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	Lonsdorf et al. Avian migration model
1	A generalizable energetics-based model of avian migration to facilitate continental-scale
2	waterbird conservation
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Abstract. Conserving migratory birds is made especially difficult because of movement 28 among spatially disparate locations across the annual cycle. In light of challenges presented by 29 the scale and ecology of migratory birds, successful conservation requires integrating objectives, 30 31 management, and monitoring across scales, from local management units to ecoregional and flyway administrative boundaries. We present an integrated approach using a spatially explicit 32 energetic-based mechanistic bird migration model useful to conservation decision-making across 33 disparate scales and locations. This model moves a mallard-like bird (Anas platyrhynchos), 34 through spring and fall migration as a function of caloric gains and losses across a continental-35 scale energy landscape. We predicted with this model that fall migration, where birds moved 36 from breeding to wintering habitat, took a mean of 27.5 days of flight with a mean seasonal 37 survivorship of 90.5% (95% CI = 89.2%, 91.9%) whereas spring migration took a mean of 23.5 38 days of flight with mean seasonal survivorship of 93.6% (95% CI = 92.5%, 94.7%). Sensitivity 39 analyses suggested that survival during migration was sensitive to flight speed, flight cost, the 40 amount of energy the animal could carry and the spatial pattern of energy availability, but 41 generally insensitive to total energy availability per se. Nevertheless, continental patterns in the 42 bird-use days occurred principally in relation to wetland cover and agricultural habitat in the fall. 43 Bird-use days were highest in both spring and fall in the Mississippi Alluvial Valley and along 44 the coast and near-shore environments of South Carolina. Spatial sensitivity analyses suggested 45 that locations nearer to migratory endpoints were less important to survivorship; for instance, 46 removing energy from a 1,036 km² stopover site at a time from the Atlantic Flyway suggested 47 coastal areas between New Jersey and North Carolina, including Chesapeake Bay and the North 48 Carolina piedmont, are essential locations for efficient migration and increasing survivorship 49 50 during spring migration but not locations in Ontario and Massachusetts. This sort of spatially

51	explicit information may allow decision-makers to prioritize their conservation actions toward
52	locations most influential to migratory success. Thus, this mechanistic model of avian migration
53	provides a decision-analytic medium integrating the potential consequences of local actions to
54	flyway-scale phenomena.

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- *Key words: Anas platyrhynchos*, bird survivorship, conservation, migration, migratory
 birds, mallard, North American Wetlands Conservation Act, waterfowl



58

INTRODUCTION

Achieving conservation goals over large spatial scales often requires significant financial 59 investment. Since 1997, conservation and land management expenditures by the United States 60 Federal Government exceeded \$7.7 billion annually (US Office of Management and Budget 61 2012), which constitutes as much as one-third of the global investment by governments into 62 conservation (Waldron et al. 2013). The economic cost of conservation, coupled with budget 63 limitations and the demand for accountability necessitates efficient and transparent use of 64 resources (Wilson et al. 2007). In response to the growing demand for accountability, both 65 practitioners and the academic community have advocated for strategic, business-like 66 management approaches to address these concerns (Cleary 2006, Higgins et al. 2006, U.S. Fish 67 and Wildlife Service 2006, Wilson et al. 2007). Although researchers have applied decision-68 analytic techniques to conservation biology (Walters and Hilborn 1978, Ellison 2004, Williams 69 et al. 2005, Mendoza and Martins 2006), the efficient allocation of limited resources across space 70 and time remains understudied (McDonald-Madden et al. 2008, Thogmartin et al. 2009), 71 especially for large spatial scales (Holzkämper and Seppelt 2007). 72

One challenging and pressing coarse-scale resource allocation problem involves the 73 conservation of migratory birds (Klaassen et al. 2006, 2008; Kirby et al. 2008; Runge et al. 74 2014). Migratory birds congregate in spatially disparate locations across the annual cycle (e.g., 75 breeding, migration and wintering areas). In North America, for example, some migratory birds 76 breed during summer in Canada and the northern United States and overwinter in the southern 77 United States or Latin America. Since 1948, waterfowl have been managed through a system of 78 79 four administrative flyway councils (Atlantic, Mississippi, Central, and Pacific) that are based on waterfowl migration paths and geographic boundaries, whereby state and federal are given roles 80

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 87 growing recognition that successful conservation requires integration of objectives, management, 88 89 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 90 biologists choose management actions to best achieve objectives with respect to a particular 91 management unit or wetland complex, but often strive to contribute to ecoregional objectives 92 whenever possible. A common decision of managers at the ecoregional scale (e.g., Bird 93 Conservation Regions; U.S. NABCI Committee 2000) is the spatial allocation of resources and 94 funds among sites within a region or to provide guidance to local wetland managers with regard 95 to priorities at larger scales (Thogmartin et al. 2011). Similarly, decision makers at these larger 96 scales often decide on spatial allocation of resources, but from a broader perspective and often 97 with additional considerations related to maintaining connections between breeding and 98 wintering areas and supporting migratory birds in transit. 99

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).

107

Conservation and management decision context

Decision-analytic approaches to help increase the necessary level of coordination have 108 been applied to waterfowl management since Brown and Hammack (1973) developed a model to 109 determine the net economic value of waterfowl by controlling the number of waterfowl killed by 110 hunters and the number of ponds rented for waterfowl habitat. Extensions of this work were 111 developed by Cowardin and Johnson (1979) and Brown et al. (1976). A stochastic simulation 112 model to evaluate alternative management schemes on refuging waterfowl populations was 113 developed by Frederick et al. (1987), whereas Klaasen et al. (2008) used stochastic dynamic 114 programming of spring migrating geese (Anser sp.) to evaluate a range of management scenarios 115 with respect food supplementation. In 1995, the USFWS adopted the concept of adaptive 116 resource management (Walters 1986) for regulating waterfowl harvests in the United States 117 (Williams and Johnson 1995, Nichols et al. 2007). Strategic Habitat Conservation (SHC, U.S. 118 Fish and Wildlife Service 2006) has been established as the new business model for wildlife 119 conservation within the US Fish and Wildlife Service. Strategic Habitat Conservation 120 incorporates biological planning, conservation design, delivery, monitoring and research in a 121 framework allowing adaptive and iterative management decision making. To date however, there 122 has been a lack of models incorporating density-dependent mechanisms (e.g., Sutherland 1998, 123 Taylor and Norris 2007) that would identify resources most limiting to waterfowl migration or 124 125 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 AmericanWetland Conservation Act (NAWCA).

Here, we present a model designed to integrate the basic needs of waterbirds across scales 128 and provide important insights for managers regarding the strategic placement of additional 129 resources for waterbird conservation useful in an adaptive management context. We present a 130 general continental-scale energetic-based, biological model of waterfowl migration during the 131 fall and spring and evaluate simply whether it provides results consistent with our best 132 understanding of migration and stopover dynamics. After which, we use the model to determine 133 if survivorship during migration is limited by the estimated amount of food resources. Finally, 134 we illustrate how the model could be used to evaluate the consequences of potential wetland loss 135 for the Atlantic Flyway, one of the four migratory waterfowl administrative areas for within the 136 United States (others are Mississippi, Central and Pacific, Figure 1A). 137

138

METHODS

Overview - We modeled waterfowl migration through the continent as a function of 139 140 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 towards wintering areas, with 141 migratory flight often consisting of a series of several movements or "jumps" from one stopover 142 site to another (Piersma 1987, Moore and Simons 1992, Moore et al. 1995, Drent et al. 2003, 143 Jenni and Schaub 2003, Newton 2006). When a bird leaves its breeding grounds, or one stopover 144 site for another, it must choose its next stopover site, and we assume this choice depends on the 145 stopover site's roosting and forage availability and quality, its distance from the departure site, 146 and the stopover site's distance to a final non-breeding destination. Because birds expend 147

148	considerable energy during migratory flight (Newton 2006), and there is a chance that a bird will
149	die, we assume the mortality rate increases as energy is depleted. Most birds survive, however,
150	and use the stopover site to rest and "refuel" before repeating this process until they reach a final
151	non-breeding or wintering site. In the spring, the process reverses.
152	Scale of the model and analysis
153	Waterfowl and waterbirds are commonly used as model species in the development of
154	migration models (e.g., Farmer and Wiens 1998, 1999; Weber et al. 1998, 1999; Clark and
155	Butler 1999; Beekman et al. 2002; Klaassen et al. 2006). We used the mallard as a model species
156	(Anas platyrhynchos) because of the wealth of information associated with and considerable
157	management interest in it, but the framework we describe can be applied, with proper
158	parameterization, to the complete array of migrating bird species. Determining the appropriate
159	scale is one of the most challenging decisions in modeling migratory waterfowl movements, as
160	continental populations for some species are estimated at over 5 million birds and nonbreeding
161	ranges cover thousands of square kilometers (Ridgely et al. 2005).
162	We chose to model the birds at a temporal resolution comprised of migratory jumps and a
163	spatial resolution of 1,036 km^2 (400 mile ²) stopover sites. The size of the stopover site was
164	chosen to reflect our group's expert opinion that 16 km (10 mi) is the maximum distance
165	mallards might travel from a roosting site to forage, and that anything farther would be
166	considered movement to a different stopover site, i.e. migratory movement. We modeled the
167	number and fate of flocks, i.e. groups of individuals, moving from a collection of starting sites,
168	i.e. breeding grounds, to a collection of ending sites, i.e. wintering grounds.

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We combined information from three sources to select the location and flock size starting 169 from sites at the end of the non-migratory season. First, we used National Land Cover Database 170 2006 for the United States (Fry et al. 2011) and the CSC2000v for Canada (Center for 171 Topographic Information, Earth Sciences Sector and Natural Resources Canada 2009) 172 (Appendix B) for habitat input (Fig 1A); then determined the location of the sites according to 173 range maps, provided by NatureServe (Ridgely et al. 2005), delineating the distribution of 174 mallards during breeding and wintering periods; these locations represented the potential starting 175 and ending sites for fall or spring migration, respectively (Fig. 1B). To determine the number of 176 birds to model, we used recent results of the breeding population survey (U.S. Fish and Wildlife 177 Service 2013; Fig. 1C). The land cover data were translated into shoreline roosting habitat (Fig. 178 1D) and forage quality (Fig 1E for fall and 1F for spring). To determine the number of birds 179 starting from each breeding site, we combined the spatial information of the breeding population 180 survey with information from our evaluation of forage and roosting quality (described below). 181 We weighted the number of birds by the quality of habitat within the site and the breeding 182 population survey results for the area: the quality of the habitat is described in detail below, but 183 in short, sites with more shoreline, herbaceous wetlands and woody wetlands were considered to 184 have higher quality. We used those data with our estimates of habitat quality to allocate the total 185 number of birds observed across the breeding grounds. Thus, sites with high quality and a 186 relatively large number of birds, according to breeding population counts, started with the most 187 birds. We then used the abundance of birds within these breeding sites to start/stop the migration 188 dynamics in the model. 189

We used a multistep approach to addressing the behavior of these migratory jumps. Wefirst 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.

199

Generating energetic-based landscapes

We translated continental land cover into two key habitat components of waterfowl 200 migration – roosting and forage habitat (Figs. 1D and 1E, 1F, respectively). For each 201 component, we generated a site-specific summary of habitat quality for roosting and forage. 202 Mallards require shallow water where they can both forage and roost during stopovers. Thus, we 203 assumed that a site of the highest quality would consist of areas with abundant roosting and 204 205 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 206 lower quality than foraging areas relatively near a roost area. Here we describe how we 207 delineated the quality and quantity of roost and forage. We used ArcGIS 10.1 in our analysis of 208 roost and forage. 209

210

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

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 1, 4, and 5 for parameter values). Thus, a synthetic measure of roosting habitat quality and quantity HR_{sj} provided in site *j* was:

219
$$HR_{j} = A_{j} \sum_{c=1}^{C} R_{c} p_{cj}, \qquad (equation 1.1)$$

where A_j was the area of site *j* (generally 1,036 km², except along continental shores and other irregular bodies) (Fig. 1D).

Because the US and Canadian land cover datasets do not specify a "shoreline" cover type, we generated a proxy for shoreline by turning all 30-meter 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.

227

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:

233
$$HF_j = A_j \sum_{c=1}^{C} K_c p_{cj}, \qquad (equation 1.2)$$

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 C).

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).

240
$$\overline{HF_j} = A_j \sum_{c=1}^{C} K_c p_{cj} q_{cj}, \qquad (equation 1.2.1)$$

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 D). 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

245

We modeled migration in two steps: first we analyzed a continental land cover map to 246 determine the quality of stopover sites and, then, given the quality and spatial pattern of stopover 247 sites, we modeled the movement of birds through the stopover sites as they travel to and from 248 249 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 250 spent at stopover sites and thus any mortality occurring during migration was assumed likely to 251 occur at stopover sites or as a result of decisions made at stopover sites (Taylor et al. 2011). To 252 account for these dynamics, we broke migratory movement into three linked components: 253

movement patterns, energy (fuel) dynamics, and migration survivorship. We used Matlab (ver.
7.13; Mathworks, Inc., Natick, MA) to model migration.

256

Movement Patterns

We assumed the probability a bird migrates from stopover site *i* to stopover site *j*, m_{ij} , 257 was a function of three landscape factors: 1) distance between the sites *i* to *j* relative the 258 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 259 potential final destination such as a wintering or breeding site, \hat{E}_{i} . We assumed birds would 260 travel along routes minimizing the travel distance to and from the wintering and breeding 261 grounds, while selecting higher quality stopover sites preferentially over lower quality sites. We 262 provide an overview of the three factors here, and the formal equations are described in detail in 263 Appendix D. 264

For the first factor, the distance between the sites *i* to *j* relative to bird's flight range, \hat{F}_{ij} 265 (Eq. A4-2), we assumed that when birds are migrating, the distance they travel for each 266 migration event is limited by the energetic cost of flight and their body (energetic) condition 267 (Appendix E). Individuals generally arrive at stopover habitat in a fat-depleted condition 268 (Rappole and Warner 1976, Moore and Kerlinger 1987); thus, we also assumed that birds are 269 more likely to expend nearly all stored energy, risking starvation, rather than spend very little 270 before landing to refuel with the caveat that they are less likely to risk expending all available 271 stored energy (Figure 2). 272

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 (Eq. A4-3). 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 Orian 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 (Eq. A4-4). 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 towards 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:

293
$$m_{ij} = \frac{\hat{F}_{ij}\hat{E}_j\hat{S}_j}{\sum_{j=1}^J \hat{F}_{ij}\hat{E}_j\hat{S}_j}.$$
 (equation 2)

294	It follows that the number of birds of the flock n_{ij} in site <i>i</i> moving to site <i>j</i> , is the probability of
295	migration times the number of birds in site <i>i</i> is: $n_{ij} = m_{ij}n_i$. Thus the overall movement of birds
296	can be represented by: $\hat{\mathbf{n}} = \mathbf{M}\mathbf{n}$, where M is a <i>J</i> by <i>J</i> matrix consisting of elements m_{ij} and n is a <i>J</i>
297	by 1 vector consisting of elements n_i . Note that once the bird reached an end site (either the
298	breeding ground or wintering area), we set m_{ij} to 1 for that site so the probability of moving to
299	any other site to 0. It is worth mentioning that the temporal scale is based on number of "jumps"
300	rather than time, such that the time (days) to complete migration is a model output rather than an
301	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:

307
$$\varphi_{ij} = D_{ij} \frac{\theta}{\beta}.$$
 (equation 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*, $\overline{\varphi}_i$, is:

311
$$\overline{\varphi}_{j} = \frac{\sum_{i=1}^{J} n_{ij} \varphi_{ij}}{\sum_{i=1}^{J} n_{ij}}.$$
 (equation 3.2)

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

313

Net energy gain and incorporating within-site flight costs

314 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/day (Moore and 315 Kerlinger 1987). Thus, upon reaching a stopover site, birds refuel by traveling from a roosting 316 site to a nearby foraging site. In our model, the daily net energy gain is a loaded term that 317 represents the energy gained at from forage at the stopover site minus the costs of the round trip 318 flight and normal body maintenance costs, basal metabolic rate, thermoregulatory requirements, 319 and energetic costs of daily activities other than flight (i.e., feeding, swimming, walking, 320 preening, and social behaviors). The number of days, t_i , a bird stays at stopover site j increases 321 as the amount of forage required to refuel increases and decreases as the daily net gain ζ 322 (kiloJoules/day) of an individual increases (Cherry 1982, Moore and Kerlinger 1987). 323

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:

326
$$t_{j} = \frac{\left(\Phi - \overline{\varphi}_{j}\right)}{\zeta}, \qquad (equation 4)$$

where Φ is the maximum amount of fuel (Joules) carried, i.e., the size of a bird's fuel tank, the numerator $(\Phi - \overline{\varphi}_j)$ 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 $(\Phi - \hat{\varphi}_j)$. With these assumptions, we related bird energy status μ_s to daily survivorship:

338
$$\mu_s = \mu_{\max} - (\mu_{\max} - \mu_{\min})\frac{\Delta}{\Phi}, \qquad (equation 5.1)$$

such that daily survivorship ranged from μ_{min} when birds arrived with no energy reserves to μ_{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:

- $\hat{\mu}_j = \mu^{t_j} \,. \qquad (\text{equation 5.2})$
- 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.
- 347

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 *i*'s, $\sum_{i=1}^{J} n_{ij} \varphi_{ij}$, the numerator of the flight cost

equation 6.2. Thus, available forage HF_{jk} , in site *j* for migratory jump *k* is:

353
$$HF_{jk} = HF_{jk-1} - \sum_{i=1}^{J} n_{ij}\varphi_{ij}$$
 (equation 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 thenumber of birds) and the number of birds on each site for each jump. To determine the BUDsfor each site*j*, we sum the product of the total number of birds surviving within each site*j*duringjump*k*with the analogous time spent refueling in site*j*across all*K*migratory jumps:

359
$$BUDS_{j} = \sum_{k=1}^{K} (\hat{n}_{jk} \hat{u}_{jk}) t_{jk} , \qquad (equation 7)$$

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*.

362 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

369	created a sample of 500 parameter combinations by selecting parameter values randomly from a
370	uniform distribution, each within its range of uncertainty and then generated a survivorship
371	value, μ , for each parameter set (see Range described in Appendix E).

Following methods of Cross and Beissinger (2001) and Lonsdorf et al (2009), the 372 sensitivity of survivorship to each predictor variable was indicated by its standardized regression 373

coefficient, calculated from the best fit of a multiple linear regression model: 374

 $\mu = \delta_0 + \delta_1 x_1 + ... + \delta_z x_z$, where x is one of z predictor variables (cover energy value, amount of 375

energy carried, etc.) and δ is a regression coefficient for each predictor variable. To calculate the

377 sensitivity of each site's BUDs to parametric uncertainty, we also included quadratic terms 378 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: 379

 $BUD_{i} = \delta_{0} + \delta_{1}x_{1} + \delta_{2}x_{1}^{2} + \dots + \delta_{2z-1}x_{z} + \delta_{2z}x_{z}^{2}$. For each analysis, the standardized regression 380

coefficient was calculated as the *t*-value, i.e., the regression coefficient (slope of a line given that 381 the true slope may be zero) divided by its standard error (δ/SE ; Cross and Beissinger 2001). The 382 t-value is a unitless quantity allowing one to directly compare the sensitivity among parameters 383 384 that may have different units of measurement, with the largest t-values indicating greatest sensitivity of survivorship to that parameter. 385

386

376

Model evaluation

We compared the continental model output to citizen-contributed mallard observations 387 collected through eBird (Sullivan et al. 2009) within the conterminous United States. eBird 388 observations were limited to spring and fall, 2004 2014 (eBird 2014) and from those identified 389 through complete checklists to help control for effort (Isaac et al. 2014). We further limited our 390

assessment to only those sites in which mallards were reported by eBird, because of obvious omission of mallard occurrences in the southcentral U.S. (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, $Pr(Z_{model}-Z_{eBird} > 0)$, of whether the continental model results departed significantly from eBird observations where they were collected.

398

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

We illustrate the marginal value approach by evaluating only those migratory sites 399 (according to NatureServe's range maps) that are in the Atlantic Flyway administrative area 400 (Figure 1A). We chose a relatively straightforward approach to evaluating the relative 401 importance of foraging habitat at the location of a site. We calculated the discrete marginal value 402 of a site by simply comparing the number of birds that survive if there were no food energy 403 available in the site to the number of birds that survive given current energy estimates. 404 Specifically, we define site *i*'s marginal value here as the average change in survivorship (the 405 406 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: 407

$$MV_i = \mu(kJ_i = Current) - \mu(kJ_i = 0), \qquad (equation 8)$$

where μ represents the number of birds surviving the migration, kJ_i is the number of kilo Joules present 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.

413

RESULTS

Forage - Our characterization of forage availability leads to differing patterns of bird use 414 in fall and spring (Fig. 3). The main seasonal differences were due to our assumption that 415 agricultural areas do not provide forage in spring migration as a result of prior consumption or 416 decay. Indeed, there was a 75% reduction in available food energy within the United States and 417 Canada in the spring compared to the fall because of this assumption (Fig 3A). For example, the 418 majority of the lower Mississippi alluvial valley is agricultural land so if our assumption is 419 reasonable, this region likely experiences a greater decrease in spring migration habitat quality 420 than other areas with less agricultural land. Despite the large reduction in food energy, there was 421 still an average of over 6 million kJ available per bird across the continent in the spring as 422 compared to just over 26 million kJ per bird available in the fall. 423

Survivorship - Based on USFWS breeding population surveys referenced in this paper, 424 we estimated just over 20 million birds (i.e., mallard-like ducks) at the start of fall and spring 425 426 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%427 (95% CI = 92.5%, 94.7%) during spring migration (Fig. 3B). So despite an assumed decrease in 428 available forage in spring, survivorship predicted by the model slightly increased in spring 429 migration compared to the fall migration. The difference in survival is consistent with the 430 prediction that birds spend more time during migration in the fall than spring (Fig 3C). 431

Migration - To illustrate how the model represents migration, we provide example
outputs of the model (Fig. 4) depicting migration from Canada to the southern United States. 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 U.S. (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
United States 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 446 migration was most sensitive to bird flight characteristics rather than food energy availability 447 448 (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 land 449 cover types (crops, herbaceous wetlands, shoreline and woody wetlands) did not correlate with 450 survivorship.. Despite migration being seemingly insensitive to energy provided by each land 451 cover type we did observe spatial patterns in the sensitivity of BUDs to herbaceous wetlands and, 452 in fall but not spring, agriculture habitat (Appendix F). In other words, while the spatial 453 distribution of birds landscape may be influenced to the energy provided by each land cover 454 type, the number of birds surviving migration is not. 455

456	Validation - We found predicted fall and spring BUDs generally did not differ from
457	annual depictions of BUDs as determined from eBird reports throughout the United States (Fall
458	comparison: paired t-test: t <0.001; mean difference [z_{eBird} - z_{model}] <0.001, df = 1139, p \approx 1;
459	Spring comparison: paired t-test: t<0.001; mean difference [z_{eBird} - z_{model}], df = 684, p \approx 1).
460	Significant discrepancies (departures from 0) between the model output and eBird reports were
461	observed, but these were rare (occurring in <2.5% of all observations) and generally differed
462	among years, seasons, and locations (though discrepancies were ~4 times more frequent in
463	spring than fall; further analysis of spatial discrepancies and patterns in Appendix G).
464	Marginal value - Removing one site at a time from the Atlantic Flyway suggested the
465	coastal sites between New Jersey and North Carolina, including Chesapeake Bay and the North
466	Carolina piedmont, were essential locations for increasing survivorship during spring migration

467 (Fig. 6). Locations closer to the breeding grounds (i.e., Ontario and Massachusetts) were least468 important to survivorship in migration.

469

DISCUSSION

470 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 471 flight, amount of energy available to a bird for flight, the spatial distribution of consumable 472 energy, and fuel deposition rates, we developed a reliable continental-scale model of avian 473 migration that moved birds as a function of energy gains and losses. This model, in turn, 474 provided insight into duration of stopover, timing of departure from stopover sites, migration 475 routes, the overall speed of travel, and survival during migration. We also now have a better 476 understanding of potential bottlenecks in migration (Myers 1983). Our migration model, for 477

instance, appeared to funnel birds in fall migration through a gap caused by calorically deficient 478 habitat in the Ozark highlands and the Appalachian Mountains causing large amounts of bird use 479 over relatively small areas. Northward migration, however, appeared to focus greater movement 480 481 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 (1981) suggested, 482 these looped migrations are expected to occur as a result of seasonal differences in conditions 483 encountered en route (e.g., differential availability of energy in fall versus spring). 484

Our goal of creating this continental-scale model was to provide a quantitative prediction 485 that could be incorporated into decision analyses at multiple scales and to promote integrated. 486 more financially efficient and transparent conservation decision-making through these linkages. 487 Although we did incorporate economic details, the discrete marginal value analysis we illustrated 488 (Fig. 6) is one of many ways that the model could be used to inform decision-makers about the 489 effects of land use change on migration. Using the model in scenario planning, by evaluating 490 sets of potentially funded proposals in which the selected sets were created with an *a priori* 491 strategy, would be another way to use the model in decision making. Other land acquisition or 492 493 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 494 energy generation facilities on site-specific mortality and determine what effect this stressor 495 might have on migration through other sites. 496

By predicting migratory bird response to broad-scale, distributed landscape changes (i.e. 497 management actions), the model framework promotes accountability in conservation decision-498 making that affects allocation of limited resources because it increases transparency and 499 subsequently aids in defending decisions. Furthermore, it provides a quantitative link that better 500

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represents the influence of potential consequences of local actions to continental-scale migratory 501 bird conservation and promotes observation of local implications to phenomena from changes far 502 outside one's own administrative boundary. 503

From an applied perspective the results of the model provide insights into how to direct 504 research efforts to improve decision-making. For example, if our model reasonably addresses 505 avian migration energetics, then our results imply that capturing how spatial patterns in seasonal 506 energy availability influence migration is perhaps more important than knowing exactly how 507 much energy is produced by a given habitat type. This is illustrated by the counter-intuitive 508 emergent property that greater continental availability of food energy (during fall) allows for less 509 efficient migration, at the cost of slightly increased mortality during the period of migration. Of 510 course, this is a modeled result that may not be realized in nature. For example, weather can 511 influence seasonal movement, with birds moving among known high-quality habitat otherwise 512 unavailable during inclement periods. This movement, then, would be associated with increased 513 survival rather than mortality. 514

515

Uncertainties and potential improvements to make

We suggest attempts to make the model more realistic be done in the context of a 516 decision analytic framework, so as to determine the sensitivity of a decision to the added realism. 517 In short, one should strive to determine the value of added information. There are many details 518 that could be added and we believe this flexibility is a strength. However, without a decision 519 analysis in place, there is little to guide whether investment in added detail should lead to 520 improved decision-making. With this note of caution in mind, opportunities for further model 521 development tied directly to ongoing empirical research studies could include: 522

1. Comparison of model output to empirical migration curves at specific places and time. 523 We assumed that birds departed stop-over sites as soon as they finished "refueling." 524 Thus, the amount of time spent at stop-over sites is minimized, but often birds remain at 525 526 stop-over sites for longer periods than perhaps needed for refueling. Relaxing this assumption would require more detailed assumptions about stop-over ecology. Related 527 to this is the assumption that migratory survivorship is simply a function of time. 528 2. Comparison of model-based site-to-site movement probability to satellite telemetry 529 studies. We explicitly model the probability of moving from one site to another and thus 530 can begin to parameterize this subroutine in the model using telemetry studies (e.g., 531 Krementz et al. 2011, Wall et al. 2014). Thus, one could potentially use empirical data to 532 determine if the assumptions of moving towards sites of high quality and towards a final 533

destination are supported by empirical data.

535 3. Incorporating and evaluating more detailed spatial patterns of forage. Because we

536focused on the goal of evaluating large-scale land-use planning, we used a basic national-537scale land cover data to generate our results. We believe this to be a strength of the model538as the model framework can be run on any properly parameterized land cover data set.539Proper parameterization of more detailed land cover information, however, could be540aided by wide-ranging, systematic surveys of seasonal food availability. A more detailed541land cover data set may lead to different spatial patterns in forage availability which, as542our 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

546		food value during migration. An additional limitation of our current energetic landscape
547		is that energy regrowth does not occur. Energy depletion occurs at stopover sites such
548		that birds following after others find less food for refueling. However, food availability is
549		only simply included in our model framework. A dynamic module describing food
550		energy as a function of seasonal phenology and climatic relations would allow for more
551		realistic depictions of seasonal food energy supply during avian migration. Clearly, these
552		models could be complex and are certainly beyond the scope of what we could
553		accomplish here. By having a model, however, one could determine if more effort to
554		determine forage quality would alter a decision informed by the outcome of the model.
555	5.	Evaluate consequences of inter-annual variation in spatial production of forage
556		resources for mallard-like birds. If the resource availability (especially at larger scales) is
557		highly variable among years, then the implications for conservation management are
558		likely to be very different. For example, one may wish to employ a minimum-regret
559		strategy in which a plan is designed with the worst year in mind to minimize the
560		probability of major mortality events.

561 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 562 to extend the framework. For example, birds sometimes skip suitable sites when they have 563 stored more fat than is necessary for reaching the next stop in migration. This phenomenon is 564 known as overloading (Piersma 1987). Our model only allows this overloading phenomenon in 565 the sense that the maximum amount of energy in a bird's tank was drawn from a uniform 566 distribution ranging as high as 90% greater than the mean energy carried by the animal. 567 Overloading behavior is generally thought to be rare principally because the energetic costs of 568

flight are based on the premise that flight costs increase with increasing body mass (Tucker 569 1974, Rayner 1990, Pennycuick 2008); there is an optimal body mass during flight and 570 exceeding that optimal mass may lead to deleterious consequences such as predation. Because 571 572 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 573 in the context of resiliency of migration to energy deserts, pinch-points in the migratory path 574 with less than the necessary amount of energy to support the full set of birds moving through 575 (Buehler and Piersma 2008). 576

Our estimates of survival in the spring $(\sim 93\%)$ and fall $(\sim 90\%)$ migration are concordant 577 with estimates used in a migratory metapopulation model for northern pintail (Mattsson et al. 578 2012). Nevertheless, added realism associated with survival could be useful to decision makers; 579 for instance, improvements to allow alteration to migration behavior caused by human 580 disturbance (Klaasen et al. 2006), hunter harvest (Fox and Madsen 1997, Béchet et al. 2003), and 581 predation (Moore et al. 1990) could lead to changes in the spatial patterns of BUDs. During 582 stopovers, birds may need to tradeoff energy acquisition with predator avoidance (Metcalfe and 583 Furness 1984, Whitfield 1985, Cresswell 1993, Cimprich and Moore 1999). Predation risk 584 increases with increasing exposure time (Cimprich and Moore 1999), increasing body mass 585 (Hedenström 1992, Witter and Cuthill 1993, Witter et al. 1994) and decreasing flock size (Page 586 and Whitacre 1975, Lindström 1989, Creswell 1994). In our model, body mass and exposure 587 time would be most amenable to reflecting risk from predation, principally through modification 588 of equation 6. 589

590 This continental model constrains migration movement towards an "end-site", but we 591 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.

597 Other uncertainties in our continental migration model remain, including: 598 survivorship rates of birds at stop-over sites, daily energy requirement estimates at stop-over 599 habitats, effective availability of food energy at stopover sites, seasonal deterioration in 600 energetic quality of food available at stopover sites, community-level competition for food 601 and roost sites, and potentially many others. Individuals differ in their fat stores according 602 to their age and sex (e.g., Morris 1996, Woodrey and Moore 1997, Lyons et al. 2008); we 603 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 604 605 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 606 and Boldt 2001) or first principles (Pennycuick 2008). Perhaps more difficult, because 607 differential use of stopover habitat by species is generally related to food availability (e.g., 608 Martin 1980, Graber and Graber 1983), is tuning the energy landscape to other species; to do so 609 requires species-specific information regarding the food energy value and availability of habitat, 610 information that may not be readily available for some species. 611

612 Conditions during migration can be limiting to populations if they slow a population613 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 over-wintering 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).

620

CONCLUSION

Conservation decisions for migratory birds at large scales are continuing to be made 621 using expert opinion and best judgment. The assumptions of those implicit models are especially 622 difficult to evaluate because they are hidden inside the minds of those who make them. We 623 624 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 presented above attempts to make 625 our assumptions transparent and open to review. Our goal is to promote formal improvement of 626 627 migration models and to allow one to gain insight into the potential consequences of applying incorrect assumptions. As conservationists endeavor to learn more and more about optimally 628 conserving desired species with increasingly limited funds, we must be able to address the 629 question, "how do we know when we know enough?" through formal decision analyses and the 630 quantitative integration of our knowledge in the context of decisions. We must strive to strike a 631 balance between spending the limited resources available on basic scientific understanding and 632 intelligent management to conserve our desired species. 633

634

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Supplemental Material

941 Appendices A-G are available online.



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- Table 1. Parameters used in the model. Note that some of the parameters refer to equations
- 943 described in the appendices.

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
Р	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>i</i> and <i>j</i>
ϕ	Maximum flight range (km) indexed
Ω	Proportion of maximum flight range traveled before refueling
Г	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
М	Overall site to site flight probability matrix
N	site vector of bird numbers

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β	flight speed (km/h) indexed by guild
Θ	energetic cost (kJ) of flight per hour indexed by guild
$\varphi_{i,j}$	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
М	Survivorship
t	expected time for refueling (bird-use days)
	DEDTIT

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. 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.

		Parameter	Minimum	Median	Maximum	<i>t</i> -value
neter		Shoreline	12,849	109,395	205,941	-0.88
kiloJoules provided per 30-meter		Row Crop Agriculture	185,489	324,072	462,654	1.26
	pixel					
		Herbaceous wetland	12,849	109,395	205,941	-0.73
kiloJc		Woody wetland	12,849	109,395	205,941	-0.81
		Maximum Amount of				
Flight parameters		Fuel Carried (kJ)	3,690	4,958	6,113	17.17
		Flight cost (kJ hr ⁻¹)	159	201	243	-23.90
H		Flight speed (km hr ⁻¹)	40	83	122	58.01

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953 Figure Legend

954 Figure 1. Illustration of GIS inputs and GIS analysis of habitat quality. A) Land cover map for the United States and Canada, along with administrative boundaries of four major flyways: 955 Atlantic, Mississippi, Central and Pacific. We used the land cover data to estimate roosting and 956 957 forage quality. B) NatureServe range map showing mallard duck breeding only areas (red), nonbreeding areas (blue) and areas where mallards can be found year-round (purple) (Ridgely et al. 958 2005). This layer provided potential starting and ending locations for migratory waterfowl. C) 959 Distribution of the May waterfowl breeding population (estimated in thousands of birds per 960 stopover site [1,036 km²]) for mallards which is used to estimate the starting distribution of birds 961 in the fall migration. D) Total dabbling duck roosting quality within each site (darker shades 962 indicate higher quality) based on analysis of land cover. E and F) Average of a stopover site's 963 forage availability (in 100,000 kJ) during fall and spring migration, respectively, based analysis 964 of land cover using a range of parameter estimates (Table 2). Lower availability is indicated by 965 blue, with a gradient of increasing availability from green to yellow to orange. 966 Figure 2. Gamma probability distribution function illustrating the likelihood that a mallard would 967 travel from one site to another given the distance between them. The three curves reflect the 968

969 uncertainty in energetic parameters used to predict migration by illustrating the minimum flight
970 range (dotted line), maximum flight range (dashed line) and the average flight range (solid line)

971 used in the analyses. The precise equation is described in Appendix D.

Figure 3. Summary metrics of modeled results of illustrating seasonal predicted differences in

973 migration for mallards for the: A) modeled sum of energy (kJoules) potentially available to

974 mallards across the entire area (United States and Canada), B) predicted proportion of birds

975	surviving continental migration, and C) predicted number of days necessary for completing
976	continental migration. Boxes represent 25 th and 75 th percentiles, with whiskers extending to the
977	most extreme model predictions.
978	Figure 4. A) Model result from one iteration of fall migration: each panel represents the
979	movement after a migratory jump. The upper-left panel represents the start of the model and
980	jumps proceed left to right and top to bottom. Increasing density of birds from blue (low) to

981 yellow to red (high). B) Model result from one iteration of spring migration: each panel

represents the movement after a migratory jump as in Figure 4A.

983 Figure 5. Model result of total bird-use days (BUDs) estimated for the fall (A) and spring (B)

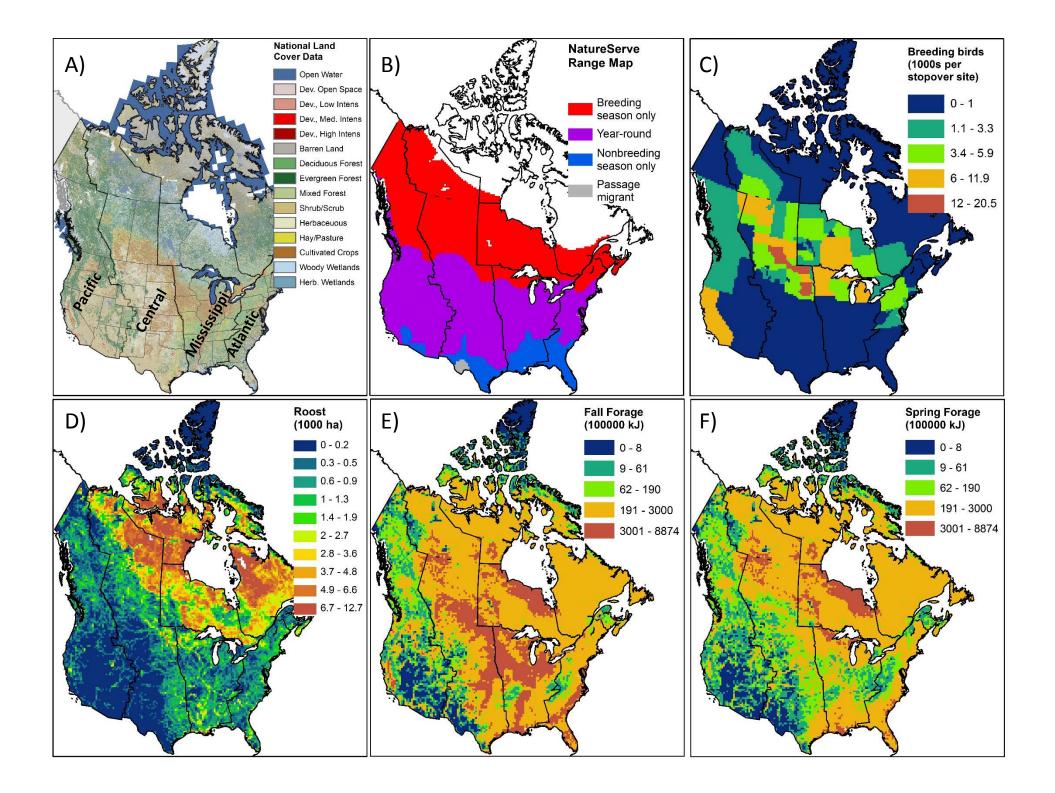
984 migration. These figures show the average of 500 iterations.

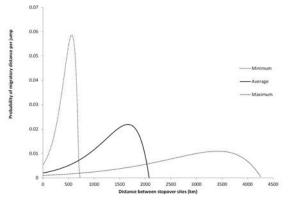
Figure 6. Marginal value analysis using the model to determine importance of sites for the

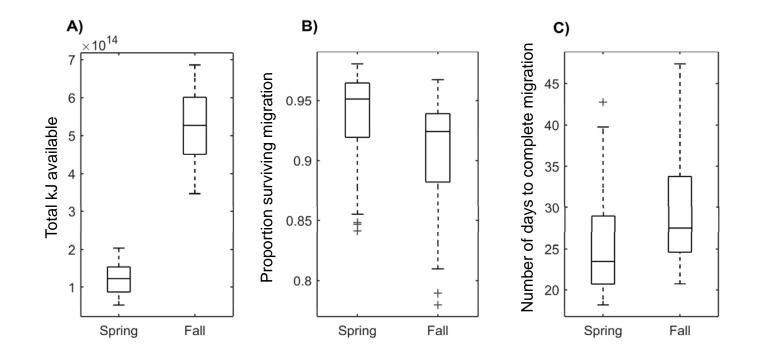
Atlantic flyway survivorship during the spring migration. The majority of sites within the

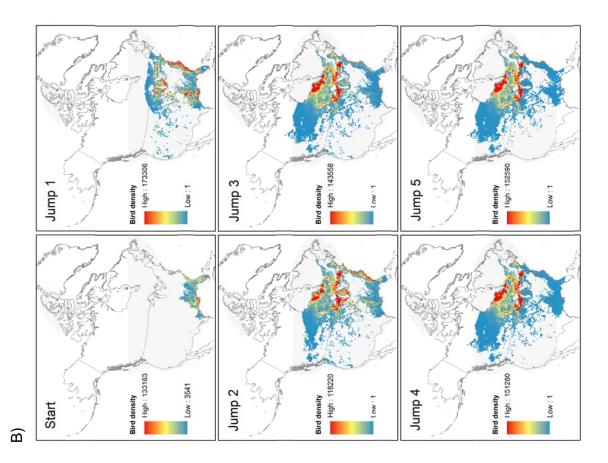
- 987 Appalachian Mountains are effectively zero (light orange) since there are comparatively few
- 988 kiloJoules available in that landscape.

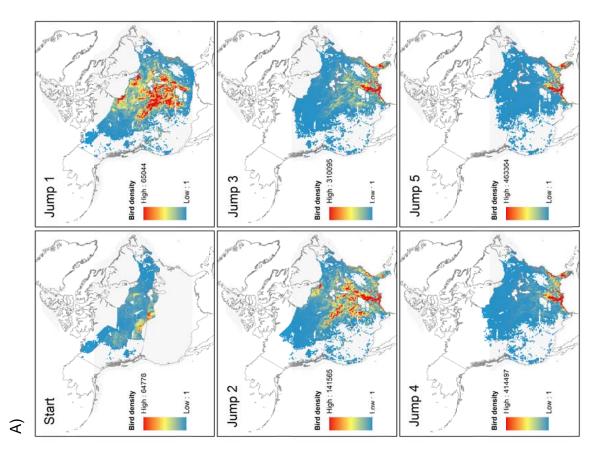
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