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A generalizable energetics-based model of avian migration to facilitate continental-scale waterbird conservation

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Abstract. Conserving migratory birds is made especially difficult because of movement among spatially disparate locations across the annual cycle. In light of challenges presented by the scale and ecology of migratory birds, successful conservation requires integrating objectives, management, and monitoring across scales, from local management units to ecoregional and flyway administrative boundaries. We present an integrated approach using a spatially explicit energetic-based mechanistic bird migration model useful to conservation decision-making across disparate scales and locations. This model moves a Mallard-like bird (*Anas platyrhynchos*), through spring and fall migration as a function of caloric gains and losses across a continental-scale energy landscape. We predicted with this model that fall migration, where birds moved from breeding to wintering habitat, took a mean of 27.5 d of flight with a mean seasonal survivorship of 90.5% (95% CI = 89.2%, 91.9%), whereas spring migration took a mean of 23.5 d of flight with mean seasonal survivorship of 93.6% (95% CI = 92.5%, 94.7%). Sensitivity analyses suggested that survival during migration was sensitive to flight speed, flight cost, the amount of energy the animal could carry, and the spatial pattern of energy availability, but generally insensitive to total energy availability per se. Nevertheless, continental patterns in the bird-use days occurred principally in relation to wetland cover and agricultural habitat in the fall. Bird-use days were highest in both spring and fall in the Mississippi Alluvial Valley and along the coast and near-shore environments of South Carolina. Spatial sensitivity analyses suggested that locations nearer to migratory endpoints were less important to survivorship; for instance, removing energy from a 1036 km^2 stopover site at a time from the Atlantic Flyway suggested coastal areas between New Jersey and North Carolina, including the Chesapeake Bay and the North Carolina piedmont, are essential locations for efficient migration and increasing survivorship during spring migration but not locations in Ontario and Massachusetts. This sort of spatially explicit information may allow decision-makers to prioritize their conservation actions toward locations most influential to migratory success. Thus, this mechanistic model of avian migration provides a decision-analytic medium integrating the potential consequences of local actions to flyway-scale phenomena.

Key words: Anas platyrhynchos; *bird survivorship; conservation; Mallard; migration; migratory birds; North American Wetlands Conservation Act; waterfowl.*

INTRODUCTION

Achieving conservation goals over large spatial scales often requires significant financial investment. From 2001 to 2008, conservation expenditures by the United States Federal Government exceed US$7 billion annually,

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which constitutes more than one-third of the global investment by governments into conservation (Waldron et al. 2013). The economic cost of conservation, coupled with budget limitations and the demand for accountability necessitates efficient and transparent use of resources (Wilson et al. 2007). In response to the growing demand for accountability, both practitioners and the academic community have advocated for strategic, business-like management approaches to address these concerns (Cleary 2006, Higgins et al. 2006, U.S. Fish and Wildlife Service 2006, Wilson et al. 2007). Although researchers have applied decision-analytic techniques to conservation biology (Walters and Hilborn 1978, Ellison 2004, Williams et al. 2005, Mendoza and Martins 2006), the efficient allocation of limited resources across space and time remains understudied (McDonald-Madden et al. 2008, Thogmartin et al. 2009), especially for large spatial scales (Holzkämper and Seppelt 2007).

One challenging and pressing coarse-scale resource allocation problem involves the conservation of migratory birds (Klaassen et al. 2006, 2008, Kirby et al. 2008, Runge et al. 2014). Migratory birds congregate in spatially disparate locations across the annual cycle (e.g., breeding, migration, and wintering areas). In North America, for example, some migratory birds breed during summer in Canada and the northern USA and overwinter in the southern USA or Latin America. Since 1948, waterfowl have been managed through a system of four administrative flyway councils (Atlantic, Mississippi, Central, and Pacific) that are based on waterfowl migration paths and geographic boundaries, whereby state and federal agencies are given roles to coordinate flyway-scale management activities (Nichols et al. 1995). From a conservation standpoint, the identification of limiting factors at such a coarse scale is challenging because of the transitory nature of bird movements which cross administrative boundaries. Cross-seasonal effects associated with temporal habitat limitations during portions of the birds' annual cycle should be considered when developing a land conservation strategy for migratory bird conservation (Greenberg and Marra 2005, Boulet and Norris 2006, Skagen 2006).

In light of these challenges presented by the scale and ecology of migratory birds, there is growing recognition that successful conservation requires integration of objectives, management, and monitoring across scales from local management units to ecoregional and flyway administrative boundaries (Mattsson et al. 2012). At the local level, wetland managers and field biologists choose management actions to best achieve objectives with respect to a particular management unit or wetland complex, but often strive to contribute to ecoregional objectives whenever possible. A common decision of managers at the ecoregional scale (e.g., Bird Conservation Regions; U.S. NABCI Committee 2000) is the spatial allocation of resources and funds among sites within a region or to provide guidance to local wetland managers with regard to priorities at larger scales (Thogmartin et al. 2011). Similarly, decision makers at these larger scales often decide on spatial allocation of resources but from a broader perspective and often with additional considerations related to maintaining connections between breeding and wintering areas and supporting migratory birds in transit.

National Wildlife Refuges (NWR) and state wildlife management areas contribute significantly to meeting the habitat needs of many waterbird species (Scott et al. 2004). However, the contribution of additional protected areas to waterbird conservation has been quantified only in limited cases (Williams et al. 1999). Additionally, cross-border coordination of wetland management actions among management areas is rare, but doing so to match waterbird migration chronologies may result in greater efficiency in waterbird conservation (Martin et al. 2007).

Conservation and management decision context

Decision-analytic approaches to help increase the necessary level of coordination have been applied to waterfowl management since Brown and Hammack (1973) developed a model to determine the net economic value of waterfowl by controlling the number of waterfowl killed by hunters and the number of ponds rented for waterfowl habitat. Extensions of this work were developed by Cowardin and Johnson (1979) and Brown et al. (2001). A stochastic simulation model to evaluate alternative management schemes on refuging waterfowl populations was developed by Frederick et al. (1987), whereas Klaassen et al. (2008) used stochastic dynamic programming of spring migrating geese (*Anser* sp.) to evaluate a range of management scenarios with respect food supplementation. In 1995, the USFWS adopted the concept of adaptive resource management (Walters 1986) for regulating waterfowl harvests in the United States (Williams and Johnson 1995, Nichols et al. 2007). Strategic Habitat Conservation (SHC; U.S. Fish and Wildlife Service 2006) has been established as the new business model for wildlife conservation within the U.S. Fish and Wildlife Service. Strategic Habitat Conservation incorporates biological planning, conservation design, delivery, monitoring, and research in a framework allowing adaptive and iterative management decision-making. To date, however, there has been a lack of models incorporating density dependent mechanisms (e.g., Sutherland 1998, Taylor and Norris 2007) that would identify resources most limiting to waterfowl migration or mechanisms for providing quantitative guidance for the annual land conservation granting decisions made under various programs (e.g., Klaassen et al. 2008), such as the North American Wetland Conservation Act (NAWCA).

We present a model designed to integrate the basic needs of waterbirds across scales and provide important insights for managers regarding the strategic placement of additional resources for waterbird conservation useful in an adaptive management context. We present a general continental-scale, energetic-based, biological model of waterfowl migration during the fall and spring and evaluate simply whether it provides results consistent with our best understanding of migration and stopover dynamics. After which, we use the model to determine if survivorship during migration is limited by the estimated amount of food resources. Finally, we illustrate how the model could be used to evaluate the consequences of potential wetland loss for the Atlantic Flyway, one of the four migratory waterfowl administrative areas for within the USA (others are Mississippi, Central, and Pacific; Fig. 1A).

METHODS

Overview

We modeled waterfowl migration through the continent as a function of energetic gains and losses, subject to the availability of requisite levels of roosting habitat and nearby forage. In the fall, birds depart breeding grounds to head toward wintering areas, with migratory flight often consisting of a series of several movements or jumps from one stopover site to another (Piersma 1987, Moore and Simons 1992, Moore et al. 1995, Drent et al. 2003, Jenni and Schaub 2003, Newton 2006). When a bird leaves its breeding grounds, or one stopover site for another, it must choose its next stopover site, and we assume this choice depends on the stopover site's roosting and forage availability and quality, its distance from the departure site, and the stopover site's distance to a final non-breeding destination. Because birds expend considerable energy during migratory flight (Newton 2006) and there is a chance that a bird will die, we assume the mortality rate increases as energy is depleted. Most birds survive,

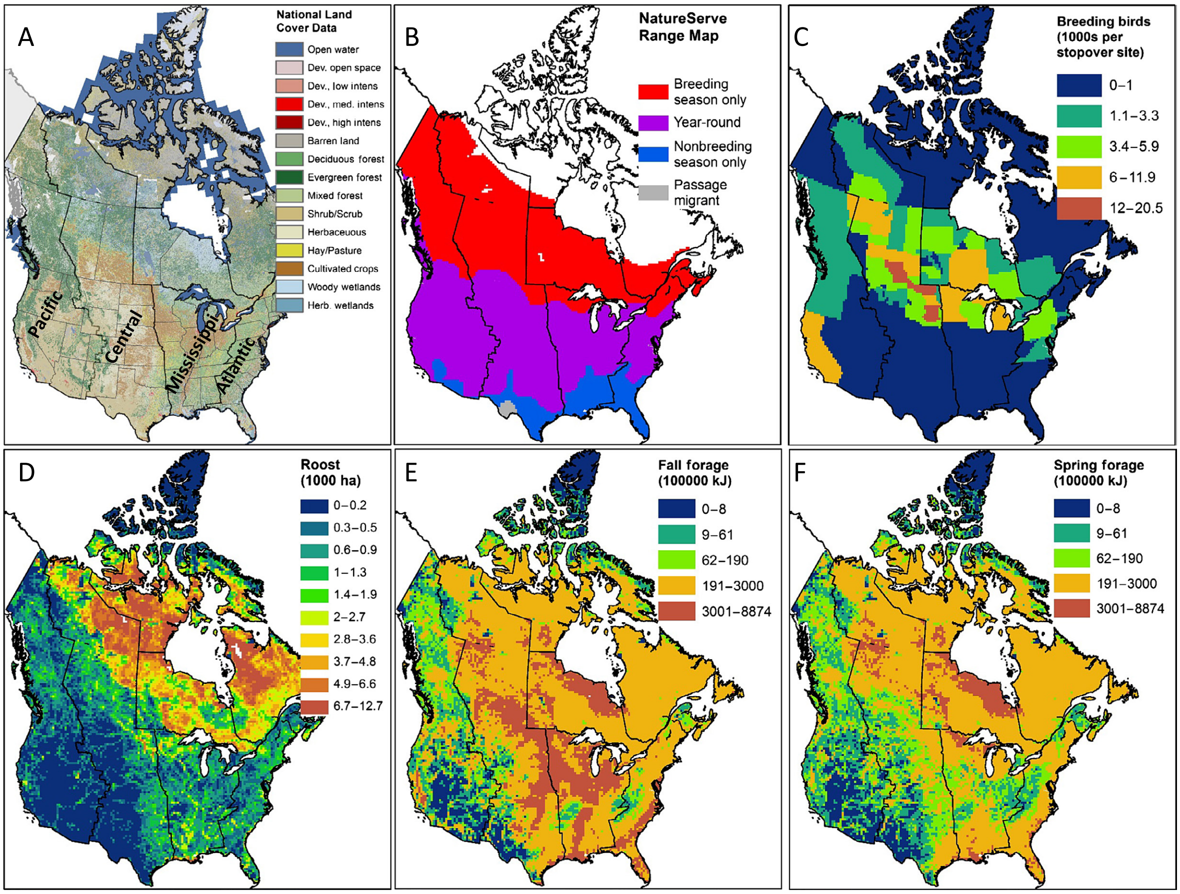

FIG. 1. Illustration of GIS inputs and GIS analysis of habitat quality. (A) Land cover map for the USA and Canada, along with administrative boundaries of four major flyways: Atlantic, Mississippi, Central, and Pacific. We used the land cover data to estimate roosting and forage quality. (B) NatureServe range map showing Mallard duck breeding only areas (red), non-breeding areas (blue) and areas where Mallards can be found year-round (purple; Ridgely et al. 2005). This layer provided potential starting and ending locations for migratory waterfowl. (C) Distribution of the May waterfowl breeding population (estimated in thousands of birds per stopover site [1036 km^2]) for Mallards, which is used to estimate the starting distribution of birds in the fall migration. (D) Total dabbling duck roosting quality within each site (darker shades indicate higher quality) based on analysis of land cover. (E, F) Average of a stopover site's forage availability (in 100000 kJ) during fall and spring migration, respectively, based analysis of land cover using a range of parameter estimates (Table 2). Lower availability is indicated by blue, with a gradient of increasing availability from green to yellow to orange.

however, and use the stopover site to rest and refuel before repeating this process until they reach a final non-breeding or wintering site. In the spring, the process reverses.

Scale of the model and analysis

Waterfowl and waterbirds are commonly used as model species in the development of migration models (e.g., Farmer and Wiens 1998, 1999, Weber et al. 1998, 1999, Clark and Butler 1999, Beekman et al. 2002, Klaassen et al. 2006). We used the Mallard as a model species (*Anas platyrhynchos*) because of the wealth of information associated with and considerable management interest in it, but the framework we describe can be applied, with proper parameterization, to the complete array of migrating bird species. Determining the appropriate scale is one of the most challenging decisions in modeling migratory waterfowl movements, as continental populations for some species are estimated at over 5 million birds and non-breeding ranges cover thousands of square kilometers (Ridgely et al. 2005).

We chose to model the birds at a temporal resolution composed of migratory jumps and a spatial resolution of 1036 km^2 (400 mile^2) stopover sites. The size of the stopover site was chosen to reflect our group's expert opinion that 16 km (10 miles) is the maximum distance Mallards might travel from a roosting site to forage and that anything farther would be considered movement to a different stopover site, i.e., migratory movement. We modeled the number and fate of flocks, i.e., groups of individuals, moving from a collection of starting sites, i.e., breeding grounds, to a collection of ending sites, i.e., wintering grounds.

We combined information from three sources to select the location and flock size starting from sites at the end of the non-migratory season. First, we used National Land Cover Database 2006 for the USA (Fry et al. 2011) and the CSC2000v for Canada (*available online*; see Appendix S2) for habitat input (Fig. 1A).[12] then determined the location of the sites according to range maps, provided by NatureServe (Ridgely et al. 2005), delineating the distribution of Mallards during breeding and wintering periods; these locations represented the potential starting and ending sites for fall or spring migration, respectively (Fig. 1B). To determine the number of birds to model, we used recent results of the breeding population survey (U.S. Fish and Wildlife Service 2013; Fig. 1C). The land cover data were translated into shoreline roosting habitat (Fig. 1D) and forage quality (Fig. 1E for fall and Fig. 1F for spring). To determine the number of birds starting from each breeding site, we combined the spatial information of the breeding population survey with information from our evaluation of forage and roosting quality (described below). We weighted the number of birds by the quality of habitat within the site and the breeding population survey results for the area: the quality of the habitat is described fully in the *Movement patterns* section, but in short, sites with more shoreline, herbaceous wetlands, and woody wetlands were considered to have higher quality. We used those data with our estimates of habitat quality to allocate the total number of birds observed across the breeding grounds. Thus, sites with high quality and a relatively large number of birds, according to breeding population counts, started with the most birds. We then used the abundance of birds within these breeding sites to start/stop the migration dynamics in the model.

We used a multistep approach to addressing the behavior of these migratory jumps. We first used a spatial analysis to evaluate the amount, quality, and configuration of migratory habitat; the result of the spatial analysis was used as an input in a deterministic migration model. Habitat quality at stopover sites was defined by quality of both roosting and foraging habitat. Specific sites representing breeding (starting) and wintering (ending) grounds were input in addition to the spatial analyses. Finally, we recognize that there is considerable parametric uncertainty in many aspects of the model, so we performed a sensitivity analysis by running the deterministic model under a range of parameter values to determine how our estimates of survivorship depend on the parameter value.

Generating energetic-based landscapes

We translated continental land cover into two key habitat components of waterfowl migration: roosting and forage habitat (Fig. 1D–F, respectively). For each component, we generated a site-specific summary of habitat quality for roosting and forage. Mallards require shallow water where they can both forage and roost during stopovers. Thus, we assumed that a site of the highest quality would consist of areas with abundant roosting and forage habitat and that the quality of forage within a site was the product of the food energy present and distance to roosting sites, such that foraging areas farther from a roost area are of lower quality than foraging areas relatively near a roost area. We describe how we delineated the quality and quantity of roost and forage. We used ArcGIS 10.1 (ESRI, Redlands CA) in our analysis of roost and forage.

Roosting

Birds use stopover periods not only for refueling but also to rest and prepare for the next migratory jump (Wikelski et al. 2003), and roosting habitat is an important feature of high-quality stopover sites. To estimate the roosting quantity of a stopover site, we determined the proportion, p, of site j that was covered by land cover c (i.e., shoreline), p_{cj}, and the roosting habitat quality provided by land cover c, R_c. Roosting habitat quality ranged from 0 (poor) to 1 (high). Table 1 shows a list of all parameters used in the model as well as their definition (see Appendices S1, S4, and S5 for parameter values). Thus, a synthetic measure of roosting habitat quality and quantity HR_{sj} provided in site j was

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[12] http://www.geobase.ca/

Table 1. Parameters used in the model are shown here.

Parameter	Definition
HR	area (km^2) of habitat for roosting within a site
HF	habitat-based quantity of forage (kiloJ) within a site
A	area (km^2) of a site
P	proportion of cover type, e.g., from National Land Cover Dataset 2006, in a site
R	suitability of cover type for roosting
K	amount of forage provided by cover type (energy value in kJoules) indexed by guild
D	distance (km) between sites indexed by i and j
φ	maximum flight range (km) indexed
Ω	proportion of maximum flight range traveled before refueling
Γ	scalar to describe shape of the gamma function for distance function
F	site to site flight probability matrix based on distance
E	site to site flight probability matrix based on distance to end
S	site to site flight probability matrix based on habitat quality
M	overall site to site flight probability matrix
N	site vector of bird numbers
β	flight speed (km/h) indexed by guild
Θ	energetic cost (kJ) of flight per hour indexed by guild
$\phi_{i,j}$	total cost (kJ) of flight between sites i and j
ζ	net energy gain (kJ) indexed by guild
Φ	maximum amount of energy (kJ in the tank) indexed by guild
Δ	energy deficit (kJ) upon arriving at a site
M	survivorship
t	expected time for refueling (bird-use days)

Note: Some of the parameters refer to equations described in the appendices.

$$HR_j = A_j \sum_{c=1}^{C} R_c p_{cj}, \tag{1.1}$$

where A_j was the area of site j (generally 1036 km^2, except along continental shores and other irregular bodies; Fig. 1D).

Because the USA and Canadian land cover datasets do not specify a shoreline cover type, we generated a proxy for shoreline by turning all 30-m pixels of open water bordering land into a new shoreline cover type (Fig. 1D). We recognize that not all shoreline pixels that we created would be considered ideal roosting habitat but without an alternative, we deemed this a reasonable approximation.

Forage quantity

Food abundance should influence the number of birds capable of passing through a site during a migration season (Schneider and Harrington 1981). To determine the forage quantity of a stopover site, we determined the proportion of site j that was covered by land cover c, p_{cj}, and the amount of forage K_c (in kiloJoules) provided by land cover c per unit area. Thus, the potential amount of forage provided in site j, HF_j, was:

$$HF_j = A_j \sum_{c=1}^{C} K_c p_{cj}, \tag{1.2}$$

where A_j was the area of site j. To determine available food energy per land cover pixel, we reviewed literature pertaining to Mallard food habits (Appendix S3).

We represent the proportion of forage within a site available to a Mallard as a function of forage location's distance to roosting sites. We assumed that the realized quality (net energy gained) of a forage site declines with increasing distance to the nearest roosting site because of increasing travel costs (Johnson et al. 2014).

$$\bar{H}\bar{F}_j = A_j \sum_{c=1}^{C} K_c p_{cj} q_{cj}, \tag{1.2.1}$$

where q_{cj} is equal to the proportion of forage available based on distance to the nearest roost site (details of how we determined q_{cj} can be found in Appendix S4). Combining the quantity of forage for fall (Fig. 1E) and spring (Fig. 1F) periods relative to roosting habitat provides overall assessment of habitat quality for fall and spring migration.

Waterbird migration

We modeled migration in two steps: first we analyzed a continental land cover map to determine the quality of stopover sites and, then, given the quality and spatial pattern of stopover sites, we modeled the movement of birds through the stopover sites as they travel to and from breeding to wintering areas. Migration occurs through a series of migratory flights between stopover sites, where the birds roost, forage, and refuel. The majority of the migration process is spent at stopover sites and thus any mortality occurring during migration was assumed likely to occur at stopover sites or as a result of decisions made at stopover sites (Taylor et al. 2011). To account for these dynamics, we broke migratory movement into three linked components: movement patterns, energy (fuel) dynamics, and migration survivorship. We used Matlab (version 7.13; Mathworks, Natick, Massachusetts, USA) to model migration.

Movement patterns

We assumed the probability a bird migrates from stopover site i to stopover site j, m_{ij}, was a function of three landscape factors: (1) distance between the sites i and j relative the Mallard's flight range, $\hat{F}_{ij}$, (2) the overall quality of site j, $\hat{S}_j$, and (3) the distance of site j to a potential final destination such as a wintering or breeding site, $\hat{E}_j$. We assumed birds would travel along routes minimizing the travel distance to and from the wintering and breeding grounds, while selecting higher quality stopover sites preferentially over lower quality sites. We provide an overview of the three factors here, and the formal equations are described in detail in Appendix S4.

For the first factor, the distance between the sites i and j relative to bird's flight range, $\hat{F}_{ij}$ (Appendix S4: Eq. S2.2), we assumed that when birds are migrating, the distance they travel for each migration event is limited by the energetic cost of flight and their body (energetic) condition (Appendix S5). Individuals generally arrive at stopover habitat in a fat-depleted condition (Rappole and Warner 1976, Moore and Kerlinger 1987); thus, we also assumed that birds are more likely to expend nearly all stored energy, risking starvation, rather than spend very little before landing to refuel with the caveat that they are less likely to risk expending all available stored energy (Fig. 2).

The second factor influencing migration is based on our assumption that the probability a migrating bird will meet its energetic requirements and achieve safe passage between breeding and wintering grounds is correlated with the intrinsic quality of stopover habitat (Moore et al. 1993, Petit 2000) of site j, $\hat{S}_j$ (Appendix S4: Eq. S3). Migrants require roosting and foraging habitat at stopovers; we assumed birds are more likely to stop over at sites with a relatively greater proportion of both roosting and forage habitat (i.e., higher quality) than sites with a lesser proportion (sensu Orians and Wittenberger 1991). Some birds will choose stopover sites that are of poorer quality than others but we assume this is less likely than choosing a site of higher quality.

Finally, we assumed that the nearer site j was to a potential final destination, the higher the probability that that a bird would select a stopover site within that site, $\hat{E}_j$ (Appendix S4: Eq. S4). Maximizing the speed of migration is an optimal strategy for migrating birds (Alerstam and Lindström 1990, Hedenström 2008). There is often no faster path than a straight line. Thus, we assumed birds migrate preferentially toward a final destination, rather than away, such that each migratory jump was more likely to move birds closer to a potential identified final destination (a site in either the specified wintering or breeding grounds).

To determine the overall movement probability from current site i to site j, we calculated the product of all three components (flight range, attractiveness, and distance to an end site), normalized by the sum of probabilities from site i to all J other sites is 1. Thus, the probability of migrating from site i to site j, m_{ij}, is

$$m_{ij} = \frac{\hat{F}_{ij}\hat{E}_j\hat{S}_j}{\sum_{j=1}^{J} \hat{F}_{ij}\hat{E}_j\hat{S}_j}. \tag{2}$$

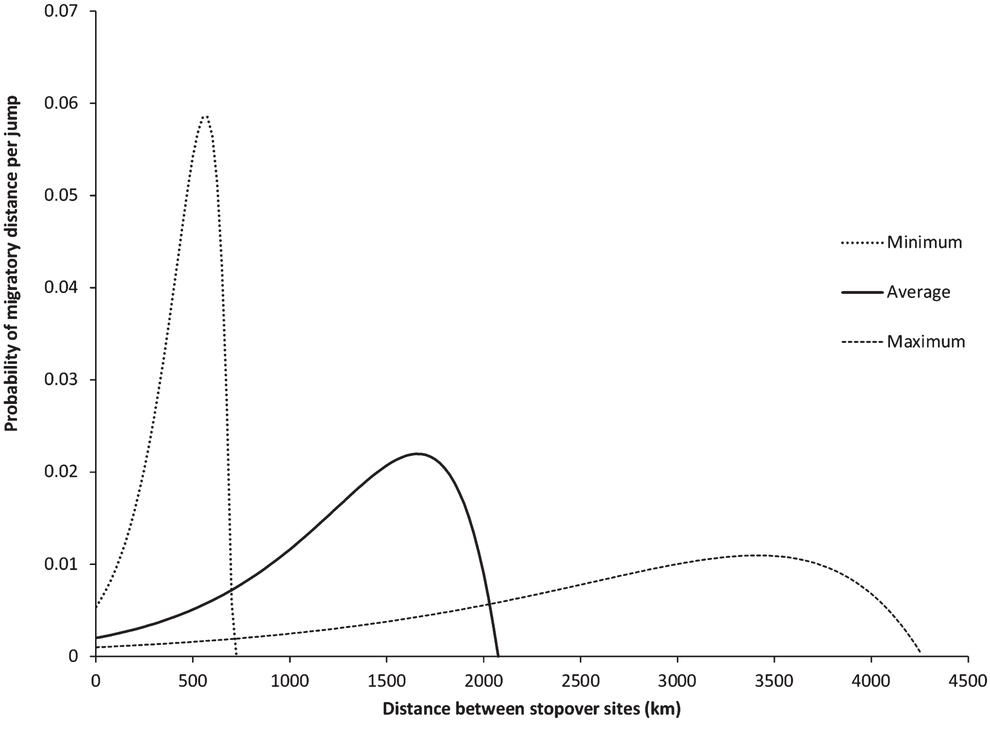

FIG. 2. Gamma probability distribution function illustrating the likelihood that a Mallard would travel from one site to another given the distance between them. The three curves reflect the uncertainty in energetic parameters used to predict migration by illustrating the minimum flight range (dotted line), maximum flight range (dashed line), and the average flight range (solid line) used in the analyses. The precise equation is described in Appendix S4.

It follows that the number of birds of the flock n_{ij} in site i moving to site j, is the probability of migration times the number of birds in site i is: $n_{ij} = m_{ij}n_i$. Thus the overall movement of birds can be represented by $\hat{\mathbf{n}} = \mathbf{Mn}$, where $\mathbf{M}$ is a J by J matrix consisting of elements m_{ij} and $\mathbf{n}$ is a J by 1 vector consisting of elements n_i. Note that once the bird reached an end site (either the breeding ground or wintering area), we set m_{ij} to 1 for that site so the probability of moving to any other site to 0. It is worth mentioning that the temporal scale is based on number of jumps rather than time, such that the time (days) to complete migration is a model output rather than an explicit input.

Energetics of migration

Birds expend energy during a migratory flight and must refuel by foraging at a stopover site. The amount of energy ϕ_{ij} expended during flight between sites i and j was a function of the distance D_{ij} (kilometers) between sites i and j, the speed of flight β (kilometers per hour), and the energetic cost θ (Joules per hour) of migratory flight:

$$\varphi_{ij} = D_{ij}\frac{\theta}{\beta}. \tag{3.1}$$

Because flocks are likely to arrive at stopover site j from multiple sites i, we calculated the average energetic cost of flight for all birds arriving at site j such that the expected cost of birds arriving at site j, $\bar{\varphi}_j$, is

$$\bar{\varphi}_j = \frac{\sum_{i=1}^{J} n_{ij}\varphi_{ij}}{\sum_{i=1}^{J} n_{ij}}. \tag{3.2}$$

Each day spent foraging or roosting at the stopover site is considered a bird-use day (BUD).

Net energy gain and incorporating within-site flight costs

Lipid stores are depleted during migration flights; some birds are capable of rapidly rebuilding these reserves in a matter of days at rates approaching 10% of body mass/d (Moore and Kerlinger 1987). Thus, upon reaching a stopover site, birds refuel by traveling from a roosting site to a nearby foraging site. In our model, the daily net energy gain is a loaded term that represents the energy gained from forage at the stopover site minus the costs of the round trip flight and normal body maintenance costs, basal metabolic rate, thermoregulatory requirements, and energetic costs of daily activities other than flight (i.e., feeding, swimming, walking, preening, and social behaviors). The number of days, t_j, a bird stays at stopover site j increases as the amount of forage required to refuel increases and decreases as the daily net gain ζ (kiloJoules/d) of an individual increases (Cherry 1982, Moore and Kerlinger 1987).

We assume that when birds landed, they do not leave until they completely refuel (cf., Erni et al. 2002). Thus the number of days it took a bird to refuel is

$$t_j = \frac{\left(\Phi - \bar{\varphi}_j\right)}{\zeta}, \tag{4}$$

where Φ is the maximum amount of fuel (Joules) carried, i.e., the size of a bird's fuel tank, the numerator $\left(\Phi - \bar{\varphi}_j\right)$ is the amount of energy needed to completely refuel and the denominator is daily net gain in Joules as described above.

Migration survivorship

Traveling long distances comes with considerable risk to migrating birds, and mortality during migration is often substantial (Greenberg 1980, Ketterson and Nolan 1983, Owen and Black 1991, Sillett and Holmes 2002, Guillemain et al. 2010). Daily survivorship was a major source of uncertainty, so we made several basic assumptions and used expert opinion to create this aspect of the model. There is a non-negligible chance each day that a bird may die, and we assumed that the mortality rate was likely to increase with increasing energy deficits $\left(\Phi - \hat{\varphi}_j\right)$. With these assumptions, we related bird energy status μ_s to daily survivorship,

$$\mu_s = \mu_{\max} - \left(\mu_{\max} - \mu_{\min}\right)\frac{\Delta}{\Phi}, \tag{5.1}$$

such that daily survivorship ranged from $\mu_{\min}$ when birds arrived with no energy reserves to $\mu_{\max}$ when they arrived with full reserves. Overall survivorship $\hat{\mu}_j$ at stopover site j is simply the cumulative product of daily survivorship over the residence time:

$$\hat{\mu}_j = \mu^{t_j}. \tag{5.2}$$

To determine the number of birds leaving site j to continue their migration, we simply calculate the product of survivorship for site j, $\hat{\mu}_j$, with the number of birds that arrived at site j, $\hat{n}_j$. Overall survivorship is simply the total number of birds that arrive to the end sites, either wintering grounds or breeding area divided by the number of birds that started.

Updating the amount of forage in a site

As birds forage at a stopover site, they deplete the available food for birds that have yet to arrive (Schneider and Harrington 1981, Moore and Yong 1991, Kelly et al. 2002). To update forage availability in site j, removing forage energy HF_{sj} from site j, we simply subtract the flight cost of all the birds arriving to site j from site is, $\sum_{i=1}^{J} n_{ij}\varphi_{ij}$, the numerator of the flight cost equation 3.2. Thus, available forage HF_{jk}, in site j for migratory jump k is

$$HF_{jk} = HF_{jk-1} - \sum_{i=1}^{J} n_{ij}\varphi_{ij} \tag{6}$$

Output

In addition to overall survivorship, we can use the logic in the model to determine bird-use days (BUDs) for each site (the number of days spent refueling per bird times the number of birds) and the number of birds on each site for each jump. To determine the BUDs for each site j, we sum the product of the total number of birds surviving within each site j during jump k with the analogous time spent refueling in site j across all K migratory jumps,

$$BUDS_j = \sum_{k=1}^{K} \left(\hat{n}_{jk}\hat{u}_{jk}\right) t_{jk}, \tag{7}$$

where the term within parentheses represents the number of birds surviving in site j during jump k and t_{jk} represents the time spent refueling at site j during jump k.

Sensitivity analysis

We used regression analysis to determine sensitivity of overall survivorship and each site's BUDs to parametric uncertainty, similar to the logistic regression approach used by McCarthy et al. (1995) in population viability analyses. Our goal was to calculate how variation in each parameter affected model-predicted survivorship during migration, independent of all other parameters in the model. Given the computational time it takes to run a single iteration and the number of parameters, exploring every combination of them was impractical. Instead, we created a sample of 500 parameter combinations by selecting parameter values randomly from a uniform distribution, each within its range of uncertainty and then generated a survivorship value, μ, for each parameter set (see range described in Appendix S5).

Following methods of Cross and Beissinger (2001) and Lonsdorf et al. (2009), the sensitivity of survivorship to each predictor variable was indicated by its standardized regression coefficient, calculated from the best fit of a multiple linear regression model, $\mu = \delta_0 + \delta_1 x_1 + \ldots + \delta_z x_z$, where x is one of z predictor variables (cover energy value, amount of energy carried, etc.) and δ is a regression coefficient for each predictor variable. To calculate the sensitivity of each site's BUDs to parametric uncertainty, we also included quadratic terms because exploratory analysis indicated that BUDs were parabolic with respect to some of the variables. Thus the linear regression model for BUDs at site j was $BUD_j = \delta_0 + \delta_1 x_1 + \delta_2 x_1^2 + \cdot + \delta_{2z-1} x_z + \delta_{2z} x_z^2$. For each analysis, the standardized regression coefficient was calculated as the *t value*, i.e., the regression coefficient (slope of a line given that the true slope may be zero) divided by its standard error (δ/SE; Cross and Beissinger 2001). The t value is a unitless quantity allowing one to directly compare the sensitivity among parameters that may have different units of measurement, with the largest t values indicating greatest sensitivity of survivorship to that parameter.

Model evaluation

We compared the continental model output to citizen-contributed Mallard observations collected through eBird (Sullivan et al. 2009) within the conterminous USA. eBird observations were limited to spring and fall, 2004–2014 (*available online*) and from those identified through complete checklists to help control for effort (Isaac et al. 2014).[13] We further limited our assessment to only those sites in which Mallards were reported by eBird because of obvious omission of Mallard occurrences in the south-central USA (K. Aagaard, *personal observation*). In a manner equivalent to the continental model, bird-use days were calculated from eBird observations. However, because means and standard deviations were different, we used standardized z scores (Zar 1999) to calculate the probability, $\Pr(Z_{\text{model}} - Z_{\text{eBird}} > 0)$, of whether the continental model results departed significantly from eBird observations where they were collected.

Determining a site's discrete marginal value to a flyway management area

We illustrate the marginal value approach by evaluating only those migratory sites (according to NatureServe's range maps) that are in the Atlantic Flyway administrative area (Fig. 1A). We chose a relatively straightforward approach to evaluating the relative importance of foraging habitat at the location of a site. We calculated the discrete marginal value of a site by simply comparing the number of birds that survive if there were no food energy available in the site to the number of birds that survive given current energy estimates. Specifically, we define site i's marginal value here as the average change in survivorship (the number of birds that survive the migration) across the range of parameter values we use in the sensitivity analysis. The marginal value of site i, MV_i, is thus

$$MV_i = \mu\left(kJ_i = Current\right) - \mu\left(kJ_i = 0\right), \tag{8}$$

where μ represents the number of birds surviving the migration, kJ_i is the number of kilo Joules present at site i. It follows that if there is no food currently present in site i, the marginal value is also 0. If survivorship decreases by effectively removing the site, the marginal value of that site is positive, and if survivorship increases, the marginal value is negative.

RESULTS

Forage

Our characterization of forage availability leads to differing patterns of bird use in fall and spring (Fig. 3). The main seasonal differences were due to our assumption that agricultural areas do not provide forage in spring

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[13] http://www.ebird.org

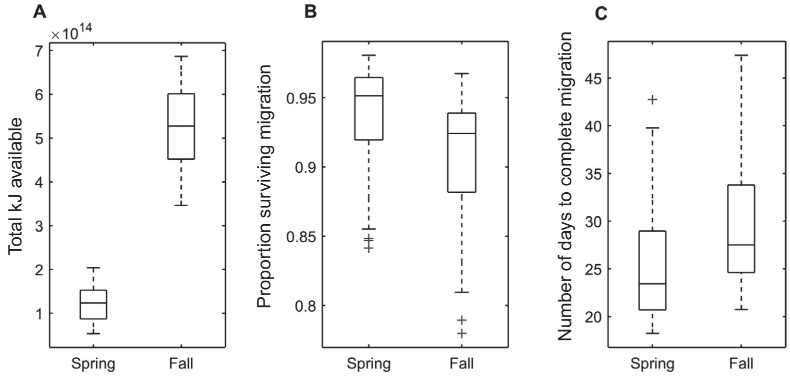

FIG. 3. Summary metrics of modeled results of illustrating seasonal predicted differences in migration for Mallards for the (A) modeled sum of energy (kJoules) potentially available to Mallards across the entire area (USA and Canada), (B) predicted proportion of birds surviving continental migration, and (C) predicted number of days necessary for completing continental migration. Boxes represent 25th and 75th percentiles, with whiskers extending to the most extreme model predictions.

migration as a result of prior consumption or decay. Indeed, there was a 75% reduction in available food energy within the USA and Canada in the spring compared to the fall because of this assumption (Fig. 3A). For example, the majority of the lower Mississippi alluvial valley is agricultural land, so if our assumption is reasonable, this region likely experiences a greater decrease in spring migration habitat quality than other areas with less agricultural land. Despite the large reduction in food energy, there was still an average of over 6 million kJ available per bird across the continent in the spring as compared to just over 26 million kJ per bird available in the fall.

Survivorship

Based on USFWS breeding population surveys referenced in this paper, we estimated just over 20 million birds (i.e., Mallard-like ducks) at the start of fall and spring migrations. Based on our assumption and the range of values used in our modeling, we projected a median survival rate of 90.5% (95% CI = 89.2%, 91.9%) during fall migration and 93.6% (95% CI = 92.5%, 94.7%) during spring migration (Fig. 3B). So despite an assumed decrease in available forage in spring, survivorship predicted by the model slightly increased in spring migration compared to the fall migration. The difference in survival is consistent with the prediction that birds spend more time during migration in the fall than spring (Fig 3C).

Migration

To illustrate how the model represents migration, we provide example outputs of the model (Fig. 4) depicting migration from Canada to the southern USA. The time step of the model was a migratory jump rather than a regular time period, i.e., daily, although these units are highly correlated. The panels in the figure represent the movement from northern breeding grounds to a set of specified sites representing wintering grounds along the southern coasts of the USA (Fig. 4A) and from those same southern wintering grounds back to the north (Fig. 4B).

Bird-use days

Total BUDs during the fall migration were highest in the Mississippi Alluvial Valley, along the coast and near-shore environments of South Carolina and southwestern Oklahoma (Fig. 5A). The broad expanse of the Prairie Pothole Region as well as western portions of the Boreal Hardwood and Eastern Tallgrass Prairie regions of the central USA provided for large numbers of ducks, but BUDs in these areas were more widely distributed than in the southern portions of the flyway. Similar results were obtained for spring migration (Fig. 6B).

Sensitivity analysis

Given the literature-informed parameters we used, we found migration was most sensitive to bird flight characteristics rather than food energy availability (Table 2). The most sensitive parameter was flight speed, followed by flight cost, and, lastly, the maximum amount of fuel carried. Variation in the energy provided to Mallards from each of the land cover types (crops, herbaceous wetlands, shoreline, and woody wetlands) did not correlate with survivorship. Despite migration being seemingly insensitive to energy provided by each land cover type, we did observe spatial patterns in the sensitivity of BUDs to herbaceous wetlands and, in fall but not spring, agriculture habitat (Appendix S6). In other words, while the spatial distribution of birds' landscape may be influenced to the energy provided by each land cover type, the number of birds surviving migration is not.

Validation

We found predicted fall and spring BUDs generally did not differ from annual depictions of BUDs as determined from eBird reports throughout the USA (fall comparison,

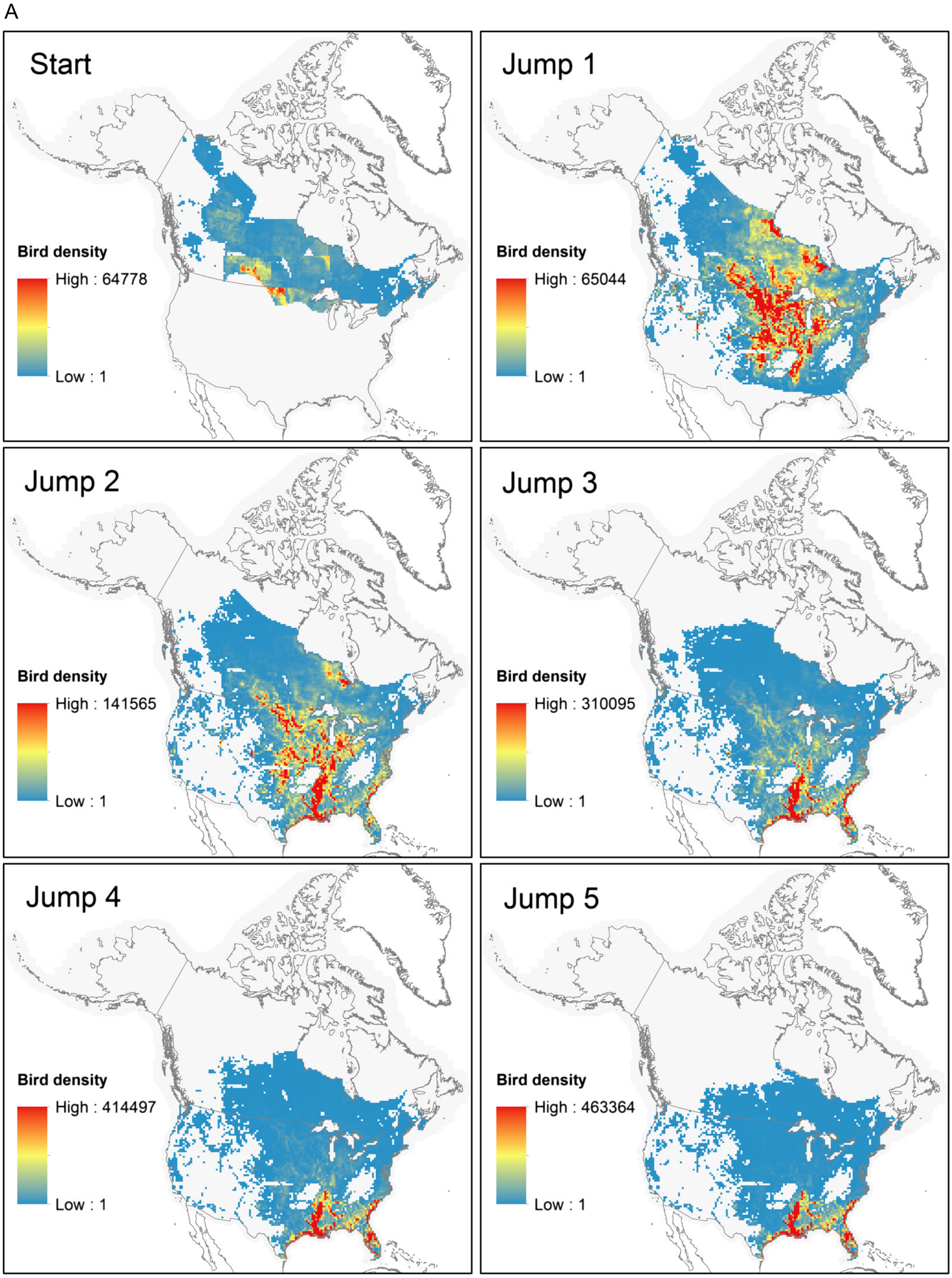

FIG. 4. (A) Model result from one iteration of fall migration. Each panel represents the movement after a migratory jump. The upper-left panel represents the start of the model and jumps proceed left to right and top to bottom. Increasing density of birds from blue (low) to yellow to red (high). (B) Model result from one iteration of spring migration. Each panel represents the movement after a migratory jump as in Fig. 4A.

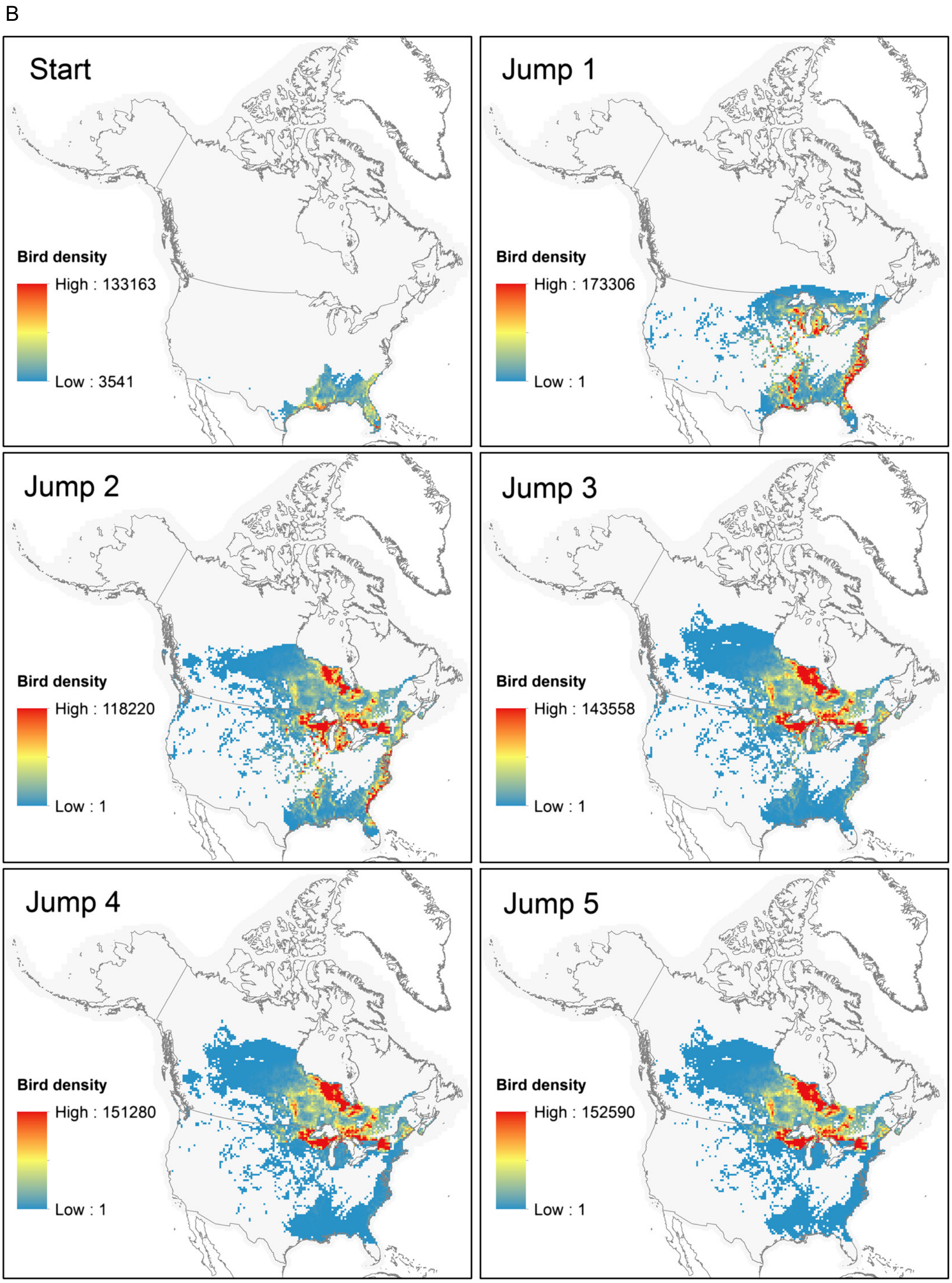

FIG. 4. (Continued)

paired *t* test, $t < 0.001$, mean difference $[z_{\mathrm{eBird}} - z_{\mathrm{model}}]$ <0.001, df = 1139, $p \approx 1$; spring comparison, paired *t* test, $t < 0.001$, mean difference $[z_{\mathrm{eBird}} - z_{\mathrm{model}}]$, df = 684, $p \approx 1$). Significant discrepancies (departures from 0) between the model output and eBird reports were observed, but these were rare (occurring in <2.5% of all observations) and generally differed among years, seasons, and locations (though discrepancies were

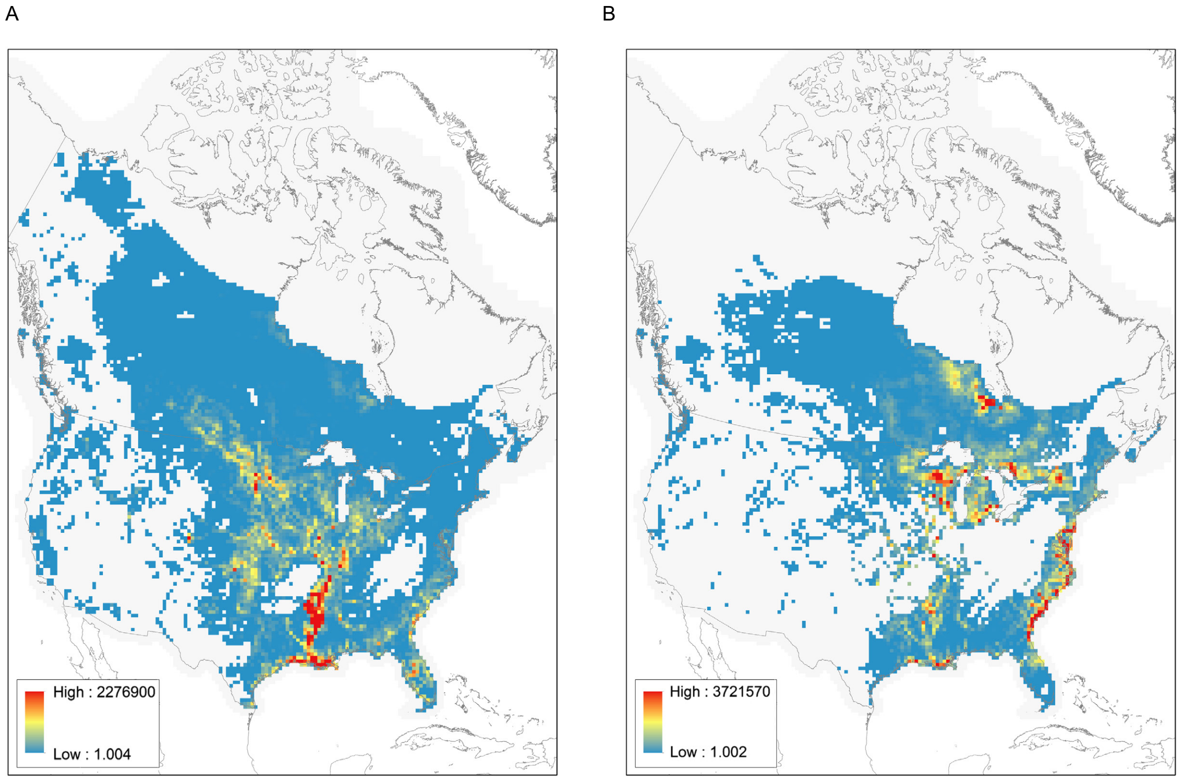

FIG. 5. Model result of total bird-use days (BUDs) estimated for the (A) fall and (B) spring migration. These figures show the average of 500 iterations.

~4 times more frequent in spring than fall; further analysis of spatial discrepancies and patterns in Appendix S7).

Marginal value

Removing one site at a time from the Atlantic Flyway suggested the coastal sites between New Jersey and North Carolina, including Chesapeake Bay and the North Carolina piedmont, were essential locations for increasing survivorship during spring migration (Fig. 6). Locations closer to the breeding grounds (i.e., Ontario and Massachusetts) were least important to survivorship in migration.

DISCUSSION

Fall and spring migration are the least understood events in the avian life cycle (Faaborg et al. 2010). However, based on our understanding of, among other things, the energetic costs of flight, amount of energy available to a bird for flight, the spatial distribution of consumable energy, and fuel deposition rates, we developed a reliable continental-scale model of avian migration that moved birds as a function of energy gains and losses. This model, in turn, provided insight into duration of stopover, timing of departure from stopover sites, migration routes, the overall speed of travel, and survival during migration. We also now have a better understanding of potential bottlenecks in migration (Myers 1983). Our migration model, for instance, appeared to funnel birds in fall migration through a gap caused by calorically deficient habitat in the Ozark highlands and the Appalachian Mountains causing large amounts of bird use over relatively small areas. Northward migration, however, appeared to focus greater movement along the Atlantic coast, east of the Appalachian mountains, which in sum with fall migration may lend evidence of looped migration (La Sorte et al. 2013). As Newton (2006) suggested, these looped migrations are expected to occur as a result of seasonal differences in conditions encountered en route (e.g., differential availability of energy in fall vs. spring).

Our goal of creating this continental-scale model was to provide a quantitative prediction that could be incorporated into decision analyses at multiple scales and to promote integrated, more financially efficient, and transparent conservation decision-making through these linkages. Although we did incorporate economic details, the discrete marginal value analysis we illustrated (Fig. 6) is one of many ways that the model could be used to inform decision makers about the effects of land-use change on migration. Using the model in scenario planning, by evaluating sets of potentially funded proposals in which the selected sets were created with an a priori strategy, would be another way to use the

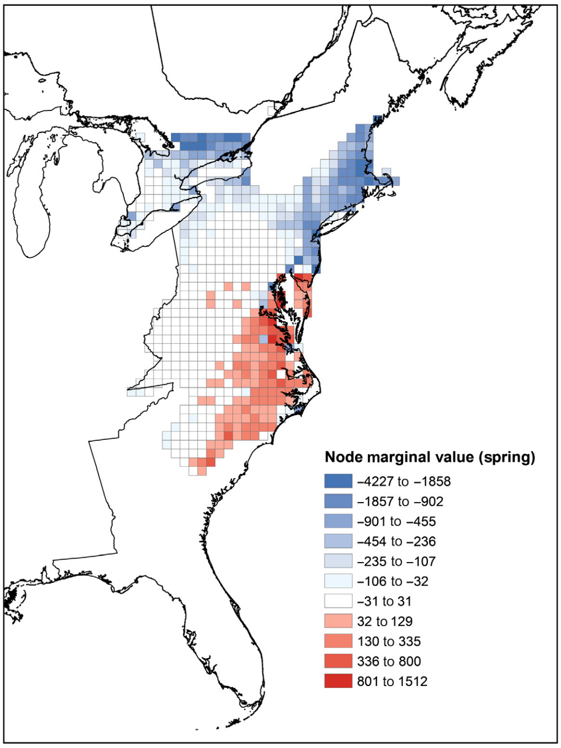

FIG. 6. Marginal value analysis using the model to determine importance of sites for the Atlantic flyway survivorship during the spring migration. The majority of sites within the Appalachian Mountains are effectively zero (light orange) since there are comparatively few kiloJoules available in that landscape.

model in decision making. Other land acquisition or restoration strategies in which larger spatial areas are targeted could be evaluated. In addition to land acquisition, the model could also be used to evaluate potential effects of, for instance, wind energy generation facilities on site-specific mortality and determine what effect this stressor might have on migration through other sites.

By predicting migratory bird response to broad-scale, distributed landscape changes (i.e., management actions), the model framework promotes accountability in conservation decision-making that affects allocation of limited resources because it increases transparency and subsequently aids in defending decisions. Furthermore, it provides a quantitative link that better represents the influence of potential consequences of local actions to continental-scale migratory bird conservation and promotes observation of local implications to phenomena from changes far outside one's own administrative boundary.

From an applied perspective, the results of the model provide insights into how to direct research efforts to improve decision-making. For example, if our model reasonably addresses avian migration energetics, then our results imply that capturing how spatial patterns in seasonal energy availability influence migration is perhaps more important than knowing exactly how much energy is produced by a given habitat type. This is illustrated by the counterintuitive emergent property that greater continental availability of food energy (during fall) allows for less efficient migration, at the cost of slightly increased mortality during the period of migration. Of course, this is a modeled result that may not be realized in nature. For example, weather can influence seasonal movement, with birds moving among known high-quality habitat otherwise unavailable during inclement periods. This movement, then, would be associated with increased survival rather than mortality.

Uncertainties and potential improvements to make

We suggest attempts to make the model more realistic be done in the context of a decision analytic framework, so as to determine the sensitivity of a decision to the added realism. In short, one should strive to determine the value of added information. There are many details that could be added, and we believe this flexibility is a strength. However, without a decision analysis in place, there is little to guide whether investment in added detail should lead to improved decision-making. With this note of caution in mind, opportunities for further model development tied directly to ongoing empirical research studies could include the following.

TABLE 2. Sensitivity of model survivorship to seven parameter values that affect the energy provided by land cover at stopover sites or flight energetic parameters.

Parameter		Minimum	Median	Maximum	*t* value
kiloJoules provided per 30-m pixel	shoreline	12,849	1,09,395	2,05,941	−0.88
	row crop agriculture	1,85,489	3,24,072	4,62,654	1.26
	herbaceous wetland	12,849	1,09,395	2,05,941	−0.73
	woody wetland	12,849	1,09,395	2,05,941	−0.81
Flight parameters	maximum amount of fuel carried (kJ)	3,690	4,958	6,113	17.17
	flight cost (kJ/h)	159	201	243	−23.90
	flight speed (km/h)	40	83	122	58.01

Notes: The minimum, maximum, and median values from 500 iterations drawn uniform random distribution of values. The magnitude of the standardized regression coefficient, the *t* value, is proportional to the relative sensitivity of the model's predicted survivorship to variation in that parameter based on multiple regression.

1) A comparison of model output to empirical migration curves at specific places and time. We assumed that birds departed stopover sites as soon as they finished refueling. Thus, the amount of time spent at stopover sites is minimized, but often birds remain at stopover sites for longer periods than perhaps needed for refueling. Relaxing this assumption would require more detailed assumptions about stopover ecology. Related to this is the assumption that migratory survivorship is simply a function of time.
2) A comparison of model-based site-to-site movement probability to satellite telemetry studies. We explicitly model the probability of moving from one site to another and thus can begin to parameterize this subroutine in the model using telemetry studies (e.g., Krementz et al. 2011, Wall et al. 2014). Thus, one could potentially use empirical data to determine if the assumptions of moving toward sites of high quality and toward a final destination are supported by empirical data.
3) Incorporating and evaluating more detailed spatial patterns of forage. Because we focused on the goal of evaluating large-scale land-use planning, we used basic national-scale land cover data to generate our results. We believe this to be a strength of the model, as the model framework can be run on any properly parameterized land cover dataset. Proper parameterization of more detailed land cover information, however, could be aided by wide-ranging, systematic surveys of seasonal food availability. A more detailed land cover dataset may lead to different spatial patterns in forage availability which, as our results suggest, is important.
4) Incorporating and evaluating more detailed estimates of forage quality. We mainly used expert opinion and literature-derived parameter values to determine the amount of forage provided. Joint Ventures can, in many instances, provide region-specific estimates of food value during migration. An additional limitation of our current energetic landscape is that energy regrowth does not occur. Energy depletion occurs at stopover sites such that birds following after others find less food for refueling. However, food availability is only simply included in our model framework. A dynamic module describing food energy as a function of seasonal phenology and climatic relations would allow for more realistic depictions of seasonal food energy supply during avian migration. Clearly, these models could be complex and are certainly beyond the scope of what we could accomplish here. By having a model, however, one could determine if more effort to determine forage quality would alter a decision informed by the outcome of the model.
5) Evaluate consequences of interannual variation in spatial production of forage resources for Mallard-like birds. If the resource availability (especially at larger scales) is highly variable among years, then the implications for conservation management are likely to be very different. For example, one may wish to employ a minimum-regret strategy in which a plan is designed with the worst year in mind to minimize the probability of major mortality events.

There are certainly additional improvements to be considered, as well, but none of those suggested above would alter the general framework. Indeed, there are likely many opportunities to extend the framework. For example, birds sometimes skip suitable sites when they have stored more fat than is necessary for reaching the next stop in migration. This phenomenon is known as overloading (Piersma 1987). Our model only allows this overloading phenomenon in the sense that the maximum amount of energy in a bird's tank was drawn from a uniform distribution ranging as high as 90% greater than the mean energy carried by the animal. Overloading behavior is generally thought to be rare, principally because the energetic costs of flight are based on the premise that flight costs increase with increasing body mass (Tucker 1974, Rayner 1990, Pennycuick 2008); there is an optimal body mass during flight and exceeding that optimal mass may lead to deleterious consequences such as predation. Because flight range is influenced by the energy available to and carried by a bird, understanding the frequency of this behavior could have important consequences to model performance, especially in the context of resiliency of migration to energy deserts, pinch-points in the migratory path with less than the necessary amount of energy to support the full set of birds moving through (Buehler and Piersma 2008).

Our estimates of survival in the spring (~93%) and fall (~90%) migration are concordant with estimates used in a migratory metapopulation model for Northern Pintail (Mattsson et al. 2012). Nevertheless, added realism associated with survival could be useful to decision makers; for instance, improvements to allow alteration to migration behavior caused by human disturbance (Klaassen et al. 2006), hunter harvest (Fox and Madsen 1997, Bechet et al. 2003), and predation (Moore et al. 1990) could lead to changes in the spatial patterns of BUDs. During stopovers, birds may need to tradeoff energy acquisition with predator avoidance (Metcalfe and Furness 1984, Whitfield 1985, Cresswell 1993, Cimprich and Moore 1999). Predation risk increases with increasing exposure time (Cimprich and Moore 1999), increasing body mass (Hedenström 1992, Witter and Cuthill 1993, Witter et al. 1994) and decreasing flock size (Page and Whitacre 1975, Lindström 1989, Creswell 1994). In our model, body mass and exposure time would be most amenable to reflecting risk from predation, principally through modification of Eq. equations 5.1 and 5.2.

This continental model constrains migration movement towards an end-site, but we recognize that migration is the dynamical interaction of navigational capacity, sociality, and complex motivational goals that we have not likely fully captured (Nathan et al. 2008, Schick et al. 2008). As a consequence, some stopover habitat may remain part of the migratory path even when such habitats should be avoided. Our modeling process, however, allows for the incorporation of such migratory inertia as deviations between reality and our model become apparent, and field research testifies to the reasons for this inertia.

Other uncertainties in our continental migration model remain, including: survivorship rates of birds at stopover sites, daily energy requirement estimates at stopover habitats, effective availability of food energy at stopover sites, seasonal deterioration in energetic quality of food available at stopover sites, community-level competition for food and roost sites, and potentially many others. Individuals differ in their fat stores according to their age and sex (e.g., Morris 1996, Woodrey and Moore 1997, Lyons et al. 2008); we ignored the potential consequences of these and other uncertainties on stopover dynamics.

While we parameterized the model to reflect the flight and foraging characteristics of a Mallard, this model framework is applicable to the migrational processes of most avian species. The flight characteristics of species are often available either through field data (e.g., Bruderer and Boldt 2001) or first principles (Pennycuick 2008). Perhaps more difficult, because differential use of stopover habitat by species is generally related to food availability (e.g., Martin 1980, Graber and Graber 1983), is tuning the energy landscape to other species; to do so requires species-specific information regarding the food energy value and availability of habitat, information that may not be readily available for some species.

Conditions during migration can be limiting to populations if they slow a population increase or cause its decline (Newton 2006). Our model provides a critical link between breeding and wintering dynamics for migrating species. This energetic-based migration model allows us to project the condition of birds entering the wintering and breeding grounds (i.e., cross-seasonal effects). If energetic-based reproduction and overwintering components were incorporated, we could model the complete life cycle of migrating species. We could, for instance, translate projected excess energy in the tanks of arriving birds into an energetically equivalent number of eggs (Drent and Daan 1980).

CONCLUSION

Conservation decisions for migratory birds at large scales are continuing to be made using expert opinion and best judgment. The assumptions of those implicit models are especially difficult to evaluate because they are hidden inside the minds of those who make them. We know this because, to our knowledge, no model of avian migration exists to support decisions in North America (but see Iwamura et al. 2014). The model we present attempts to make our assumptions transparent and open to review. Our goal is to promote formal improvement of migration models and to allow one to gain insight into the potential consequences of applying incorrect assumptions. As conservationists endeavor to learn more about optimally conserving desired species with increasingly limited funds, we must be able to address the question, How do we know when we know enough?, through formal decision analyses and the quantitative integration of our knowledge in the context of decisions. We must strive to strike a balance between spending the limited resources available on basic scientific understanding and intelligent management to conserve our desired species.

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LITERATURE CITED

Alerstam, T., and Å. Lindström. 1990. Optimal bird migration: the relative importance of time, energy, and safety. Pages 331–351 *in* E. Gwinner, editor. Bird migration: physiology and ecophysiology. Springer Press, Berlin, Germany.

Bechet, A., J.-F. Giroux, G. Gauthier, J. D. Nichols, and J. E. Hines. 2003. Spring hunting changes the regional movements of migrating Greater Snow Geese. Journal of Applied Ecology 40:553–564.

Beekman, J. H., B. A. Nolet, and M. Klaassen. 2002. Skipping swans: fuelling rates and wind conditions determine differential use of migratory stopover sites of Bewick's Swans *Cygnus bewickii*. Ardea 90:437–460.

Boulet, M., and D. R. Norris. 2006. The past and present of migratory connectivity. Ornithological Monograph 61:1–13.

Brown, G. M., and J. Hammack. 1973. Dynamic economic management of migratory waterfowl. Review of Economics and Statistics 55:73–82.

Brown, S., C. Hickey, B. Harrington and R. Gill, eds. 2001. United States shorebird conservation plan, Second edition. Manomet Center for Conservation Sciences, Manomet, Massachusetts, USA.

Bruderer, B., and A. Boldt. 2001. Flight characteristics of birds: I. Radar measurements of speeds. Ibis 143:178–204.

Buehler, D. M., and T. Piersma. 2008. Travelling on a budget: predictions and ecological evidence for bottlenecks in the annual cycle of long-distance migrants. Philosophical Transactions of the Royal Society of London B: Biological Sciences 363:247–266.

Carver, E. 2009. Birding in the United States: a demographic and economic analysis. Addendum to the 2006 National Survey of Fishing, Hunting, and Wildlife-associated Recreation. US Fish and Wildlife Service, Division of Economics. Arlington, Virginia.

Cherry, J. D. 1982. Fat deposition and length of stopover of migrant White-crowned Sparrows. Auk 99:725–732.

Cimprich, D. A., and F. R. Moore. 1999. Energetic constraints and predation pressure during stopover. Pages 834–846 *in* N. J. Adams, and R. H. Slotow, editors. Proceeding of the 22nd International Ornithological Congress. Durban, South Africa.

Clark, C. W., and R. W. Butler. 1999. Fitness components of avian migration: a dynamic model of Western Sandpiper migration. Evolutionary Ecology Research 1:443–457.

Cleary, D. 2006. The questionable effectiveness of science spending by international conservation organizations in the tropics. Conservation Biology 20:733–738.

Cowardin, L. M., and D. H. Johnson. 1979. Mathematics and Mallard management. Journal of Wildlife Management 43:18–35.

Cresswell, W. 1993. Escape responses by redshanks *Tringa totanus* on attack by avian predators. Animal Behaviour 46:609–611.

Creswell, W. 1994. Flocking is an effective anti-predation strategy in Redshank, *Tringa totanus*. Animal Behaviour 47:433–442.

Cross, P. C., and S. R. Beissinger. 2001. Using logistic regression to analyze the sensitivity of PVA models: a comparison of methods based on African wild dog models. Conservation Biology 15:1335–1346.

Drent, R. H., and S. Daan. 1980. The prudent parent: energetic adjustments in avian breeding. Ardea 68:225–252.

Drent, R., C. Both, M. Green, J. Madsen, and T. Piersma. 2003. Pay-offs and penalties of competing migratory schedules. Oikos 103:274–292.

Ellison, A. M. 2004. Bayesian inference in ecology. Ecology Letters 7:509–520.

Erni, B., F. Liechti, and B. Bruderer. 2002. Stopover strategies in passerine bird migration: a simulation study. Journal of Theoretical Biology 219:479–493.

Faaborg, J., et al. 2010. Conserving migratory land birds in the New World: Do we know enough? Ecological Applications 20:398–418.

Farmer, A. H., and J. A. Wiens. 1998. Optimal migration schedules depend on the landscape and the physical environment: a dynamic modeling view. Journal of Avian Biology 29:405–415.

Farmer, A. H., and J. A. Wiens. 1999. Models and reality: time-energy trade-offs in Pectoral Sandpiper (*Calidris melanotos*) migration. Ecology 80:2566–2580.

Fox, A. D., and J. Madsen. 1997. Behavioural and distributional effects of hunting disturbance on waterbirds in Europe: implications for refuge design. Journal of Applied Ecology 34:1–13.

Frederick, R. B., W. R. Clark, and E. E. Klaas. 1987. Behavior, energetics, and management of refuging waterfowl: a simulation model. Wildlife Monographs 96:3–35.

Fry, J., G. Xian, S. Jin, J. Dewitz, C. Homer, L. Yang, C. Barnes, N. Herold, and J. Wickham. 2011. Completion of the 2006 National Land Cover Database for the conterminous United States. Photogrammetric Engineering and Remote Sensing 77:858–864.

Graber, J. W., and R. R. Graber. 1983. Feeding rates of Warblers in spring. Condor 85:139–150.

Greenberg, R. 1980. Demographic aspects of long-distance migration. Pages 493–516 *in* A. Keast, and E. Morton, editors. Migrants in the neotropics. Smithsonian Institution Press, Washington, D.C., USA.

Greenberg, R., and P. P. Marra, editors. 2005. Birds of two worlds: the ecology and evolution of migration. Johns Hopkins University Press, Baltimore, Maryland, USA.

Guillemain, M., J. M. Bertout, T. K. Christensen, H. Poysa, V. M. Vaananen, P. Triplet, V. Schricke, and A. D. Fox. 2010. How many juvenile Teal *Anas crecca* reach the wintering grounds? Flyway-scale survival rate inferred from wing age-ratios. Journal of Ornithology 151:51–60.

Hedenström, A. 1992. Flight performance in relation to loads in birds. Journal of Theoretical Biology 158:535–537.

Hedenström, A. 2008. Adaptations to migration in birds: behavioural strategies, morphology and scaling effects. Philosophical Transactions of the Royal Society of London B: Biological Sciences 363:287–299.

Higgins, J. V., J. L. Touval, R. S. Unnasch, S. Reichle, D. C. Oren, W. R. Waldman, and J. M. Hoekstra. 2006. Who needs to spend money on conservation science anyway? Conservation Biology 20:1566–1567.

Holzkämper, A., and R. Seppelt. 2007. Evaluating cost-effectiveness of conservation management actions in an agricultural landscape on a regional scale. Biological Conservation 136:117–127.

Isaac, N. J. B., A. J. van Strien, T. A. August, M. P. de Zeeuw, and D. B. Roy. 2014. Statistics for citizen science: extracting signals of change from noisy ecological data. Methods in Ecology and Evolution 5:1052–1060.

Iwamura, T., R. A. Fuller, and H. P. Possingham. 2014. Optimal management of a multispecies shorebird flyway under sea-level rise. Conservation Biology 28:1710–1720.

Jenni, L., and M. Schaub. 2003. Behavioural and physiological reactions to environmental variation in bird migration: a review. Pages 155–171 *in* P. Berthold, E. Gwinner, and E. Sonneschein, editors. Avian Migration. Springer, Berlin, Germany.

Johnson, W. P., P. M. Schmidt, and D. P. Taylor. 2014. Foraging flight distances of wintering ducks and geese: a review. Avian Conservation and Ecology 9:2.

Kelly, J. F., L. S. Delay, and D. M. Finch. 2002. Density-dependent mass gain by Wilson's Warblers during stopover. Auk 119:210–213.

Ketterson, E., and V. Nolan. 1983. The evolution of differential migration. Current Ornithology 1:357–402.

Kirby, J. S., A. J. Stattersfield, S. H. M. Butchart, M. I. Evens, R. F. A. Grimmett, V. R. Jones, J. O'Sullivan, G. M. Tucker, and I. Newton. 2008. Newton. Key conservation issues for migratory land- and waterbird species on the world's major flyways. Bird Conservation International 18:49–73.

Klaassen, M., S. Bauer, J. Madsen, and I. Tombre. 2006. Modelling behavioural and fitness consequences of disturbance for Geese along their spring flyway. Journal of Applied Ecology 43:92–100.

Klaassen, M., S. Bauer, J. Madsen, and H. Possingham. 2008. Optimal management of a Goose flyway: migrant management at a minimum cost. Journal of Applied Ecology 45:1446–1452.

Krementz, D. G., K. Asante, and L. W. Naylor. 2011. Spring migration of Mallards from Arkansas as determined by satellite telemetry. Journal of Fish and Wildlife Management 2:156–168.

La Sorte, F. A., D. Fink, W. M. Hochachka, J. P. DeLong, and S. Kelling. 2013. Population-level scaling of avian migration speed with body size and migration distance for powered fliers. Ecology 94:1839–1847.

Lindström, Å. 1989. Finch flock size and risk of hawk predation at a migratory stopover site. Auk 106:225–232.

Lonsdorf, E., C. Kremen, T. Ricketts, R. Winfree, N. Williams, and S. Greenleaf. 2009. Modelling pollination services across agricultural landscapes. Annals of Botany 103:1589–1600.

Lyons, J. E., J. A. Collazo, and C. G. Guglielmo. 2008. Plasma metabolites and migration physiology of

Semi-palmated Sandpipers: refueling performance at five latitudes. Oecologia 155:417–427.

Martin, T. E. 1980. Diversity and abundance of spring migratory birds using habitat islands on the Great Plains. Condor 82:430–439.

Martin, T. G., I. Chadès, P. Arcese, P. P. Marra, H. P. Possingham, and D. R. Norris. 2007. Optimal conservation of migratory species. PLoS One 2:e751.

Mattsson, B. J., M. C. Runge, J. H. Devries, G. S. Boomer, J. M. Eadie, D. A. Haukos, J. P. Fleskes, D. N. Koons, W. E. Thogmartin, and R. G. Clark. 2012. A modeling framework for integrated harvest and habitat management of North American waterfowl: case-study of Northern Pintail metapopulation dynamics. Ecological Modelling 225:146–158.

McCarthy, M. A., M. A. Burgman, and S. Ferson. 1995. Sensitivity analysis for models of population viability. Biological Conservation 73:93–100.

McDonald-Madden, E., P. W. J. Baxter, and H. P. Possingham. 2008. Subpopulation triage: how to allocate conservation effort among populations. Conservation Biology 22:656–665.

Mendoza, G. A., and H. Martins. 2006. Multi-criteria decision analysis in natural resource management: a critical review of methods and new modelling paradigms. Forest Ecology and Management 230:1–22.

Metcalfe, N. B., and R. W. Furness. 1984. Changing priorities: the effect of premigratory fattening on the trade-off between foraging and vigilance. Behavioral Ecology and Sociobiology 15:203–206.

Moore, F. R., and P. Kerlinger. 1987. Stopover and fat deposition by North American Wood-Warblers (Parulinae) following spring migration over the Gulf of Mexico. Oecologia 74:47–54.

Moore, F. R., and T. R. Simons. 1992. Habitat suitability and stopover ecology of Neotropical landbird migrants. Pages 345–355 *in* J. M. Hagen, and D. W. Johnson, editors. Ecology and conservation of Neotropical migrant landbirds. Smithsonian Institution, Washington, D.C., USA.

Moore, F. R., and W. Yong. 1991. Evidence of food-based competition among passerine migrants during stopover. Behavioral Ecology and Sociobiology 28:85–90.

Moore, F. R., P. Kerlinger, and T. R. Simons. 1990. Stopover on a gulf coast barrier island by spring trans-gulf migrants. The Wilson Bulletin 102:487–500.

Moore, F. R., S. A. Gauthreaux Jr, P. Kerlinger, and T. R. Simons. 1993. Stopover habitat: management implications and guidelines. Pages 58–69 *in* D. M. Finch, and P. W. Stangel, editors. Status and management of Neotropical migratory birds, 21-25 September 1992, Estes Park, Colorado. General Technical Report RM-229, U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.

Moore, F. R., S. A. Jr Gauthreaux, P. Kerlinger, and T. R. Simons. 1995. Habitat requirements during migration: important link in conservation. Pages 121–144 *in* T. E. Martin and D. M. Finch, editors. Ecology and management of Neotropical birds. Oxford University, Oxford, UK.

Morris, S. R. 1996. Mass loss and probability of stopover by migrant warblers during spring and fall migration. Journal of Field Ornithology 67:456–462.

Myers, J. P. 1983. Conservation of migrating shorebirds: staging areas, geographic bottlenecks, and regional movements. American Birds 37:23–25.

Nathan, R., W. M. Getz, E. Revilla, M. Holyoak, R. Kadmon, D. Saltz, and P. E. Smouse. 2008. A movement ecology paradigm for unifying organismal movement research. Proceedings of the National Academy of Sciences USA 105:19052–19059.

Newton, I. 2006. Can conditions experienced during migration limit the population levels of birds? Journal of Ornithology 147:146–166.

Nichols, J. D., F. A. Johnson, and B. K. Williams. 1995. Managing North American waterfowl in the face of uncertainty. Annual Review of Ecology and Systematics 26:177–199.

Nichols, J. D., M. C. Runge, F. A. Johnson, and B. K. Williams. 2007. Adaptive harvest management of North American waterfowl populations: a brief history and future prospects. Journal of Ornithology 148(Suppl. 2): S343–S349.

Orians, G. H., and J. F. Wittenberger. 1991. Spatial and temporal scales in habitat selection. American Naturalist 137:S29–S49.

Owen, M., and J. M. Black. 1991. A note on migration mortality and its significance in goose population dynamics. Ardea 79:195–196.

Page, G., and D. F. Whitacre. 1975. Raptor predation on wintering shorebirds. Condor 77:73–83.

Pennycuick, C. J. 2008. Modelling the flying bird. Theoretical Ecology Series, Volume 5, Academic Press/Elsevier, Burlington, Massachusetts, USA.

Petit, D. R. 2000. Habitat use by landbirds along nearctic-neotropical migration routes: implications for conservation of stopover habitats. Studies in Avian Biology 20: 15–33.

Piersma, T. 1987. Hop, jump, or skip? Constraints on migration of arctic waders by feeding, fattening, and flight speed. Limosa 60:185–194 [in Dutch, with English summary].

Rappole, J. H., and D. W. Warner. 1976. Relationships between behavior, physiology and weather in avian transients at a migration stopover site. Oecologia 26:193–212.

Rayner, J. M. V. 1990. The mechanics of flight and bird migration performance. Pages 283–299 *in* E. Gwinner, editor. Bird migration: the physiology and ecophysiology. Springer, Berlin, Germany.

Ridgely, R. S., T. F. Allnutt, T. Brooks, D. K. McNicol, D. W. Mehlman, B. E. Young, and J. R. Zook. 2005. Digital distribution maps of the birds of the Western Hemisphere, version 2.1. NatureServe, Arlington, Virginia, USA.

Runge, C. A., T. G. Martin, H. P. Possingham, S. G. Willis, and R. A. Fuller. 2014. Conserving mobile species. Frontiers in Ecology and the Environment 12:395–402.

Schick, R. S., S. R. Loarie, F. Colchero, B. D. Best, A. Boustany, D. A. Conde, P. N. Halpin, L. N. Joppa, C. M. McClellan, and J. S. Clark. 2008. Understanding movement data and movement processes: current and emerging directions. Ecology Letters 11:1338–1350.

Schneider, D. C., and B. A. Harrington. 1981. Timing of shorebird migration in relation to prey depletion. Auk 98:801–811.

Scott, J. M., T. Loveland, K. Gergely, J. Strittholt, and N. Staus. 2004. National Wildlife Refuge system: ecological context and integrity. Natural Resources Journal 44:1041–1055.

Sillett, T. S., and R. T. Holmes. 2002. Variation in survivorship of a migratory songbird throughout its annual cycle. Journal of Animal Ecology 71:296–308.

Skagen, S. K. 2006. Migration stopovers and the conservation of arctic-breeding Calidridine Sandpipers. Auk 123:313–322.

Sullivan, B. L., C. L. Wood, M. J. Iliff, R. E. Bonney, D. Fink, and S. Kelling. 2009. eBird: a citizen-based bird observation network in the biological sciences. Biological Conservation 142:2282–2292.

Sutherland, W. J. 1998. The effect of local change in habitat quality on populations of migratory species. Journal of Applied Ecology 35:418–421.

Taylor, C. M., and D. R. Norris. 2007. Predicting conditions for migration: effects of density dependence and habitat quality. Biology Letters 3:280–284.

Taylor, P. D., S. A. Mackenzie, B. G. Thurber, A. M. Calvert, A. M. Mills, L. P. McGuire, and C. G. Guglielmo. 2011. Landscape movements of migratory birds and bats reveal an expanded scale of stopover. PLoS One 6:e27054.

Thogmartin, W. E., J. A. Fitzgerald, and M. T. Jones. 2009. Conservation design: Where do we go from here? Proceedings of the International Partners in Flight Conference 4:426–436.

Thogmartin, W. E., B. A. Potter, and G. J. Soulliere. 2011. Bridging the conservation design and delivery gap for wetland bird habitat maintenance and restoration in the Midwestern United States. Journal of Conservation Planning 7:1–12.

Tucker, V. A. 1974. Energetics of natural avian flight. Pages 298–328 *in* R. A. Paynter, editor. Avian energetics. Publication No. 15 of the Nuttall Ornithological Club, Cambridge, Massachusetts, USA.

U.S. Fish and Wildlife Service. 2006. Strategic habitat conservation: a report from the National Ecological Assessment Team. U.S. Fish and Wildlife Service, Arlington, Virginia, USA.

U.S. Fish and Wildlife Service. 2013. Waterfowl population status, 2013. U.S. Department of the Interior, Washington, D.C., USA.

U.S. NABCI Committee. 2000. North American Bird Conservation Initiative: bird conservation region descriptions, a supplement to the North American Bird Conservation Initiative Bird Conservation Regions Map. http://www.nabci-us.org/bcrs.htm.

Waldron, A., A. O. Mooers, D. C. Miller, N. Nibbelink, D. Redding, T. S. Kuhn, J. T. Roberts, and J. L. Gittleman. 2013. Targeting global conservation funding to limit immediate biodiversity declines. Proceedings of the National Academy of Sciences of the United States of America 110:12144–12148.

Wall, J., G. Wittemyer, B. Klinkenberg, and I. Douglas-Hamilton. 2014. Novel opportunities for wildlife conservation and research with real-time monitoring. Ecological Applications 24:593–601.

Walters, C. J. 1986. Adaptive management of renewable resources. Macmillan, New York, New York, USA.

Walters, C. J., and R. Hilborn. 1978. Ecological optimization and adaptive management. Annual Review of Ecology and Systematics 8:157–188.

Weber, T. P., B. J. Ens, and A. I. Houston. 1998. Optimal avian migration: a dynamic model of fuel stores and site use. Evolutionary Ecology 12:377–401.

Weber, T. P., A. I. Houston, and B. J. Ens. 1999. Consequences of habitat loss at migratory stopover sites: a theoretical investigation. Journal of Avian Biology 30:416–426.

Whitfield, D. P. 1985. Raptor predation on wintering waders in south-east Scotland. Ibis 127:554–558.

Wikelski, M., E. M. Tarlow, A. Raim, R. H. Diehl, R. P. Larkin, and G. H. Visser. 2003. Costs of migration in free-flying songbirds. Nature 423:704.

Williams, B. K., and F. A. Johnson. 1995. Adaptive management and the regulation of waterfowl harvests. Wildlife Society Bulletin 23:430–436.

Williams, B. K., M. D. Koneff, and D. A. Smith. 1999. Evaluation of waterfowl conservation under the North American Waterfowl management plan. Journal of Wildlife Management 63:417–440.

Williams, J. C., C. S. ReVelle, and S. A. Levin. 2005. Spatial attributes and reserve design models: a review. Environmental Modeling and Assessment 10:163–181.

Wilson, K. A., et al. 2007. Conserving biodiversity efficiently: what to do, where, and when. PLoS Biology 5:e223.

Witter, M. S., and I. S. Cuthill. 1993. The ecological costs of avian fat storage. Philosophical Transactions of the Royal Society B 340:73–92.

Witter, M. S., I. S. Cuthill, and R. H. C. Bonser. 1994. Experimental investigations of mass-dependent predation risk in the European Starling, *Sturnus vulgaris*. Animal Behaviour 48:201–222.

Woodrey, M. S., and F. R. Moore. 1997. Age-related differences in the stopover of fall landbird migrants on the coast of Alabama. Auk 114:695–707.

Zar, J. H. 1999. Biostatistical analysis, Fourth edition. Prentice Hall, Upper Saddle River, New Jersey, USA.

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Data Availability

Data associated with this paper have been deposited in Dryad: http://dx.doi.org/10.5061/dryad.23n6p