use of natural resources presents great challenges worldwide (Sutherland, 2001; Lertzman, 2009). Decisions in natural resource management are particularly complex when achieving

---

[*] Corresponding author at: U.S. Geological Survey, Western Ecological Research Center, California LCC, 3020 State Univ. Drive East, Suite 2007, Sacramento, CA 95819, United States. Tel.: +1 706 534 0896.
E-mail address: bmattsson@usgs.gov (B.J. Mattsson).

0304-3800/$ – see front matter. Published by Elsevier B.V.
doi:10.1016/j.ecolmodel.2011.10.028

these goals requires management at multiple spatial scales by multiple entities representing diverse approaches to management (Runge et al., 2006; Whittingham et al., 2007; McAlpine et al., 2008). A prominent example of this is management of migratory waterfowl species, many of which exhibit a continental distribution and spatial heterogeneity in demographic rates (Saether et al., 2008). A specific challenge in managing waterfowl is that habitat and harvest management actions are often implemented at local or regional scales, whereas concerns about waterfowl population dynamics reside at the continental scale. Integrating these management actions and evaluating their consequences at broader spatial scales remains an outstanding but important task to ensure sustainability of waterfowl populations.

Natural resource agencies in North America, including the U.S. Fish and Wildlife Service (USFWS) and the Canadian Wildlife Service (CWS) have a mandate to enact broad-scale habitat protection and restoration through programs such as the North American Waterfowl Management Plan (NAWMP; Anonymous, 1986) and to set waterfowl harvest regulations consistent with the Migratory Bird Treaty Act. Although these two broad activities are designed to affect the same populations of waterfowl, the objectives of habitat and harvest management programs are not integrated (Runge et al., 2006). Indeed, recent biological reviews identified deficiencies in NAWMP program performance and prioritized the steps needed to improve decision processes (Anderson et al., 2007). In 2005, the NAWMP Committee and the Adaptive Harvest Management Task Force for the International Association of Fish and Wildlife Agencies commissioned a Joint Task Group to develop options and recommendations for clarifying NAWMP population objectives and their use in harvest management (Anderson et al., 2007). This same year, the NAWMP Committee also commissioned an Assessment Steering Committee (ASC) to conduct a continental biological assessment of the NAWMP (Assessment Steering Committee, 2007). These reviews challenged NAWMP to implement formal measures to substantiate how actions taken by joint ventures (JVs; i.e., partnerships responsible for implementing bird conservation plans within one or more contiguous ecoregions) contribute to achieving NAWMP goals. Further recommendations suggested more effective methods of setting harvest regulations by developing a coherent decision support framework explicitly linking habitat conditions to harvest opportunity. The NAWMP is currently undergoing a revision that could be improved by incorporating such a coherent decision framework.

One of the needs identified by the Joint Task Group was an integrated modeling framework for making simultaneous predictions about the effects of harvest and habitat management (Anderson et al., 2007). In the United States, predictive models have been used to inform decision-making regarding waterfowl harvest regulations through an application of adaptive harvest management at the continental level (USFWS, 2009b). Concurrently, predictive habitat models at the JV scale have been used to support planning activities in some JVs under NAWMP (Neraasen and Nelson, 1999; Prairie Habitat Joint Venture, 2009). Despite these parallel efforts, there is no formal link between the predictive models used in these two endeavors, nor is there a formal recognition that the outcomes of each management program affect the outcomes of the other (Runge et al., 2006).

Our focus is on the northern pintail (*Anas acuta*; hereafter, pintail), which serves as a useful model species to examine the potential of integrating harvest and habitat management for waterfowl in North America for several reasons: (1) continental population dynamics are largely driven by processes occurring in a few key breeding and non-breeding areas (Miller et al., 2001); (2) there is a growing toolkit of regionally based and spatially explicit population and habitat models (Podruzny et al., 2002; Voldseth et al., 2007; Saether et al., 2008); (3) there is an extensive empirical database to use in models of population dynamics and of the recent landscape changes that have affected those dynamics (Zimpfer et al., 2009; Natural Resources Canada, 2010; U.S. Geological Survey, 2010); and (4) there is considerable conservation concern for this species (Miller et al., 2001). The pintail is a medium-sized dabbling duck that feeds on plant seeds and invertebrates in a variety of wetland and agricultural habitats, breeds from Alaska to the northern Great Plains, and winters primarily along the Gulf and Pacific coasts (Austin and Miller, 1995). Since 1995, unlike most other waterfowl species, the pintail population has remained well below the NAWMP goal of 5.6 million birds across breeding populations. For example, in 2009, the breeding population of pintail in traditional survey areas was 43% below the NAWMP goal and 20% below the long-term average (USFWS, 2009a). Failure of the pintail population to respond positively to improved wetland conditions on the Canadian Prairies and northward shifts in the spring population distribution suggest persistent changes in population–environment interactions. Several hypotheses could explain low pintail populations, but considerable uncertainty remains regarding how population dynamics are influenced by land use and wetland changes, harvest and disease impacts, and breeding population redistribution (Podruzny et al., 2002; Runge and Boomer, 2005). In response to these knowledge gaps, the Pintail Action Group, comprised of non-government, state, and federal agencies, was formed in 2003 following a 2001 workshop focused on concerns about pintail populations (Miller et al., 2001). Endorsed by the NAWMP Committee, the Pintail Action Group supports planning, coordination, and evaluation of pintail management and research actions across North America. The Pintail Action Group provided the impetus to build and evaluate the performance of a continental metapopulation model explicitly accounting for habitat and harvest influences. The vision is that this model may serve as a case study for applying such a formal modeling approach to management and conservation of other taxa.

Our objective, then, is to develop and evaluate the performance of a metapopulation model that serves as a template and enables us to examine, for the first time, the consequences of alternative management strategies involving habitat conditions and hunting on both harvest opportunity and carrying capacity (i.e., equilibrium population size in the absence of harvest) for a migratory game bird at a continental scale. Rather than producing an endpoint platform for population assessment and management, the model is designed to demonstrate the utility of a predictive approach capturing the essential dynamics of the population as simply as possible while accounting for variation in habitat quality, habitat quantity, and harvest regulations. We use the model to conduct a prototype analysis designed to examine the potential influence of the functional relationships regarding key vital rates and habitat condition in each population on continental-scale population dynamics and to focus attention on the key underlying assumptions upon which migratory gamebird management is based (Delgado and Gomez-Skarmeta, 1998). Specifically, we develop submodel structures capturing important population processes during breeding, fall migration, winter, and spring migration. The metapopulation model represents spatial structure encompassing core breeding and nonbreeding areas and temporal structure encompassing the annual cycle. With this model structure, we explore how habitat management may affect pintail population dynamics and harvest potential at the continental scale. Specifically, we conduct a perturbation analysis to explore how the interaction between harvest rate and habitat management actions on the breeding and nonbreeding grounds affects continental carrying capacity and sustainable harvest of pintails. We then propose future steps in model development, including submodel refinement and parameter estimation, which will be needed prior to use of this model to inform decision makers.

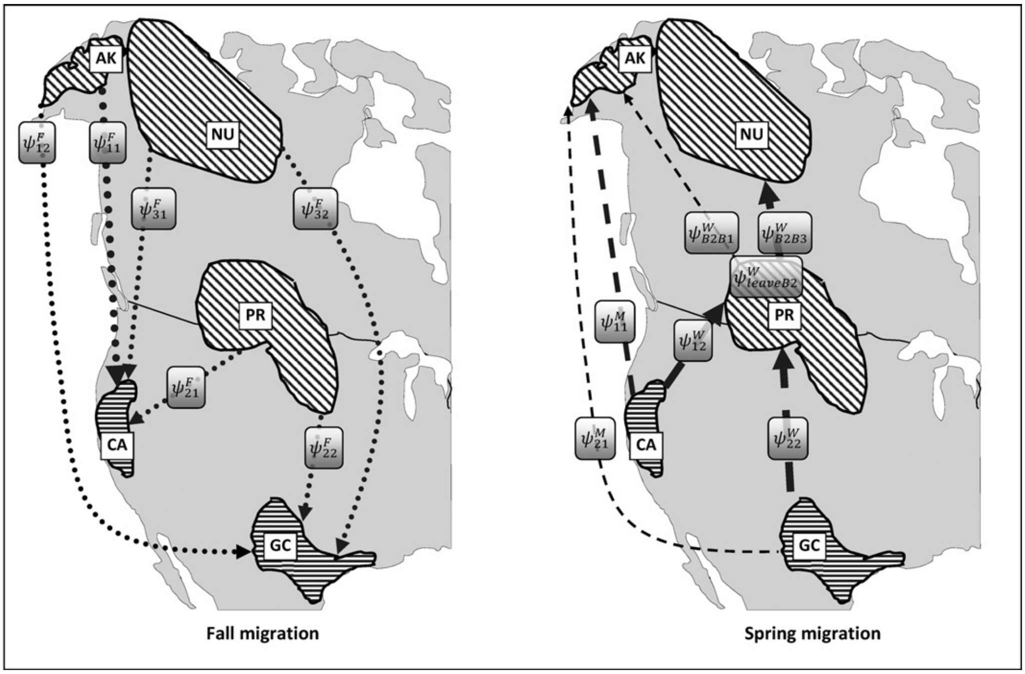


Fig. 1. Spatial representation of a metapopulation model for northern pintail (*Anas acuta*) in North America, which includes fall migration (F; left) and spring migration (W; right) between three breeding populations (1. AK = Alaska; 2. PR = Prairie Pothole; 3. NU = Northern Unsurveyed) and two nonbreeding populations (1. CA = California; 2. GC = Gulf Coast). Arrows indicate generalized points of departure and arrival during spring migration (dashed) and fall migration (dotted). Each arrow is labeled by respective migration route probabilities (ψ). Pintails that arriving in PR may then continue onto NU or to AK according to a density-dependent probability ($\psi_{leaveB2}^{W}$). Width of arrow indicates relative frequency by which pintails are expected to migrate between populations during a given season.

2. Model and methods

The conceptual foundation for this model is based on our understanding of pintail dynamics through the waterfowl population and harvest surveys and banding programs of the U.S. Fish and Wildlife and Canadian Wildlife Services (USFWS, 2007, 2009a,b) along with state and provincial partners, representing one of the most extensive cooperative wildlife monitoring efforts in the world. Annual data from these programs provide estimates of continental breeding population size and distribution, habitat conditions (e.g., wetland numbers [May ponds] in prairie survey strata), and key demographic parameters for most waterfowl species including pintail (Nichols et al., 1995). In structuring and parameterizing our model, we have drawn on insights from retrospective examination of these data (e.g., Johnson and Grier, 1988; Hestbeck, 1995; Runge and Boomer, 2005; Rice et al., 2010), original field research (Miller et al., 2005; Richkus et al., 2005; Haukos et al., 2006; Fleskes et al., 2007), unpublished data, and where data are lacking, expert judgment.

The model is spatially structured around three core breeding populations and two nonbreeding populations (Fig. 1). We acknowledge that each of the populations defined here may be comprised of multiple genetically distinguishable populations, but we refer to these collections of individuals that are collocated in space and time as populations for the purpose of this paper. The core breeding populations represent demographically distinct populations of pintails from nesting through completion of brood rearing and include Alaska (AK; breeding population 1, Prairie Pothole (PR; breeding population 2, and Northern Unsurveyed (NU; breeding population 3). Rather than representing a geographic area *per se*, the NU population is included to capture the observed dynamic that in dry years pintails overfly the PR (Podruzny et al., 2002; Runge and Boomer, 2005). The core nonbreeding populations are those areas occupied by pintails from post-harvest through completion of spring migration and include California (CA; nonbreeding population 1) and Gulf Coast (GC; nonbreeding population 2). With the exception of the AK and NU populations, each of these populations occupies multiple JVs. Therefore, we refer to Alaska and each collection of JVs (i.e., Prairie Pothole, California, and Gulf Coast) as geographical regions in the context of management actions affecting vital rates of populations. Specifying functional forms of density dependence at this regional scale provides an important linkage between local or JV-scale habitat conditions and continental-scale population dynamics. Pintails are accounted for by sex and age, with two age classes: juveniles become adults when they survive from fledging until the end of the hunting season, and these hatch-year birds may begin breeding during the subsequent breeding season. The model breaks the annual cycle into three discrete seasons: breeding (i.e., nesting through completion of brood rearing; April 15–August 15), fall through mid-winter (i.e., fall migration through the end of hunting season; August 15–January 15), and late winter through spring (i.e., post-harvest through completion of spring migration, henceforth post-harvest; January 15–April 15; Fig. 2). Note that the transition dates between seasons may vary among populations and years and are therefore approximations.

2.1. Breeding season

The metapopulation model begins with adult males and females on the breeding grounds at the start of the breeding period, which corresponds with the annual breeding population survey conducted by USFWS, CWS, and partner agencies. The number of breeding males in year t and breeding population i is given by $N_i^{\text{B♂}}(t)$ and the number of breeding females by $N_i^{\text{B♀}}(t)$. In the first transition in the model, the numbers of adult males and females in the fall flight (i.e., at the beginning of the fall migration, F) are calculated by multiplying breeding-season survival probability by the number of breeding adults (a) for each breeding population i:

$$\begin{aligned} N_i^{\text{Fa♂}}(t) &= S_i^{\text{F♂}} \cdot N_i^{\text{B♂}}(t), \\ N_i^{\text{Fa♀}}(t) &= S_i^{\text{B♀}} \cdot N_i^{\text{B♀}}(t), \end{aligned} \qquad (1)$$

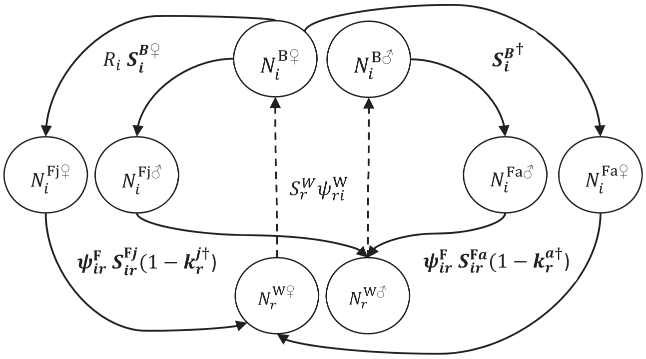


Fig. 2. Life-cycle representation of metapopulation model for northern pintail (*Anas acuta*) in North America. Population size (N) for males (♂) and females (♀) is evaluated annually (indicated by circles) using submodels (multipliers between arrows for males and females) based on probability of survival (S), probability of migration (ψ), hunting mortality (k), and/or age ratio (R) at the beginning of each of three seasons, including breeding (B), fall migration through the end of hunting season (F), and winter through completion of spring migration (W). Breeding and nonbreeding populations are indexed by i and r, respectively. Some terms are assumed to be constant across years (highlighted in bold), others are distinguished by sex only (†), and other terms are distinguished by sex and by adult (a) and juvenile (j) age classes. Dashed arrows accommodate crossing arrows. For example, adult males transition from a fall population ($N_i^{\text{Fa♂}}$) to a post-harvest population ($N_r^{\text{W♂}}$) based on the movement probability between these populations (ψ_{ir}^{F}) and their survival during this transition ($S_{ir}^{\text{Fa}}(1-k_r^{\text{a♂}})$). Density-dependent overflight movements between the Prairie Pothole and the remaining two breeding populations are not represented here but are represented in Fig. 1.

where $S_i^{\text{B♂}}$ and $S_i^{\text{B♀}}$ denote probabilities of survival for adult males and adult females during the breeding season in population i.

The population-specific number of juvenile (j) males and females at the start of fall migration (F) assumes a 50:50 sex ratio and is found by multiplying the number of females in the fall flight by the age ratio (R_i; the number of juvenile females divided by the number of adult females in the fall flight) in each breeding population i:

$$N_i^{\text{Fj♂}}(t) = N_i^{\text{Fj♀}}(t) = N_i^{\text{Fa♀}}(t)\cdot R_i(t).$$

Based on current continental-scale survey efforts, the best empirical measure of productivity at the continental scale is the age ratio in the fall flight, which is calculated by adjusting the age ratio in the harvest by the different vulnerabilities of juveniles (Runge and Boomer, 2005). While direct, empirical estimates of population-specific age ratios are currently unavailable, empirical estimates for the continental age ratio were used to help parameterize this model (see Section 2.6). The number of adult females surviving the summer multiplied by age ratio therefore determines the number of young produced. The annual fall flight, then, is the sum of surviving adults and young produced during the preceding summer. The dynamics of the age-ratios are influenced by habitat and environmental conditions on the breeding grounds and the size of the breeding populations (density-dependence), as discussed below (see Section 2.4).

2.2. Fall migration through hunting season

To make the transition from the breeding population to the wintering population, adult and juvenile pintails must choose a migration path, as well as survive migration and the hunting season. The fall migration probability, ψ_{ir}^{F}, represents the fraction of the fall population from breeding population i that moves to nonbreeding population r. These birds experience a fall migration survival rate of $S_{ir}^{\text{F}(g)}$ that is the complement of natural mortality during this period, where g represents the age and sex class of the birds. Finally, birds moving from breeding population i to nonbreeding population r are also exposed to hunting mortality, (k_r), which is equivalent to the harvest rate (h_r) with an additional crippling loss (c). Thus, noting that juveniles become indistinguishable from adults in the model after their first hunting season, the population- and sex-specific post-hunting season population sizes are given by:

$$N_r^{\text{W♂}}(t) = \sum_{r=1}^{2}\sum_{i=1}^{3}[N_i^{\text{Fa♂}}(t)\cdot\psi_{ir}^{\text{F}}\cdot S_{ir}^{\text{Fa♂}}\cdot(1-k_r^{\text{a♂}})$$

$$+N_{\text{i}}^{\text{Fj♂}}(t)\cdot\psi_{ir}^{\text{F}}\cdot S_{ir}^{\text{Fj♂}}\cdot(1-k_r^{\text{j♂}})],$$

$$N_r^{\text{W♀}}(t) = \sum_{r=1}^{2}\sum_{i=1}^{3}[N_i^{\text{Fa♀}}(t)\cdot\psi_{ir}^{\text{F}}\cdot S_{ir}^{\text{Fa♀}}\cdot(1-k_r^{\text{a♀}})$$

$$+N_{\text{i}}^{\text{Fj♀}}(t)\cdot\psi_{ir}^{\text{F}}\cdot S_{ir}^{\text{Fj♀}}\cdot(1-k_r^{\text{j♀}})].$$

The fall migration probabilities are constrained, in that the fractions of pintails migrating to each nonbreeding population from a particular breeding population must sum to 1:

$$\psi_{12}^{\text{F}} = 1-\psi_{11}^{\text{F}},\quad \psi_{22}^{\text{F}} = 1-\psi_{21}^{\text{F}},\quad\text{and}\quad \psi_{32}^{\text{F}} = 1-\psi_{31}^{\text{F}}.$$

We further assume, for this initial prototype, that birds from the NU population migrate to the wintering grounds in the same proportions as birds from the PR population. Thus,

$$\psi_{31}^{\text{F}} = \psi_{21}^{\text{F}}\quad\text{and}\quad \psi_{32}^{\text{F}} = \psi_{22}^{\text{F}}.$$

Finally, the number of pintails harvested (H) across age and sex classes each year at the continental scale is given by:

$$H(t) = \sum_{r=1}^{2}\sum_{i=1}^{3}(N_i^{\text{Fa♂}}(t)\cdot\psi_{ir}^{\text{F}}\cdot S_{ir}^{\text{Fa♂}}\cdot h_r^{\text{a♂}} + N_i^{\text{Fj♂}}(t)\cdot\psi_{ir}^{\text{F}}\cdot S_{ir}^{\text{Fj♂}}\cdot h_r^{\text{j♂}}$$

$$+N_i^{\text{Fa♀}}(t)\cdot\psi_{ir}^{\text{F}}\cdot S_{ir}^{\text{Fa♀}}\cdot h_r^{\text{a♀}} + N_i^{\text{Fj♀}}(t)\cdot\psi_{ir}^{\text{F}}\cdot S_{ir}^{\text{Fj♀}}\cdot h_r^{\text{j♀}}).$$

The harvest rate for nonbreeding population cohorts is given by:

$$h_r^{\text{a♂}} = k_r^{\text{a♂}}(1-c),\quad h_r^{\text{j♂}} = k_r^{\text{j♂}}(1-c),$$

$$h_r^{\text{a♀}} = k_r^{\text{a♀}}(1-c),\quad h_r^{\text{j♀}} = k_r^{\text{j♀}}(1-c)$$

and the harvest rate at the continental scale is given by:

$$h(t) = \frac{H(t)}{N^{\text{F}\bullet}(t)},\quad\text{where}$$

$$N^{\text{M}\bullet}(t) = \sum_{r=1}^{2}\sum_{i=1}^{3}(N_i^{\text{Fa♂}}(t)\cdot\psi_{ir}^{\text{F}}\cdot S_{ir}^{\text{Fa♂}} + N_i^{\text{Fj♂}}(t)\cdot\psi_{ir}^{\text{F}}\cdot S_{ir}^{\text{Fj♂}}$$

$$+N_i^{\text{Fa♀}}(t)\cdot\psi_{ir}^{\text{F}}\cdot S_{ir}^{\text{Fa♀}} + N_i^{\text{Fj♀}}(t)\cdot\psi_{ir}^{\text{F}}\cdot S_{ir}^{\text{Fj♀}}),$$

where $N^{\text{M}\bullet}(t)$ is the number of birds in mid-winter just after fall migration and before harvest.

2.3. Mid-winter through completion of spring migration

To make the transition from the nonbreeding grounds back to the breeding grounds, pintails must survive the post-harvest season, choose a migration path, and survive migration. This period is noted in equations that follow as W. Similar to fall migration, the spring migration probability, ψ_{ri}^{W}, represents the fraction of the population from nonbreeding population r that moves to breeding population i. These birds experience a survival rate of S_r^{W} that reflects survival from post-harvest through completion of spring migration; we assume this depends only on where the birds spent the winter (r), and not on the migration path. Furthermore, we assume that birds initially migrate either to PR or AK (but not to

NU). In the case of pintails that arrive initially in PR from either nonbreeding population, they must then choose, based on local pintail density and environmental conditions, whether to breed in the PR or to migrate to NU or AK for the breeding season (see Section 2.4). Thus, the breeding-population-specific numbers of males and females at the beginning of the breeding season are calculated by accounting for the number of individuals that survive winter and move from each nonbreeding population to each breeding population (i.e., CA–AK, GC–AK; CA–PR, GC–PR; CA–PR–AK, GC–PR–AK; CA–PR–NU, GC–PR–NU).

First, the number of males and females that breed in AK ($i = 1$) is the sum of the number that fly directly from the nonbreeding grounds and those that initially arrive in PR and then may decide to continue to AK (Fig. 1; see Section 2.4):

$$\begin{aligned}
N_1^{\mathrm{B}\text{♂}}(t+1) &= N_1^{\mathrm{W}\text{♂}}(t)\cdot S_1^{\mathrm{W}}(t)\cdot \psi_{11}^{\mathrm{W}} + N_2^{\mathrm{W}\text{♂}}(t)\cdot S_2^{\mathrm{W}}(t)\cdot \psi_{21}^{\mathrm{W}}\\
&\quad + (N_1^{\mathrm{W}\text{♂}}(t)\cdot S_1^{\mathrm{W}}(t)\cdot \psi_{12}^{\mathrm{W}}\\
&\quad + N_2^{\mathrm{W}\text{♂}}(t)\cdot S_2^{\mathrm{W}}(t)\cdot \psi_{22}^{\mathrm{W}})\cdot \psi_{leaveB2}^{\mathrm{W}}(t)\cdot \psi_{B2B1}^{\mathrm{W}},\\
N_1^{\mathrm{B}\text{♀}}(t+1) &= N_1^{\mathrm{W}\text{♀}}(t)\cdot S_1^{\mathrm{W}}(t)\cdot \psi_{11}^{\mathrm{W}} + N_2^{\mathrm{W}\text{♀}}(t)\cdot S_2^{\mathrm{W}}(t)\cdot \psi_{21}^{\mathrm{W}}\\
&\quad + (N_1^{\mathrm{W}\text{♀}}(t)\cdot S_1^{\mathrm{W}}(t)\cdot \psi_{12}^{\mathrm{W}}\\
&\quad + N_2^{\mathrm{W}\text{♀}}(t)\cdot S_2^{\mathrm{W}}(t)\cdot \psi_{22}^{\mathrm{W}})\cdot \psi_{leaveB2}^{\mathrm{W}}(t)\cdot \psi_{B2B1}^{\mathrm{W}},
\end{aligned}$$

where $\psi_{leaveB2}^{\mathrm{W}}(t)$ is the proportion of individuals that arrive initially in PR that then flyover to AK or NU (henceforth, flyover ratio), and ψ_{B2B1}^{W} is the proportion of the flyover individuals that go to AK (henceforth, AK flyover proportion; Fig. 1).

Next, the number of males and females that breed in PR includes those individuals that arrive from the nonbreeding grounds and stay in PR rather than departing for the other breeding populations (see Section 2.4).

$$\begin{aligned}
N_2^{\mathrm{B}\text{♂}}(t+1) &= (N_1^{\mathrm{W}\text{♂}}(t)\cdot S_1^{\mathrm{W}}(t)\cdot \psi_{12}^{\mathrm{W}}\\
&\quad + N_2^{\mathrm{W}\text{♂}}(t)\cdot S_2^{\mathrm{W}}(t)\cdot \psi_{22}^{\mathrm{W}})\cdot (1-\psi_{leaveB2}^{\mathrm{W}}(t)),\\
N_2^{\mathrm{B}\text{♀}}(t+1) &= (N_1^{\mathrm{W}\text{♀}}(t)\cdot S_1^{\mathrm{W}}(t)\cdot \psi_{12}^{\mathrm{W}}\\
&\quad + N_2^{\mathrm{W}\text{♀}}(t)\cdot S_2^{\mathrm{W}}(t)\cdot \psi_{22}^{\mathrm{W}})\cdot (1-\psi_{leaveB2}^{\mathrm{W}}(t)).
\end{aligned}$$

Finally, the number of males and females that breed in NU includes those individuals that arrive from the nonbreeding grounds in PR and then decide to continue on to NU (see Section 2.4):

$$\begin{aligned}
N_3^{\mathrm{B}\text{♂}}(t+1) &= (N_1^{\mathrm{W}\text{♂}}(t)\cdot S_1^{\mathrm{W}}(t)\cdot \psi_{12}^{\mathrm{W}}\\
&\quad + N_2^{\mathrm{W}\text{♂}}(t)\cdot S_2^{\mathrm{W}}(t)\cdot \psi_{22}^{\mathrm{W}})\cdot \psi_{leaveB2}^{\mathrm{W}}(t)\cdot \psi_{B2B3}^{\mathrm{W}},\\
N_3^{\mathrm{B}\text{♀}}(t+1) &= (N_1^{\mathrm{W}\text{♀}}(t)\cdot S_1^{\mathrm{W}}(t)\cdot \psi_{12}^{\mathrm{W}}\\
&\quad + N_2^{\mathrm{W}\text{♀}}(t)\cdot S_2^{\mathrm{W}}(t)\cdot \psi_{22}^{\mathrm{W}})\cdot \psi_{leaveB2}^{\mathrm{W}}(t)\cdot \psi_{B2B3}^{\mathrm{W}}.
\end{aligned}$$

As with the fall migration probabilities, the spring migration probabilities are constrained such that the proportions of pintails migrating directly from either nonbreeding population to PR or AK (Fig. 1) must sum to 1:

$\psi_{12}^{\mathrm{W}} = 1 - \psi_{11}^{\mathrm{W}}$ and $\psi_{22}^{\mathrm{W}} = 1 - \psi_{21}^{\mathrm{W}}$.

Similarly, the AK and NU flyover proportions (Fig. 1) must also sum to 1:

$$\psi_{B2B1}^{\mathrm{W}} = 1 - \psi_{B2B3}^{\mathrm{W}}.$$

When calculating breeding population sizes, we assume that the migration and survival probabilities are not age- or sex-specific. However, the ratio of initial arrivals in PR that depart for more northern populations is assumed to vary with population size (density-dependent) and with the number of ponds in PR (see Section 2.4). These equations complete the annual cycle; population change in year $t+1$ can now be projected starting with Eq. (1).

2.4. Crucial submodels

To this point, the model is an age- and sex-structured metapopulation model, tracking juvenile and adult males and females between three breeding areas and two nonbreeding areas, while accounting for reproductive and survival rates. To be useful for evaluating the potential effects of habitat and harvest management on pintail harvest and population dynamics, external and internal mechanisms of regulation need to be included. External regulatory mechanisms arise from the effects of management actions on demographic processes; internal regulatory mechanisms arise from density dependence. Density-dependence is thought to influence at least three parameters: age ratio in the fall flight (i.e., density-dependent productivity), flyover ratio, and post-harvest survival (Runge and Boomer, 2005; Anderson et al., 2007).

First, there is evidence that pintail production is density-dependent at the continental scale, in the sense that fall age-ratios are smaller in years when the breeding population size is larger, all other things equal (Runge and Boomer, 2005). Further, in PR, the age ratio is also affected by environmental conditions (as measured by “May ponds”). Thus, population-specific age ratios are a function of the number of breeding adults (Fig. 3) and, in PR, May pond abundance:

$$\begin{aligned}
&R_i(t) = e^{X_i}(t),\\
&X_1(t) = \alpha_{10} + \alpha_{11}\cdot N_1^{\mathrm{B}\bullet}(t),\\
&X_2(t) = \alpha_{20} + \alpha_{21}\cdot N_2^{\mathrm{B}\bullet}(t) + \alpha_{22}\cdot P_2^{\mathrm{B}}(t),\\
&X_3(t) = \alpha_{30} + \alpha_{31}\cdot N_3^{\mathrm{B}\bullet}(t),\\
&N_i^{\mathrm{B}\bullet}(t) = N_i^{\mathrm{B}\text{♂}}(t) + N_i^{\text{♀}\bullet}(t),
\end{aligned} \qquad (2)$$

where $R_i(t)$ denotes the population-specific age ratio, $X_i(t)$ denotes regression parameters for age ratio including population size, and $P_2^{\mathrm{B}}(t)$ denotes the number of ponds in PR during the breeding season (in the simulations that follow, the number of ponds is set to the long-term mean of 3.2 million; Runge and Boomer, 2005). Note that, whereas PR age ratio is expected to be a function of both population density and May pond abundance (Eq. (2); Runge and Boomer, 2005), AK and NU age ratios are simply a function of population density. Therefore, depending on the abundance of May ponds in PR and population-specific population densities, age ratios may differ substantially between breeding populations during any given year. Here, we assume an exponential functional form based on findings by Runge and Boomer (2005).

Second, emigration probability is positively related to population density in a number of animal taxa (for review see Matthysen, 2005), including waterfowl (Lindberg et al., 1998), and accounting for this form of density dependence in metapopulation models is crucial for making appropriate inferences about population dynamics (Hovestadt et al., 2010). There is evidence that the proportion of pintails that overfly the prairies (and move on to NU or AK) is a function of PR water conditions (Podruzny et al., 2002; Runge and Boomer, 2005). It stands to reason that this proportion might also be affected by pintail abundance, although there is not yet empirical evidence for this effect. To allow exploration of this hypothesis, we included parameters representing density-dependent overflight from PR to AK or NU. Thus, of the pintails that arrive initially in PR, the proportion that then migrate to one of the

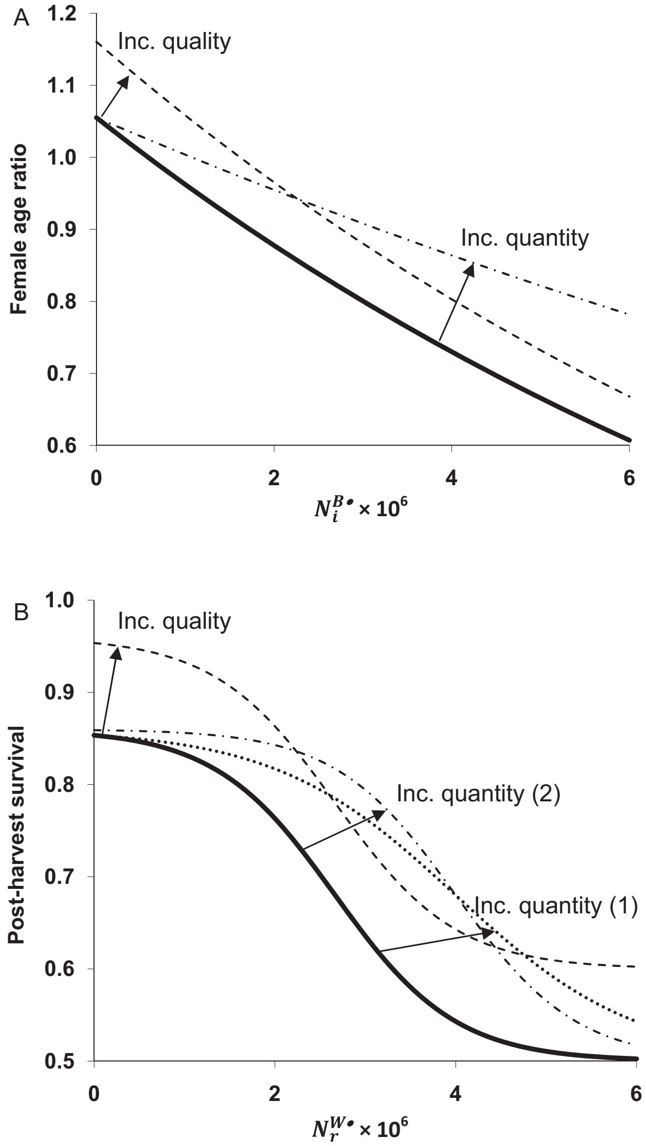


Fig. 3. Hypothetical representation of increasing habitat condition by modifying population-specific density-dependent relationships for fall age ratio (A) and post-harvest survival (B) of northern pintail. Increasing the log-scale intercept (dashed line in A) relative to a baseline (solid line in A) represents an improvement in breeding habitat quality, because pintails produce more young regardless of breeding population size ($N_i^{B\bullet}$). When the log-scale slope (dash-dotted line in A) becomes less steep, this indicates an increase in breeding habitat quantity, because improvement in age ratio depends on density. Likewise, an increase in the limits (i.e., minimum and maximum) of post-harvest survival (dashed line in B) relative to the baseline (solid line in B) reflects an improvement in nonbreeding habitat quality, because pintails have higher survival regardless of density. Improvement in nonbreeding habitat quantity can be represented in one of two ways: (1) flatten the logit-scale slope (dotted line in B) or (2) increase the logit-scale intercept to shift the curve to the right (dash-dotted line in B). Under both scenarios, the increase in post-harvest survival is contingent on post-harvest population size ($N_r^{W\bullet}$).

other breeding populations is potentially influenced by the number of pintails that arrive initially in PR as well as May pond abundance in PR:

$$\psi^{W}_{leaveB2}(t) = \psi^{W}_{leaveB2,\max} \cdot \frac{1}{1+e^{-Y(t)}},$$

$$Y(t) = \delta_0 + \delta_1 \cdot \sum_{r=1}^{2}(N_r^{W\bullet}(t) \cdot S_r^{W}(t) \cdot \psi^{W}_{r2}) + \delta_2 \cdot P_2^{B}(t),$$

$$N_r^{W\bullet}(t) = N_r^{W\text{♂}}(t) + N_r^{W\text{♀}}(t),$$

where $\psi^{W}_{leaveB2}(t)$ denotes the annual proportion of pintails arriving in PR that then depart for one of the other breeding populations, $\psi^{W}_{leaveB2,\max}$ denotes the maximum probability that pintails arriving initially in PR will continue onto AK or NU, $Y(t)$ denotes regression parameters for $\psi^{W}_{leaveB2}(t)$ including the number arriving on the nonbreeding grounds, and $P_2^{B}(t)$ denotes the PR May pond abundance as in Eq. (2). Here, we assume a logistic functional form with a maximum value.

Third, it has been suggested that post-harvest survival may be density-dependent at a continental scale (USFWS, 2007). As pintail populations increase, food availability may become limiting on nonbreeding grounds and/or spring migration routes, leading to reduced likelihood of survival. To capture this hypothesis, nonbreeding-population probabilities of post-harvest survival are a function of population size in mid-winter (Fig. 3):

$$S_r^{W}(t) = S^{W}_{r,\min} + \frac{S^{W}_{r,\max} - S^{W}_{r,\min}}{1+e^{-Z_r(t)}}, \qquad (3)$$
$$Z_r(t) = \beta_{r0} + \beta_{r1} \cdot N_r^{W\bullet}(t),$$

where $S^{W}_{r,\min}$ and $S^{W}_{r,\max}$ denote the minimum and maximum post-harvest survival probabilities, and $Z_r(t)$ denotes the regression prediction based on a bounded logit model for estimating the effect of post-harvest population size on S_r^{W}.

2.5. Formal integration of habitat and harvest management

To better motivate an understanding of our modeling framework for integrating waterfowl harvest and habitat management, we illustrate some of the underlying assumptions about the mechanisms for population regulation. We begin with a general assumption that pintail population dynamics are regulated by external (i.e., habitat and harvest management) and internal (i.e., density-dependent) mechanisms. Further, we assume that the external mechanisms of habitat and harvest management interact with the internal mechanism of density dependence. Though harvest has already been incorporated in decision models for management of North American waterfowl at the continental scale (USFWS, 2009b), habitat management has yet to be incorporated. Here, we incorporate parameters in our model that represent habitat management actions by JVs. We assume that these actions can influence habitat condition through two dimensions related to density dependence: habitat quality and habitat quantity.

Within this conceptual framework, we think that changes in habitat quality and habitat quantity can be captured by modifying parameters in the population-specific density-dependent functions (Anderson et al., 2007). Suppose that habitat quality represented the inverse of the degree to which grassland is fragmented within PR or the energetic capacity of wetlands in GC; and habitat quantity represented the total area of grassland in PR or the total area of shallow wetlands in GC. How would changes in habitat quality or quantity manifest in pintail demographic rates? We might view an increase in habitat *quality* as an effect that raised breeding or survival rates across all densities, that is, an effect that shifted a density-dependent relationship upward (Fig. 3). Indeed, fragmentation of grassland in agricultural landscapes has been linked to lower pintail nest survival perhaps due to reduced predator densities or activity (Guyn and Clark, 1999; Drever et al., 2007). Thus, an increase in PR habitat quality would raise the reproductive rate across all densities (Fig. 3a), which occurs in Eq. (2) when the log-scale intercept (i.e., α_{20}) is increased. Likewise, an increase in GC habitat quality would raise the post-harvest survival rate across all densities (Fig. 3b), which occurs in Eq. (3) when the lower and upper limits of post-harvest survival rates (i.e., $[S^{WM}_{r,\min}, S^{WM}_{r,\max}]$) are increased. On the other hand, we might view an increase in habitat *quantity* as an effect that allowed breeding or survival rates to remain high at higher population sizes, that is, an effect that shifted or stretched a density-dependent relationship to the right (Fig. 3). Therefore, an increase in PR habitat quantity (say, by adding grassland area while holding the degree of fragmentation constant) would raise the reproductive rates at higher densities (Fig. 3a), which occurs in Eq. (2) when the log-scale slope (α_{21}) becomes less steep (i.e., approaches zero). Likewise, an increase in GC habitat quantity would increase the population size at which post-harvest survival rate dropped (Fig. 3b), which occurs in Eq. (3) when the logit-scale intercept (i.e., β_{r0}) is increased or when the slope (i.e., β_{r1}) is decreased. Thus, at least at the level of thinking about changing habitat quantity or quality, habitat management can be captured in our model through the parameters in the density-dependent relationships (henceforth key parameters). The challenge in further development of the model is to make more mechanistic links between specific habitat management actions and their demographic consequences. The submodel structure we have presented, though, provides the template for this mechanistic linkage.

Taken together then, we assume that habitat management by JVs has a direct influence and harvest management has an indirect influence on population-specific vital rates through density-dependent mechanisms, and these influences interact as they scale up to continental population dynamics. In particular, we assume that continental harvest management actions reduce the mid-winter population size ($N_r^{\mathrm{W}\bullet}$) and therefore influence the density-dependent survival rate during the subsequent post-harvest period (S_r^{WM}) Eq. (3). In this way, habitat management could interact with harvest management decisions by altering harvest potential and realized harvest levels, which together can influence waterfowl population dynamics (Anderson et al., 2007). Here, we develop a modeling framework that enables us to examine the degree to which population-specific levels of habitat condition interact with continental fall harvest levels to affect pintail population dynamics and harvest opportunity. By providing a mechanism, through density-dependent relationships, to incorporate the demographic effects of habitat management, our model allows simultaneous prediction of the effects of harvest and habitat management on continental population dynamics.

2.6. Baseline model parameterization and evaluation

We began the analysis with a baseline parameterization that is based on three sources of information: (1) predictions from a model that is used to inform continental-scale pintail harvest management (USFWS, 2007), (2) pintail annual survival estimates (Rice et al., 2010), and (3) parameter values for pintail population dynamics (Runge and Boomer, 2005). Parameter values for the model and their sources are listed in Table 1. We derived parameter values from published and unpublished literature as well as our own judgment. This model parameterization, then, allows us to conduct a prototype analysis to demonstrate the utility of the modeling framework: refinements will require further consultation with waterfowl experts, as well as formal estimation methods.

For example, while literature values were available for minimum and maximum values for vital rates, no literature values were available to determine the regression coefficients in submodels for these vital rates (i.e., age ratio, spring migration route probabilities, and post-harvest survival). In this case, parameter values were chosen to produce results that are consistent with literature values for derived parameters like breeding population size and age ratios. In the case of population-specific post-harvest survival minima and maxima, we determined parameter values by adjusting literature values to better distinguish non-harvest mortality from harvest mortality. For density dependence of age ratio, literature values were available that pooled breeding populations at the continental level (Runge and Boomer, 2005). We used these values to represent the baseline scenario.

To evaluate the performance of the prototype model with the baseline parameter values, we compared model predictions at the continental level with those from published sources for annual survival rate, carrying capacity, maximum sustained yield (MSY), maximum sustained harvest rate, and equilibrium population size at MSY. For annual survival rate, we used a calculation for adult females that migrate between AK and CA as a reference annual survival rate:

$$S_{11}^{\mathrm{a}♀} = S_{11}^{\mathrm{Fa}♀} \cdot (1 - k_1^{\mathrm{a}♀}) \cdot S_1^{\mathrm{WM}} \cdot S_1^{\mathrm{B}♀}.$$

We calculated the continental post-harvest survival annually as follows:

$$S^{\mathrm{W}}(t) = \frac{\sum_{r=1}^{2} N_r^{\mathrm{W}\bullet}(t) \cdot S_r^{\mathrm{W}}(t)}{\sum_{r=1}^{2} N_r^{\mathrm{W}\bullet}(t)}.$$

We calculated continental fall age ratio annually as follows:

$$R(t) = \frac{\sum_{i=1}^{3} N_i^{\mathrm{Fj}♀}(t)}{\sum_{i=1}^{3} N_i^{\mathrm{Fa}♀}(t)}.$$

We defined equilibrium as the point when a focal parameter value at year T was equal to that parameter value at year $T-1$. For carrying capacity (K), we calculated the equilibrium breeding population size in the absence of harvest:

$$K = N^{\mathrm{B}\bullet}(eq|h=0) = \sum_{i=1}^{3} [N_i^{\mathrm{B}\bullet}(T|h=0)] = \sum_{i=1}^{3} [N_i^{\mathrm{B}\bullet}(T-1|h=0)].$$

For MSY, we calculated the maximum equilibrium harvest as

$$H^* = \max_{0 \le h \le 0.3} H(T) = \max_{0 \le h \le 0.3} H(T-1).$$

For maximum sustainable harvest rate, we calculated the harvest rate at which harvest during year T was maximized:

$$h^* = \mathit{arg}\max_{0 \le h \le 0.3} H(T) = \mathit{arg}\max_{0 \le h \le 0.3} H(T-1).$$

We calculated equilibrium harvest rate as total harvest divided by pre-harvest population size:

$$h(eq) = \frac{H(T)}{N^{\mathrm{M}\bullet}(T)} = \frac{H(T-1)}{N^{\mathrm{M}\bullet}(T-1)}.$$

We calculated equilibrium continental breeding population size as

$$N^{\mathrm{B}\bullet}(eq) = \sum_{i=1}^{3} N_i^{\mathrm{B}\bullet}(T) = \sum_{i=1}^{3} N_i^{\mathrm{B}\bullet}(T-1).$$

Likewise, we calculated equilibrium pre-harvest population size as

$$N^{\mathrm{M}\bullet}(eq) = \sum_{r=1}^{2} N_r^{\mathrm{M}\bullet}(T) = \sum_{r=1}^{2} N_r^{\mathrm{M}\bullet}(T-1).$$

Finally, we calculated the equilibrium population size at MSY as:

$$N^* = N^{\mathrm{B}\bullet}(eq|h=h^*) = \sum_{i=1}^{3} N_i^{\mathrm{B}\bullet}(T|h=h^*) = \sum_{i=1}^{3} N_i^{\mathrm{B}\bullet}(T-1|h=h^*).$$

2.7. Perturbation analysis

To represent some of the possible alternative scenarios for improved habitat conditions for pintail on the breeding and

Table 1
Parameter values for submodels that comprise a metapopulation model for northern pintail in North America. Parameters in bold were perturbed to represent management scenarios. See Appendix 1 for definitions of variables.

Variables	Values	Sources
Breeding season		
$N_1^{B♂}, N_1^{B♀}(t=0)$	930,000/2	USFWS (2009a)
$N_2^{B♂}, N_2^{B♀}(t=0)$	$0.86 \times 2{,}295{,}000/2$	USFWS (2009a)
$N_3^{B♂}, N_3^{B♀}(t=0)$	$0.14 \times 2{,}295{,}000/2$	USFWS (2009a)
$[S_i^{B♂}, S_i^{B♀}]$	[0.98, 0.81]	Richkus et al. (2005) and Brasher et al. (2006)
Intercepts for age ratios [α_{10}; $\boldsymbol{\alpha_{20}}$; α_{30}]	[0[a]; **0 or 0.1**; −1[a]][b]	
Slopes for age ratios [$\alpha_{11} = \alpha_{31}$; α_{21}; α_{22}]	[−0.00000015[a]; −0.12; −0.00000008; 0.01][b]	
$P_2^B(t)$, in millions	3.2	
Fall migration through hunting season		
$\psi_{11}^F, S_{11}^{Fa}, S_{22}^{Fa}, S_{21}^{Fa}, S_{32}^{Fa}, S_{31}^{Fa}$	0.90[b]	
S_{12}^{Fa}	0.85[b]	
$S_{11}^{Fj}, S_{22}^{Fj}, S_{21}^{Fj}, S_{32}^{Fj}, S_{31}^{Fj}$	0.80[b]	
S_{12}^{Fj}	0.75[b]	
ψ_{22}^F, ψ_{32}^F	0.50[b]	
c	0.20	USFWS (2007)
Baseline kill rate $\boldsymbol{k^{a♀}}$ [c]	**0:0.2, $\boldsymbol{n = 20}$**	
$[k^{a♂}, k^{j♂}, k^{j♀}] \times k^{a♀}$ [c]	$[1.25, 2.75, 2] \times k^{a♀}$	(J.P. Runge, unpublished data)
Mid winter through spring migration		
ψ_{11}^W	0.54[b]	Miller et al. (2005)
ψ_{22}^W	0.9	Haukos et al. (2006)
ψ_{B2B3}^W	0.9[b]	
$\psi_{leaveB2,\max}^W$	0.7[b]	
Regression coefficients for $\psi_{B2B3}^W(t) : [\delta_0, \delta_1, \delta_2]$	[−3,0.000001, 0.1][a]	
$[S_{1,\min}^W = S_{2,\min}^W, S_{1,\max}^W = S_{2,\max}^W]$	[0.84, 0.96][b]	Fleskes et al. (2007), Lee et al. (2007), and Anderson (2008)
Regression coefficients for $S_r^W(t)[\beta_0; \boldsymbol{\beta_{20}}; \beta_{11} = \beta_{21}]$	[4; **4 or 4.4**; −0.0000015][a]	

[a] Adjusted to ensure realistic, equilibrium solutions.
[b] Judgment of authors, sometimes adjusted from literature values.
[c] For this analysis, we assume that kill rate is equivalent between nonbreeding populations.

nonbreeding grounds, we conducted a multivariate perturbation analysis (Beissinger and Westphal, 1998). Specifically, we examined equilibrium population conditions for pintail across a continuum of harvest rates while perturbing the following parameter variables from baseline conditions to represent improved habitat conditions: (1) 10% increase PR habitat quality (i.e., increase α_{20} [Eq. (2)] by the natural log of 1.1; Fig. 4); and (2) 10% increase in GC habitat quantity (i.e., increase β_{20} [Eq. (3)] by 10%; Fig. 5). Here, we modified the intercepts in the density-dependent relationships for PR and GC, respectively. The slopes may also be adjusted to reflect changes in habitat quantity and habitat quality for the respective populations. We chose these variables and percentages to represent alternatives for permanent shifts in environmental conditions as a result of habitat management. Ranges of focal variables for the perturbation analyses are listed in Table 1. With at least four output parameters of interest, a formal sensitivity analysis requires further input from subject experts and stakeholders on how to best represent the management goals (e.g., some utility function that integrates H^* and N^*). Such a sensitivity analysis is therefore beyond the scope of this paper but should be considered once the objectives have been more explicitly developed. Here, we instead focus our analysis on four output parameters and two of the key input parameters that we expect to be influenced through management efforts (i.e., PR habitat quality and GC habitat quantity) as a demonstration of the utility of this modeling approach and to motivate further model developments and eventual implementation of an adaptive management program. For purposes of this example, habitat conditions in the other core populations (i.e., CA, AK, and NU) were assumed to remain at current levels; further analysis could focus on additional scenarios (e.g., rice habitat loss and alternative management programs in CA or climate-change effects in AK). The number of breeding pintails and the number of pintails harvested at year 100 in the simulation are used to represent equilibrium population size and sustainable annual yield, respectively. We confirmed that these predictions reached equilibrium by inspecting population trajectories.

3. Results

Under the baseline parameterization, the model predicts a continental carrying capacity of 5.51 million breeding pintails, an equilibrium population size at MSY of 2.8 million, maximum sustainable yield of 460,000, and maximum sustainable harvest rate of 13% (accounting for differential vulnerability among age and sex classes). These predictions were in general agreement with those from the current pintail harvest strategy (hereafter, strategy; Table 2); indeed, the predicted yield curve (Fig. 6c) closely resembles the yield curve derived from the model used in the pintail harvest strategy (USFWS, 2007). The predicted continental reproductive rates and annual survival rates also closely match the harvest strategy. The predicted continental age-ratio as the population size approaches 0 was 1.00 (compared to 1.06 based on the analysis of age-ratio data by Runge and Boomer, 2005); the predicted continental age-ratio at a breeding population size of 5.5 million was 0.64 (compared to 0.64 in Runge and Boomer, 2005). At MSY, the reference annual survival rate ($S_{11,baseline}^{a♀}$) equals 0.62, which is within the standard error of an estimate that is based

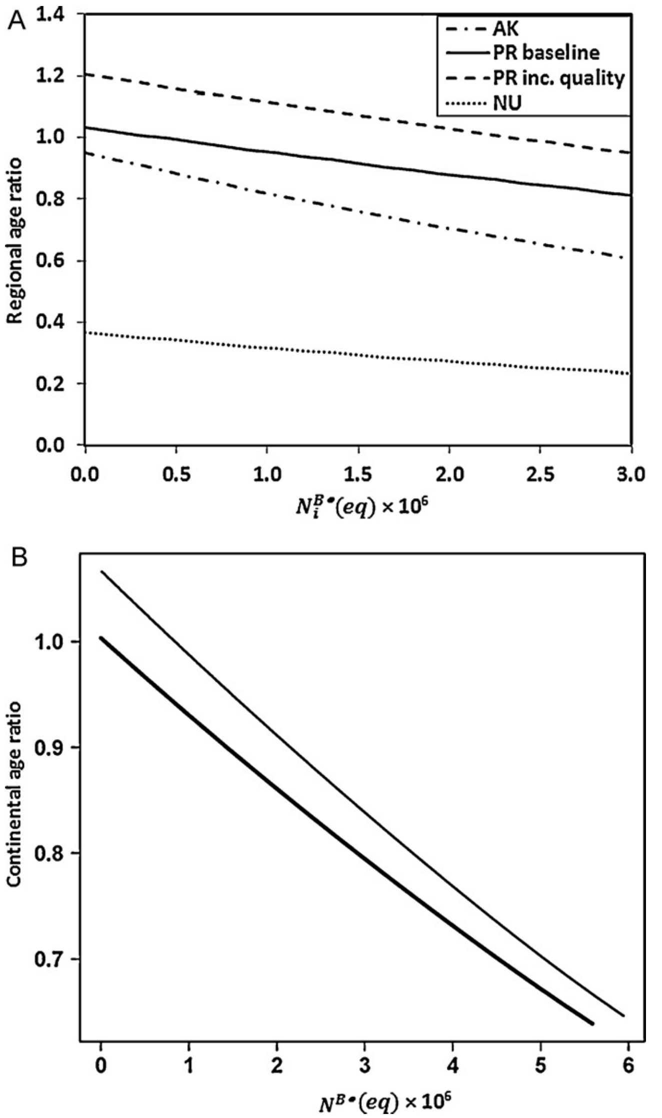


Fig. 4. Expected relationship between fall age ratio (i.e., juvenile females/adult females) and breeding population size for northern pintail (*Anas acuta*) at individual population (A; $N_i^{B\bullet}(eq)$) and continental (B; $N^{B\bullet}(eq)$) scales. Note that scales of axes differ between graphs A and B. In (A) the dash-dotted line represents Alaska (AK), and the dotted line represents northern unsurveyed (NU) areas. The remaining lines represent the Prairie Pothole population (PR) with varying upland habitat conditions reflected by the form of density-dependence: thick solid = baseline habitat quality; dashed = increased habitat quality.

on continent-wide mark-recapture data (0.65 ± 0.10 SE; Rice et al., 2010).

3.1. Influence of Prairie Pothole habitat quality and Gulf Coast habitat quantity

Changes in pintail population dynamics and harvest are evident when improving PR habitat quality by 10% regardless of GC habitat quantity (Fig. 6). Increases in K and H^* are larger when increasing habitat quality in PR (α_{20}) than when increasing habitat quantity in GC (β_{20}; Fig. 6). If just PR habitat quality increases, K increases by 6% from 5.51 to 5.86 million (Fig. 6b), MSY increases by 18% from 460 to 543 thousand pintails (Fig. 6c), equilibrium population size at MSY (N^*) increases by 11% from 2.8 to 3.1 million pintails (Fig. 6c), and the harvest rate at MSY (h^*) increases by 15% from 0.13 to 0.15 (Fig. 6d). If just GC habitat quantity increases, K increases by 1.4% from 5.51 to 5.59 million in the absence of harvest (Fig. 6b), MSY increases by 1.1% from 460 to 465 thousand pintails (Fig. 6c), N^* remains virtually constant at 2.8 million pintails (Fig. 6c), and h^* also remains constant at 0.13 (Fig. 6d). When both PR habitat quality and GC habitat quantity are increased by 10%, compared to the baseline, K increases by 8% from 5.51 to 5.94 million in the absence of harvest (Fig. 6b), MSY increases by 18% from 460 to 545 thousand pintails (Fig. 6c), N^* increases by 11% from 2.8 to 3.1 million pintails (Fig. 6c), and h^* increases by 15% from 0.13 to 0.15 (Fig. 6d).

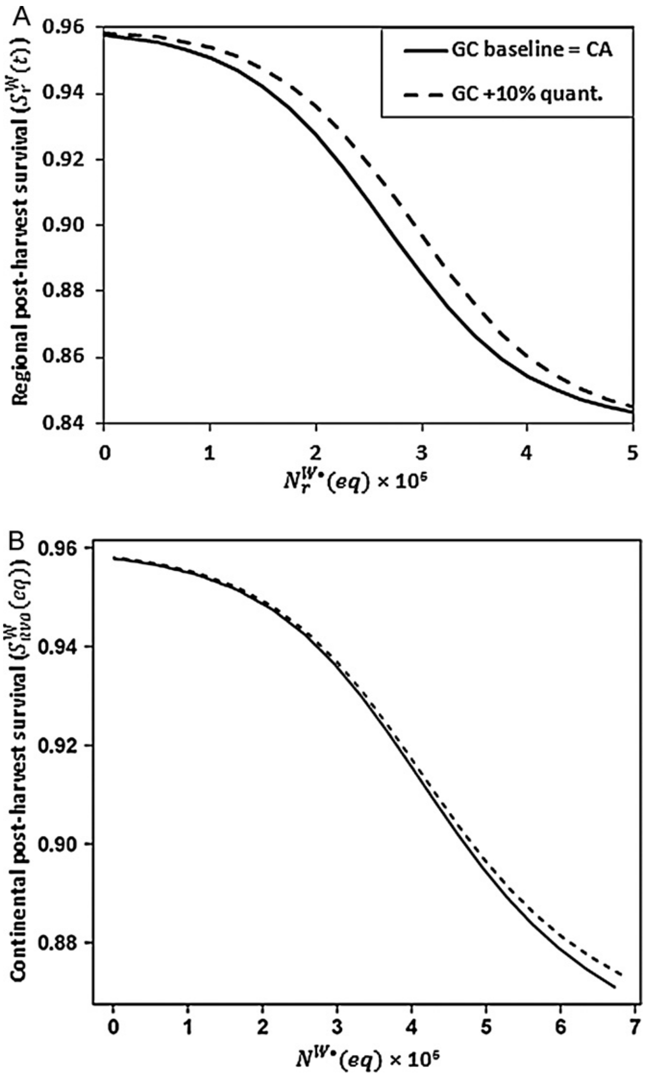


Fig. 5. Expected relationship between post-harvest survival and post-harvest population size of northern pintail (*Anas acuta*) at individual population (A; $N_r^{W\bullet}(eq)$) and continental (B; $N^{W\bullet}(eq)$) scales, with a minimum survival probability of 0.84 and a maximum of 0.96. Note that scales of axes differ between graphs A and B. The solid lines represent CA and baseline habitat quantity in GC, whereas the dashed lines represent improved habitat quantity in GC.

4. Discussion

For the first time, to our knowledge, we have shown how waterfowl harvest and habitat management can be integrated in a single modeling framework. This approach addresses directly the challenges put forth by the Joint Task Group (Anderson et al., 2007) and more importantly provides a common framework for two critical decision contexts. First, this framework enables forecasts about how habitat changes (whether management-related or external) will change the carrying capacity for waterfowl, as well as the

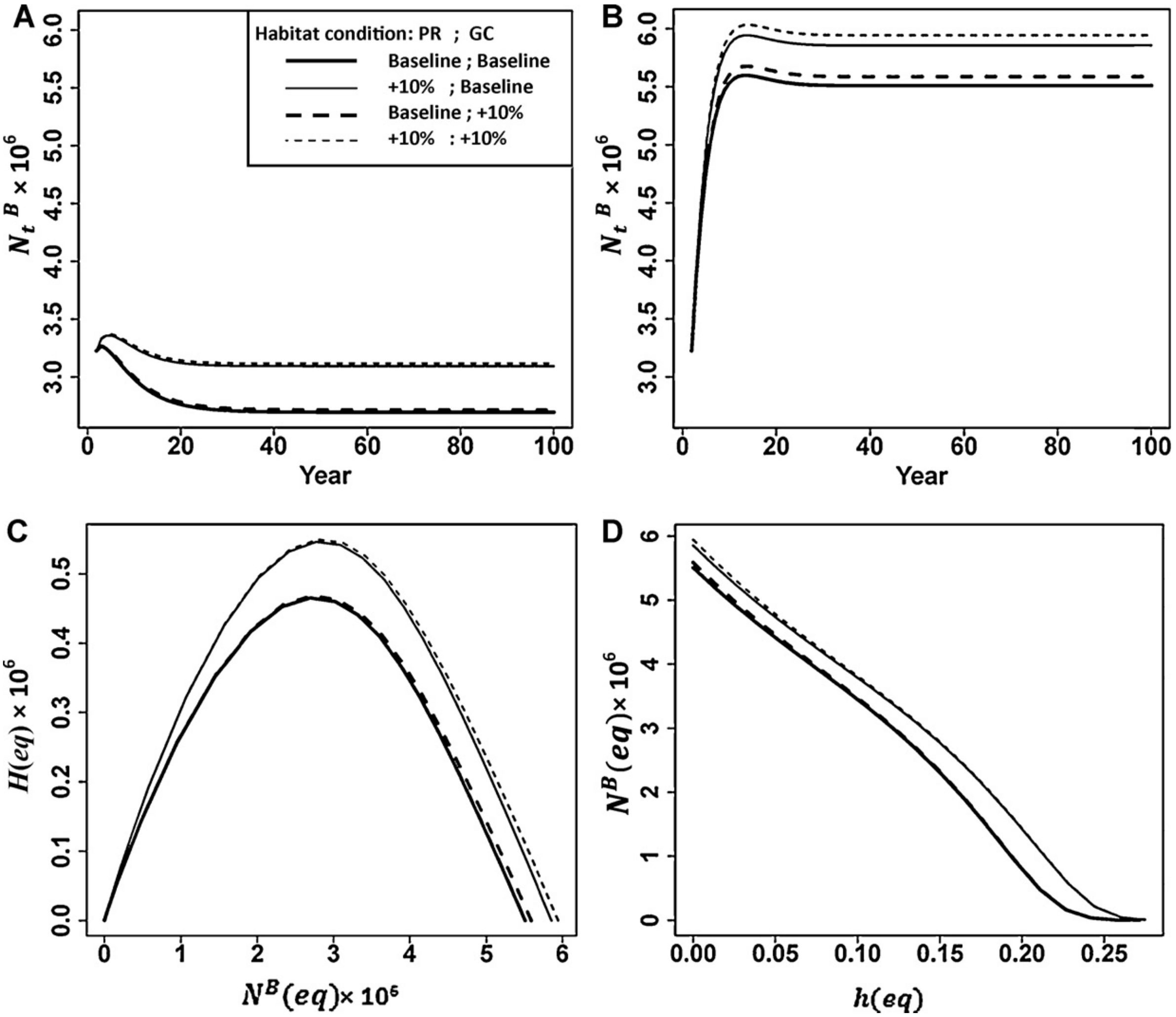


Fig. 6. Expected effects of habitat condition and harvest rate on the continental northern pintail (*Anas acuta*) population and harvest opportunity. Graphs A and B show population trajectories in millions at start of breeding (N_t^B) with no harvest (A) and with a moderate baseline harvest rate (($h_{i2}^{a♀} = 0.08$; B)). Graph C shows the expected relationship between equilibrium population size ($N^W(eq)$) and sustainable harvest ($H(eq)$). Graph D shows the expected relationship between $N^{B\bullet}(eq)$ and equilibrium harvest rate ($h(eq)$). Line type represents habitat quality in the Prairie Pothole (PR) population and habitat quantity in the Gulf Coast (GC) population relative to the baseline level.

harvest potential. This is important in order to evaluate not only habitat management decisions, but also the consequences of habitat loss through external forces. Specifically, managers can use this framework to examine consequences of alternative strategies for joint-venture (JV) scale and regional-scale habitat management on continental-scale carrying capacity and sustainable harvest. In addition, this modeling framework can be used to evaluate harvest management decisions in the face of a changing habitat. Scenarios we evaluated here to demonstrate the approach involved varying regional-scale life-history dynamics, including age ratio in the Prairie Pothole (PR) population and post-harvest survival along the Gulf Coast (GC). Based on our model and analysis, the largest proportional increase in carrying capacity and sustainable harvest was seen when increasing a proxy for habitat quality in PR (Fig. 6). In contrast, increasing a proxy for habitat quantity in GC (Fig. 5) had a somewhat weaker influence on carrying capacity and sustainable harvest of pintails, regardless of habitat quality in PR. These findings and underlying assumptions must be critically evaluated, however, before conclusive management recommendations can be made. As such, our modeling exercise represents a conceptual advance and provides a template that can be used to integrate habitat and harvest management for waterfowl.

Table 2
Comparison of continental-scale predictions from baseline parameterization of a northern pintail metapopulation model with previously published continental estimates (Runge and Boomer, 2005; USFWS, 2007). Predictions for comparison include carrying capacity (K in millions), maximum sustained yield (MSY in millions), harvest rate at MSY (h^*), equilibrium population size at MSY (N^* in millions), equilibrium post-harvest survival ($S^W(eq)$) as a function of equilibrium post-harvest population size ($N^{W\bullet}(eq)$ in millions), and fall age ratio ($R(eq)$) as a function of breeding population size (in millions).

	Baseline parameterization (this paper)	Literature estimate	% difference
K	5.51	5.50[a]	0.18
MSY	0.46	0.49[a]	5.74
h^*	0.13	0.13[a]	0.00
N^*	2.80	3.09[a]	9.39
$S^W(N^{W\bullet}(eq)=0)$	0.96	0.96[b]	0.00
$S^W(N^{W\bullet}(eq)=6)$	0.88	0.88[b]	0.00
$R(N^{B\bullet}(eq)=0)$	1.00	1.06[b]	5.00
$R(N^{B\bullet}(eq)=5.5)$	0.64	0.64[b]	0.00

[a] Based on pintail harvest strategy (USFWS, 2007).

[b] Based on previous modeling effort focused on continental density dependence (Runge and Boomer, 2005).

The biggest challenge to achieving this integration is formally linking population dynamics and management decisions across spatial scales. Habitat management occurs at local to regional scales, but population dynamics and harvest potential are assessed at the continental scale. Effective decisions about habitat and harvest management efforts, furthermore, require

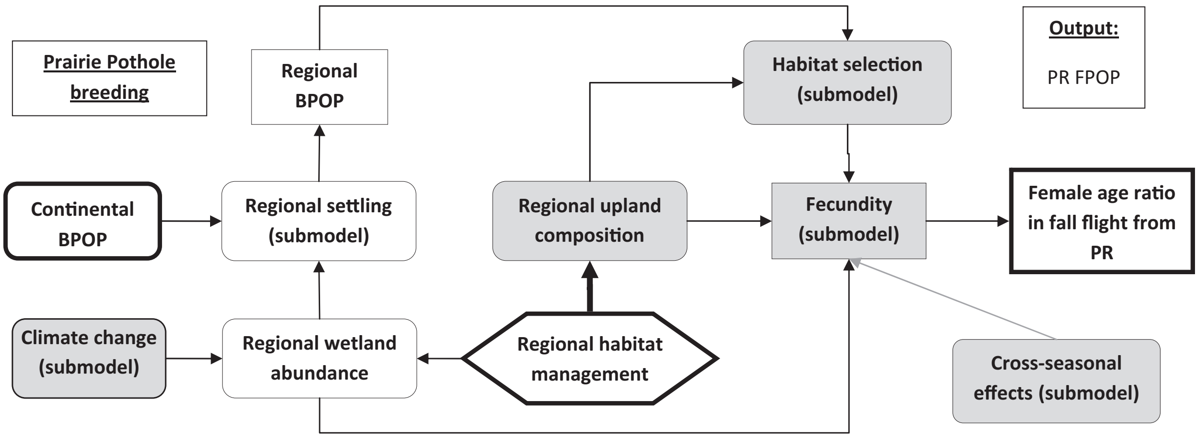


Fig. 7. Conceptual model linking habitat management actions, continental breeding population size (BPOP), and age ratio in the fall flight (FPOP) from the Prairie Pothole population (PR) for northern pintail (*Anas acuta*) in North America. White boxes are components included in the current model, whereas gray boxes are recognized as important components to be considered in future modeling efforts. These components include submodels for habitat selection and fecundity that explicitly link specific habitat management actions to reproductive output. Additional components include a climate change submodel to represent an external control of May ponds in PR, and a submodel for cross-seasonal effects of overwintering conditions on fecundity.

evaluating trade-offs to achieve multiple management objectives simultaneously at multiple spatial scales (Gregory and Long, 2009). For waterfowl harvest management, the decision context involves how to set harvest regulations to meet a complex set of objectives, including sustainable harvest, hunter satisfaction, and non-consumptive uses for continental waterfowl populations. For waterfowl habitat management to achieve continental-scale objectives, the decision context involves resource allocation among regions to most efficiently achieve management objectives at the continental level. For waterfowl habitat management to achieve JV-scale objectives, the decision context involves identifying the particular management actions (e.g., acquisition of land or easements, management methods, etc.) that most efficiently contribute to objectives at both the JV and continental levels. Part of all three decision contexts is anticipated system change—the uncertain environmental consequences induced by climate change and the intensification of land and water use in the face of demands for fuel and energy in landscapes that are critical to the reproduction and survival of North American waterfowl (Bethke and Nudds, 1995; Galatowitsch et al., 2009; Mooij et al., 2009). Understanding the connections between habitat and harvest management programs involves specifying linkages between JV and continental scales, and this is crucial for structuring an integrated predictive model. Thus, to improve the efficacy of waterfowl management, a comprehensive, predictive modeling approach is needed to formally integrate habitat and harvest management throughout the annual cycle of migratory species, while linking habitat changes at fine scales to population responses at the continental level, and accounting for the potential impacts of system change.

In this predictive modeling framework, we have shown that the solution to linking dynamics across scales lies in the regional scale density-dependent relationships for reproduction and post-harvest survival. In particular, habitat conditions (at least partially dictated by management actions) at the local level give rise to density-dependent relationships at the regional level, through a number of potential limiting mechanisms, like competition for space, energy, or mates. These regional scale density-dependent processes, in turn, scale up to influence population dynamics at the continental level, as shown in the model in this paper and others (Runge and Johnson, 2002; Runge and Boomer, 2005). So, the nexus of local- and continental-scale dynamics are these regional scale density-dependent relationships. Understanding this nexus opens tremendous potential to link dynamics across scales but presents a considerable challenge, because the demographic relationships at the regional level have not been a traditional topic of study. Addressing this challenge was the vision of the Joint Task Group (Anderson et al., 2007) and the charge of the Assessment Steering Committee (2007), and we have provided an example application here for northern pintail.

Fully specifying the details of mechanistic models that link local-scale processes to regional density-dependent relationships remains a challenge, and this is a purpose of JV assessment efforts (Assessment Steering Committee, 2007). In this paper, we have only provided a coarse way of modeling the effects of habitat management, but detailed models could be developed that link demographic responses at the regional level with on-the-ground habitat management actions. The level of detail specified in such regional models will depend on the scale of habitat management by JVs and the capacity of JVs to model the effects of these habitat actions. These regional models would be designed to predict how habitat management actions scale up to affect the regional density-dependent relationships. For example in the Prairie Pothole region, we fully expect the population-specific breeding submodel to be developed further to incorporate explicit drivers of reproduction, including local-scale habitat management actions, cross-seasonal effects, and climate change (Fig. 7; see Section 2.5). This will require input from managers and will be essential to explicitly integrate harvest and habitat management at the relevant scales.

At this point, the model we have presented is a framework to inform the integration of habitat and harvest management for waterfowl; it will need additional development before it should be used to address specific management decisions. Specifically, critical assessment of model structure and parameters will be needed concerning alternate forms of density dependence, parameterization of management influence on vital rates, incorporation of epistemic uncertainty and demographic stochasticity, and exploration of error propagation (Reed et al., 2002). Such development will require formal parameter estimation, for example, through a Bayesian implementation of an integrated population model to predict latent parameters based on empirical data (Schaub and Abadi, 2011).

Here, we briefly discuss four potential model refinements that could improve the predictive ability of this modeling framework. First, our model assumes that adult female breeding-season survival rates are constant across years and conspecific densities. As such, we assumed that adult female breeding-season survival rates were unrelated to the redistribution of breeding populations between populations (i.e., PR–AK, PR–NU). Female breeding-season survival, however, may be lower in years of higher reproductive effort (i.e., females are more vulnerable to predators when nesting; Devries et al., 2003), and accounting for this covariation between reproduction and survival could improve model predictions. Second, the scenarios we presented for the effect of potential habitat management actions in the GC and PR warrant further evaluation, particularly in linking them more specifically to on-the-ground management actions. Third, additional model structure would allow incorporation of cross-seasonal effects hypothesized to be important to waterfowl population dynamics. Previous research has suggested that habitat conditions on wintering grounds and migration stopovers may influence subsequent reproduction through the mechanism of body condition (Heitmeyer and Fredrickson, 1981; Raveling and Heitmeyer, 1989; Devries et al., 2008), and incorporating these cross-seasonal effects could improve predictions at the continental level. Fourth, as a null hypothesis, we assumed that the proportion of pintails that migrate in fall from PR to CA is equal to that of pintails that migrate from PR to GC. A skewed proportion, however, would alter our inferences regarding the relative importance of habitat management in these two nonbreeding regions. For any of these refinements, alternative models can be used to express uncertainty, and a formal analysis of the expected value of perfect information (Runge et al., 2011) could be used to identify crucial sources of uncertainty that could be the focus of monitoring and adaptive management.

We believe the modeling framework we have presented in this paper will have a number of important uses. First, the predictive model allows formal, integrated assessment of pintail status and harvest potential. Second, the framework can be used to guide management decisions, particularly regarding habitat management among and within JVs. Third, this modeling framework could serve as a prototype template for integrated habitat and harvest management of both waterfowl and non-waterfowl species. Fourth, the framework can be used to identify sources of uncertainty that have a high expected value of information, and thus should be the focus of monitoring and adaptive management.

Acknowledgements

This modeling effort was an initiative of the Pintail Action Group under the auspices of the NAWMP Science Support Team. For their contribution of time, data, ideas, and/or comments on previous versions of this manuscript, we would like to thank Mike Anderson, Paul Flint, Karla Guyn, Mark Koneff, Mike Miller, David Miller, Seth Mott, Jonathan Runge, Todd Sanders, and Robert Trost, and an anonymous reviewer. Funding for this project was provided by the U.S. Fish and Wildlife Service (Division of Bird Habitat Conservation, Division of Migratory Bird Management), the U.S. Geological Survey Science Support Partnership Program (Project #09-R2-03), Ducks Unlimited Canada's Institute for Wetland and Waterfowl Research, Environment Canada, and the University of California (Davis).

Appendix 1. Definitions of variables used in equations for metapopulation model for northern pintail in North America.

	Description
Breeding season	
$N_i^{\text{B♂}}(t), N_i^{\text{B♀}}(t), N_i^{\text{B•}}(t)$	Annual number of males, females, and all birds in breeding population *i*
$S_i^{\text{B♂}}, S_i^{\text{B♀}}$	Probability of survival during breeding for males, females in breeding population *i*
$R_i(t)$	Fall-flight age ratio in breeding population *i*
P_2^B	Number of May ponds in the Prairie Pothole population
$X_i(t)$	Population-specific regression parameters for $R_i(t)$, such as breeding population size
Fall migration through hunting season	
$N_i^{\text{Fa♂}}(t), N_i^{\text{Fj♂}}(t), N_i^{\text{Fa♀}}(t), N_i^{\text{Fj♀}}(t)$	Annual number of birds in each sex and age class at the start of fall migration in breeding population *i*
$S_{ir}^{\text{Fa♂}}, S_{ir}^{\text{Fj♂}}, S_{ir}^{\text{Fa♀}}, S_{ir}^{\text{Fj♀}}$	Probability of survival for each sex and age class while migrating from breeding population *i* to nonbreeding population *r*
ψ_{ir}^{F}	Probability of using migration route from breeding population *i* to nonbreeding population *r*
c	Crippling loss rate; proportion of pintails that die but are not harvested
$k^{\text{Fa♂}}, k^{\text{Fj♂}}, k^{\text{Fa♀}}, k^{\text{Fj♀}}$	Probability of mortality due to hunting including crippling loss (kill rate), accounting for differential vulnerability among age and sex classes during fall migration
$N_r^{\text{W•}}(t)$	Annual number of males and females at end of hunting season in nonbreeding population *r*
$H(t)$	Annual number of birds harvested
$N^{\text{M•}}(t)$	Annual number of birds just after fall migration and before harvest
$h(t)$	Annual proportion of birds harvested relative to $N^{\text{M•}}(t)$
Post-harvest through spring migration	
$N_r^{\text{W♂}}(t), N_r^{\text{W♀}}(t), N_r^{\text{W•}}(t)$	Annual number of males, females, and all birds alive post-harvest in nonbreeding population *r*
ψ_{ri}^{W}	Probability of using migration route from nonbreeding population *r* to breeding population *i*
$\psi_{B2B1}^{\text{W}}, \psi_{B2B3}^{\text{W}}$	Probability of using density-dependent migration route from PR to AK, PR to NU
$\psi_{leaveB2,\max}^{\text{W}}$	Maximum density-dependent probability that birds arriving in PR (breeding population 2) will migrate to one of the other two breeding populations
$\psi_{leaveB2}^{\text{W}}(t)$	Annual density-dependent probability that birds arriving in PR will migrate to one of the other two breeding populations
$Y(t)$	Regression parameters for $\psi_{leaveB2}^{\text{W}}(t)$, such as number of pintails arriving on the nonbreeding grounds
$S_{r,\max}^{\text{W}}$	Maximum survival probability in nonbreeding population *r*
$S_{r,\min}^{\text{W}}$	Minimum survival probability in nonbreeding population *r*
$S_r^{\text{W}}(t)$	Survival probability in nonbreeding population *r*
$Z_r(t)$	Regression parameters for $S_r^{\text{W}}(t)$, such as post-harvest population size

References

Anderson, J.T., 2008. Survival, habitat use, and movements of female northern pintails wintering along the Texas coast. MS Thesis, Texas A&M University, Kingsville, TX.

Anderson, M.G., Caswell, D., Eadie, J.M., Herbert, J.T., Huang, M., Humburg, D.D., Johnson, F.A., Koneff, M.D., Mott, S.E., Nudds, T.D., Reed, E.T., Ringelman, J.K., Runge, M.C., Wilson, B.C., 2007. Report from the Joint Task rou for clarifying North American waterfowl management plan population objectives and their use in harvest management. U.S. Fish and Wildlife Service, Arlington, VA.

Anonymous, 1986. North American Waterfowl Management Plan: a strategy for cooperation.

Assessment Steering Committee, 2007. North American Waterfowl Management Plan: continental progress assessment final report. North American Waterfowl Management Plan, Plan Committee, Washington, DC.

Austin, J.E., Miller, M.R., 1995. Northern pintail (*Anas acuta*). Cornell Lab of Ornithology. URL: http://bna.birds.cornell.edu/bna/species/163.

Beissinger, S.R., Westphal, M.I., 1998. On the use of demographic models of population viability in endangered species management. J. Wildl. Manage. 62, 821–841.

Bethke, R.W., Nudds, T.D., 1995. Effects of climate-change and land-use on duck abundance in Canadian Prairie-Parklands. Ecol. Appl. 5, 588–600.

Brasher, M.G., Arnold, T.W., Devries, J.H., Kaminski, R.M., 2006. Breeding-season survival of male and female mallards in Canada's prairie-parklands. J. Wildl. Manage. 70, 805–811.

Delgado, M., Gomez-Skarmeta, A.F., 1998. A methodology to model fuzzy systems using fuzzy clustering in a rapid-prototyping approach. Fuzzy Sets Syst. 97, 287–301.

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

Devries, J.H., Citta, J.J., Lindberg, M.S., Howerter, D.W., Anderson, M.G., 2003. Breeding-season survival of mallard females in the Prairie Pothole Region of Canada. J. Wildl. Manage. 67, 551–563.

Drever, M.C., Nudds, T.D., Clark, R.G., 2007. Agricultural policy and nest success of prairie ducks in Canada and the United States. Avian Conserv. Ecol. 2, URL: http://www.ace-eco.org/vol2/iss2/art5/.

Fleskes, J.P., Yee, J.L., Yarris, G.S., Miller, M.R., Casazza, M.L., 2007. Pintail and mallard survival in California relative to habitat, abundance, and hunting. J. Wildl. Manage. 71, 2238–2248.

Galatowitsch, S., Frelich, L., Phillips-Mao, L., 2009. Regional climate change adaptation strategies for biodiversity conservation in a midcontinental region of North America. Biol. Conserv. 142, 2012–2022.

Gregory, R., Long, G., 2009. Using structured decision making to help implement a precautionary approach to endangered species management. Risk Anal. 29, 518–532.

Guyn, K.L., Clark, R.G., 1999. Factors affecting survival of northern pintail ducklings in Alberta. Condor 101, 369–377.

Haukos, D.A., Miller, M.R., Orthmeyer, D.L., Takekawa, J.Y., Fleskes, J.P., Casazza, M.L., Perry, W.M., Moon, J.A., 2006. Spring migration of northern pintails from Texas and New Mexico, USA. Waterbirds 29, 127–136.

Heitmeyer, M.E., Fredrickson, L.H., 1981. Do wetland conditions in the Mississippi Delta hardwoods influence mallard recruitment? Trans. N. Am. Wildl. Nat. Resour. Conf. 46, 44–57.

Hestbeck, J.B., 1995. Response of northern pintail breeding populations to drought, 1961–92. J. Wildl. Manage. 59, 9–15.

Hovestadt, T., Kubisch, A., Poethke, H.J., 2010. Information processing in models for density-dependent emigration: a comparison. Ecol. Model. 221, 405–410.

Johnson, D.H., Grier, J.W., 1988. Determinants of breeding distributions of ducks. Wildl. Monogr. 100.

Lee, C.K., Taylor, J.P., Haukos, D.A., Andersen, M.C., 2007. Winter survival of northern pintails in the Middle Rio Grande Valley, New Mexico. West. N. Am. Nat. 67, 79–85.

Lertzman, K., 2009. The paradigm of management, management systems, and resource stewardship. J. Ethnobiol. 29, 339–358.

Lindberg, M.S., Sedinger, J.S., Derksen, D.V., Rockwell, R.F., 1998. Natal and breeding philopatry in a Black Brant, Branta bernicla nigricans, metapopulation. Ecology 79, 1893–1904.

Matthysen, E., 2005. Density-dependent dispersal in birds and mammals. Ecography 28, 403–416.

McAlpine, C.A., Rhodes, J.R., Bowen, M.E., Lunney, D., Callaghan, J.G., Mitchell, D.L., Possingham, H.P., 2008. Can multiscale models of species' distribution be generalized from region to region? A case study of the koala. J. Appl. Ecol. 45, 558–567.

Miller, M.R., Duncan, D.C., Guyn, K.L., Flint, P.L., Austin, J.E., 2001. The northern pintail in North America: the problem and a prescription for recovery, Sacramento, CA.

Miller, M.R., Takekawa, J.Y., Fleskes, J.P., Orthmeyer, D.L., Casazza, M.L., Perry, W.M., 2005. Spring migration of northern pintails from California's Central Valley wintering area tracked with satellite telemetry: routes, timing, and destinations. Can. J. Zool. 83, 1314–1332.

Mooij, W.M., Domis, L.N.D., Janse, J.H., 2009. Linking species- and ecosystem-level impacts of climate change in lakes with a complex and a minimal model. Ecol. Model. 220, 3011–3020.

Natural Resources Canada, 2010. GeoGratis: Geospatial Data Available Online. Earth Sciences Sector. Natural Resources Canada, Ottawa, Ontario.

Neraasen, T.G., Nelson, J.W., 1999. Landscape planning and management in agro-ecosystems: the Canadian prairie experience. In: Baydack III, R.K.C.H., Haufler, J.B. (Eds.), Practical Approaches to the Conservation of Biological Diversity. Island Press, Washington, DC, pp. 141–165.

Nichols, J.D., Johnson, F.A., Williams, B.K., 1995. Managing North-American waterfowl in the face of uncertainty. Annu. Rev. Ecol. Syst. 26, 177–199.

Podruzny, K.M., Devries, J.H., Armstrong, L.M., Rotella, J.J., 2002. Long-term response of northern pintails to changes in wetlands and agriculture in the Canadian Prairie Pothole Region. J. Wildl. Manage. 66, 993–1010.

Prairie Habitat Joint Venture, 2009. Prairie Habitat Joint Venture Implementation Plan 2007–2012. Report of the prairie habitat joint venture. Environment Canada, Edmonton, Canada.

Raveling, D.G., Heitmeyer, M.E., 1989. Relationships of population size and recruitment of pintails to habitat conditions and harvest. J. Wildl. Manage. 53, 1088–1103.

Reed, J.M., Mills, L.S., Dunning, J.B., Menges, E.S., McKelvey, K.S., Frye, R., Beissinger, S.R., Anstett, M.C., Miller, P., 2002. Emerging issues in population viability analysis. Conserv. Biol. 16, 7–19.

Rice, M.B., Haukos, D.A., Dubovsky, J.A., Runge, M.C., 2010. Continental survival and recovery rates of northern pintails using band-recovery data. J. Wildl. Manage. 74, 778–787.

Richkus, K.D., Rohwer, F.C., Chamberlain, M.J., 2005. Survival and cause-specific mortality of female northern pintails in southern Saskatchewan. J. Wildl. Manage. 69, 574–581.

Runge, M.C., Boomer, G.S., 2005. Population dynamics and harvest management of the continental northern pintail population. U.S. Fish and Wildlife Service report, Laurel, MD.

Runge, M.C., Johnson, F.A., 2002. The importance of functional form in optimal control solutions of problems in population dynamics. Ecology 83, 1357–1371.

Runge, M.C., Converse, S.J., Lyons, J.E., 2011. Which uncertainty? Using expert elicitation and expected value of information to design an adaptive program. Biological Conservation 144, 1214–1223.

Runge, M.C., Johnson, F.A., Anderson, M.G., Koneff, M.D., Reed, E.T., Mott, S.E., 2006. The need for coherence between waterfowl harvest and habitat management. Wildl. Soc. Bull. 34, 1231–1237.

Saether, B.E., Lillegard, M., Grotan, V., Drever, M.C., Engen, S., Nudds, T.D., Podruzny, K.M., 2008. Geographical gradients in the population dynamics of North American prairie ducks. J. Anim. Ecol. 77, 869–882.

Schaub, M., Abadi, F., 2011. Integrated population models: a novel analysis framework for deeper insights into population dynamics. Journal of Ornithology 152, 227–237.

Sutherland, W.J., 2001. Sustainable exploitation: a review of principles and methods. Wildl. Biol. 7, 131–140.

U.S. Geological Survey, 2010. Multi-Resolution Land Characteristics (MRLC) Consortium. Earth Resources Observation and Science Center, Sioux Falls, South Dakota.

USFWS, 2007. Northern Pintail Harvest Strategy. Division of Migratory Bird Management, U.S. Fish and Wildlife Service, Department of Interior, Washington, DC.

USFWS, 2009a. Waterfowl Population Status. U.S. Department of the Interior, Washington, DC.

USFWS, 2009b. Adaptive harvest management: 2009 hunting season. U.S. Department of the Interior. Washington, DC. URL: http://www.fws.gov/migratorybirds/NewReportsPublications/AHM/Year2009/2009-AHM-report(Final).pdf.

Voldseth, R.A., Johnson, W.C., Gilmanov, T., Guntenspergen, G.R., Millett, B.V., 2007. Model estimation of land-use effects on water levels of northern prairie wetlands. Ecol. Appl. 17, 527–540.

Whittingham, M.J., Krebs, J.R., Swetnam, R.D., Vickery, J.A., Wilson, J.D., Freckleton, R.P., 2007. Should conservation strategies consider spatial generality? Farmland birds show regional not national patterns of habitat association. Ecol. Lett. 10, 25–35.

Zimpfer, N.L., Rhodes, W.E., Silverman, E.D., Zimmerman, G.S., Koneff, M.D., 2009. Trends in duck breeding populations, 1955–2009. U.S. Department of the Interior, Fish and Wildlife Service, Laurel, MD.