How will predicted land-use change affect waterfowl spring stopover ecology? Inferences from an individual-based model

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Summary

1. Habitat loss, habitat fragmentation, overexploitation and climate change pose familiar and new challenges to conserving natural populations throughout the world. One approach conservation planners may use to evaluate the effects of these challenges on wildlife populations is scenario planning.

2. We developed an individual-based model to evaluate the effects of future land use and land cover changes on spring-migrating dabbling ducks in North America. We assessed the effects of three Intergovernmental Panel on Climate Change emission scenarios (A1B, A2 and B1) on dabbling duck stopover duration, movement distances and mortality. We specifically focused on migration stopover duration because previous research has demonstrated that individuals arriving earlier on the nesting grounds exhibit increased reproductive fitness.

3. Compared to present conditions, all three scenarios increased stopover duration and movement distances of agent ducks.

4. Although all three scenarios presented migrating ducks with increased amounts of wetland habitat, scenarios also contained substantially less cropland, which decreased overall carrying capacity of the study area.

5. *Synthesis and applications.* Land-use change may increase waterfowl spring migration stopover duration in the midcontinent region of North America due to reduced landscape energetic carrying capacity. Climate change will alter spatial patterns of crop distributions with corn and rice production areas shifting to different regions. Thus, conservation planners will have to address population-level energetic implications of shifting agricultural food resources and increased uncertainty in yearly precipitation patterns within the next 50 years.

Key-words: agent-based model, *Anas platyrhynchos*, climate change, dabbling duck, land cover change, land-use change, mallard, migration asynchrony, stopover area, stopover duration

Introduction

Wildlife populations face numerous conservation challenges, including habitat loss and climate change (Primack 2014). As a result, conservation planners have designed protected area networks to account for landscape composition, structure and function in wildlife conservation efforts (Margules & Pressey 2000). However, protected area networks are ecologically linked to surrounding landscapes, and changing land-use practices proximate to protected areas may impede conservation effectiveness (Hansen & DeFries 2007). Thus, conservation planners need information on how future land-use changes may affect the ability of protected area networks to conserve wildlife populations (Hamilton et al. 2013).

One tool that conservation planners may use to evaluate the implications of future land-use changes on protected area networks is scenario planning (Peterson, Cumming & Carpenter 2003). Generally, scenario planning allows decision-makers to consider the effects of multiple factors on complex systems characterized by high levels of uncertainty. In ecology and conservation, scenario planning may involve individual-based models (IBMs) that include adaptive animal behaviours and stochastic processes (Frederick, Clark & Klaas 1987; Grimm & Railsback 2005; McLane et al. 2011). Thus, IBMs provide conservation planners with a means to examine the potential effects of future scenarios, altered resource distributions and other novel landscape-level changes on wildlife populations (Peterson, Cumming & Carpenter 2003; McLane et al. 2011).

Individual-based models focus on modelling individual components in a complex system. As a result, IBMs integrate a bottom-up approach to modelling, and population-level metrics such as movement distances and survival 'emerge' from collective behaviours of individual agents in the model (Grimm & Railsback 2005). In IBMs, agents and/or individuals simultaneously interact with one another, and with the environment, to achieve a specified goal or objective (Railsback & Grimm 2012). To facilitate realistic representations of complex ecological systems, agents often possess some knowledge of the environment and adapt to altered environmental conditions. Consequently, IBMs provide an ideal framework to examine the implications of future land-use change on wildlife populations.

Waterfowl use a network of protected wetlands throughout the annual cycle (i.e. yearly migration and reproduction cycle) and are an ideal taxa to examine the effectiveness of protected area networks (Beatty et al. 2014a). Individual-based models have been previously developed to examine the effects of management regimes, land use/land cover change, and other environmental changes on waterbird populations. For example, Frederick, Clark & Klaas (1987) developed a model to examine the effects of alternative management approaches on lesser snow geese *Chen caerulescens* within a prominent fall migration stopover area. In contrast, Miller et al. (2014) developed an IBM to examine effects of environmental change on wintering waterfowl populations. In another model, Pettifor et al. (2000) developed a spatially explicit model for barnacle geese *Branta leucopsis* and brant *Branta bernicla* to highlight the importance of habitat loss within the context of spatially explicit annual cycle IBM. In addition, general purpose IBM programmes have been developed recently with a focus on environmental change and foraging wildlife populations (Stillman 2008; Stillman & Goss-Custard 2010). However, no IBMs have been developed that focus on spring-migrating waterfowl.

Spring stopover areas are important elements of the annual cycle for waterfowl because they provide energy for migration and essential nutrients for nesting when food resources are limited (Arzel, Elmberg & Guillemain 2006; Straub et al. 2012). In this study, we developed an IBM to assess the effects of land cover and land-use change at spring migration stopover areas on dabbling duck populations. Specifically, we modelled the effects of different Intergovernmental Panel on Climate Change (IPCC) emission scenarios (A1B, A2 and B1) and associated land use and cover on dabbling duck spring migration stopover duration in North America. We predicted that spring migration stopover duration would decrease with increased wetland availability in future scenarios. We chose to model spring stopover duration because empirical research has demonstrated that ducks arriving earlier on the nesting grounds have a fitness advantage over those arriving later (Anteau & Afton 2004; Devries et al. 2008). Thus, shorter stopover durations within a population may lead to earlier migration chronology and, consequently, elevated reproductive success and recruitment.

Materials and methods

MODEL DESCRIPTION

We developed an IBM to evaluate effects of land-use change on dabbling duck spring migration stopover duration in the midcontinent region of North America. Although a detailed description of the model is included in the Supporting Information (Appendix S1, Supporting Information) along with model script (Appendix S2), we provide a brief outline here. Agents in the model resembled mallards *Anas platyrhynchos*, which are generalist dabbling ducks and the focus of extensive management programmes throughout North America (Johnson et al. 1997; Drilling, Titman & McKinney 2002). Virtual mallards (hereafter 'mallards') arrived on a 60 km × 60 km landscape (250 × 250 m pixels) during spring migration with depleted energetic reserves from inbound travel. Mallards moved, foraged and roosted in the model environment to increase energetic reserves and continue spring migration. Each mallard had five dynamic variables that monitored behaviour, movement distances, lipid reserves, consumed food and consumed energy (Table 1). Each pixel was assigned one of six land cover types: emergent wetlands, woody wetlands, open water, corn agriculture, soya bean agriculture or other. Pixels had six variables that related land cover, food abundance and other factors (Table 1). All land cover types, with the

Table 1. Descriptions of variables used in an individual-based model to examine the effects of climate scenarios on dabbling duck stopover duration

Entity	Variable	Description	Units
Global	*Hour*	Hour 0 was first hour of day (0:00 to 1:00)	–
	Day	Day 0 was first model day	–
	Flight-cost	Energetic cost of flight	kcal km^{-1}
	Forage-rate	Energetic cost of foraging	kcal h^{-1}
	Roost-rate	Energetic cost of activities other than foraging	kcal h^{-1}
	Food-max	Maximum amount of food a duck could consume in one 24-h period	g
	Attack	Search efficiency during foraging	m^2 s^{-1}
	Handling-time	Amount of time 1 g of food is manipulated before consumption	h
	Crop-flood-prop	Proportion of crop pixels in model world with is-flooded = 1	–
	Wetland-flood-prop	Proportion of wetland pixels in model world with is-flooded = 1	–
Mallard	*Behaviour*	Behavioural motivation	'foraging' or 'not foraging'
	Step lengths	List that contained distance moved with each time step	Number of pixels
	Food-consumed	Amount of food consumed in current 24-h period	g
	Energy-consumed	Energy within consumed food in current 24-h period	kcal
	Lipid-reserves	Total amount of energy stored as lipids	kcal
Pixel	*Habitat*	Land cover of pixel	See text
	Food-pixel	Amount of food in pixel	g
	TME	Total metabolizable energy of food in pixel	kcal g^{-1}
	Is-flooded	Indicator variable for hydrological status of pixel	0 = not flooded, 1 = flooded
	Patch	Identified groups of pixels with identical habitat and *is-flooded* values	See Appendix S1
	Patch-size	Number of pixels in patch	Number of pixels

exception of other and open water, contained food for mallards. We ran the model with an hourly time step for 60 days. We censored birds that did not depart the focal area after 60 days because these individuals were less likely to nest and/or nest successfully (Bêty, Giroux & Gauthier 2004; Devries *et al.* 2008). In addition, we did not model predation *per se*; thus, censored individuals may represent birds especially vulnerable to predation in the initial steps of the simulation.

We parameterized the model with a plausible range of values based on the literature and performed sensitivity analyses to evaluate the effects of parameter values on mallard stopover duration (Appendix S3). In addition to sensitivity analyses, we tested the model using pattern-oriented modelling (POM). Pattern-oriented modelling ensures a model reproduces patterns relevant to the model's purpose at multiple levels (Grimm & Railsback 2012). We focused on two specific metrics to validate our model: stopover duration and daily flight distance. In a study that examined mallard movement in Japan, stopover duration ranged from 7 to 28 days (Yamaguchi *et al.* 2008), whereas another study in North America estimated a mean stopover duration of 12 days (Krementz, Asante & Naylor 2011). Finally, a study that examined stopover duration of dabbling ducks using weather radar in Illinois, USA, documented a mean value of 28 days (O'Neal, Stafford & Larkin 2012). Mean stopover duration for present conditions in our model was 19·53 days, which is within the range of values observed in these empirical studies. For daily flight distances, we compared distances from models to a mallard global positioning system satellite telemetry data set from spring 2010 and 2011. We selected empirical bird locations that overlapped with our study area and log10 transformed daily flight distances for both simulated and empirical data sets. Empirical mean daily flight distance was 4·87 km with a 95% confidence interval of 2·39–7·35 km. Simulation mean daily flight distances overlapped with empirical values with a mean of 1·84 and 95%

confidence interval of 0·84–2·84 km. Thus, our model presented a sound mechanistic representation of our study system.

SCENARIOS

We simulated mallard spring migration stopover behaviour based on land use and land cover (LULC) projections in the US Geological Survey's report on carbon stocks, carbon sequestration and greenhouse gas fluxes (Zhu *et al.* 2010). The LULC change model generated spatially explicit representations of land cover for each year from 2011 to 2050 based on the IPCC Special Report on Emission Scenarios (Nakicenovic *et al.* 2000). Thus, for each year after 2011, the model generated three distinct land cover products associated with three different emission scenarios (Sohl *et al.* 2007; Sohl & Sayler 2008; Zhu *et al.* 2010). Scenario A1B assumed a balanced global energy portfolio, generating

Table 2. Landscape composition for the study area based on three Intergovernmental Panel on Climate Change emission scenarios (A1B, A2 and B1) compared to landscape composition from 2010

	Scenarios			
Land cover	CDL 2010*	A1B	A2	B1
Corn	19·78	11·99	12·16	11·75
Soya beans	24·29	14·88	15·16	14·63
Other	48·72	63·66	63·28	63·72
Emergent wetlands	0·25	1·61	1·61	1·63
Open water	2·79	2·71	2·60	2·93
Woody wetlands	4·17	5·16	5·18	5·33

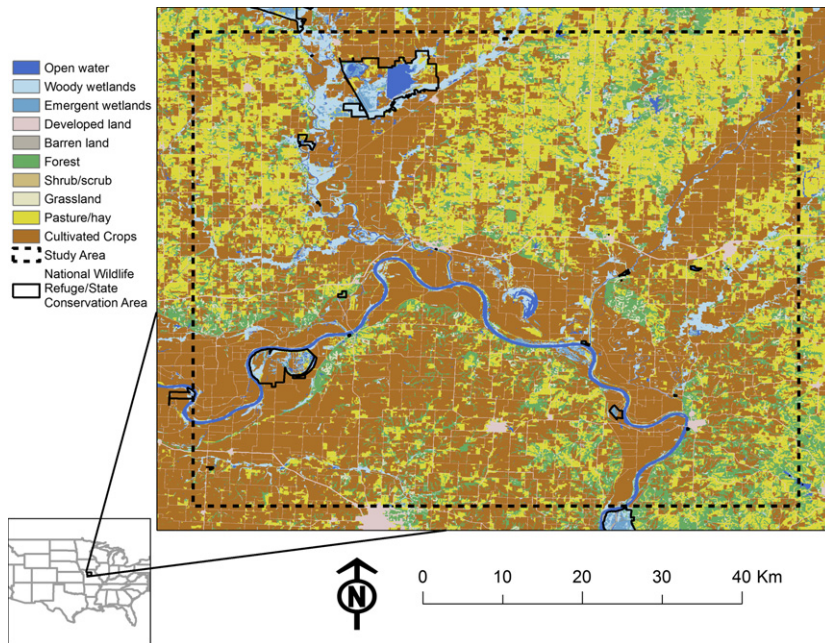*National Agricultural Statistics Service Cropland Data Layer 2010.

Fig. 1. Land use and land cover for the study area in central Missouri, USA. The dashed line represents the study area and black polygons represent state conservation areas or National Wildlife Refuges.

moderate emission levels (Nakicenovic *et al.* 2000). Scenario A2 assumed energy sources varied according to region with a high level of greenhouse gas emissions (Nakicenovic *et al.* 2000). Scenario B1 described a global transition to sustainable energy, generating low greenhouse gas emissions (Nakicenovic *et al.* 2000). Consequently, landscape composition varied among the three IPCC scenarios and present-day conditions for our study area (Table 2).

We examined mallard spring migration stopover duration at a wetland complex in central Missouri, USA, for three different scenarios in 2050 and present conditions as a reference (Fig. 1). We performed a total of four analyses, and for each analysis, we varied significant parameter(s) identified in our sensitivity analyses (Appendix S3). We ran 20 simulations for each parameter and scenario combination to thoroughly examine the effects of LULC change on mallard spring migration stopover duration. We examined stopover duration with a linear regression that included scenario (present day, A1B, A2 and B1) as a factor in addition to parameters identified as significant from sensitivity analyses. Although the goal of the model was to examine effects of LULC change on stopover duration, we examined differences in the number of mortalities and movement step length distances among scenarios. We did not include censored birds in analyses for stopover duration, number of mortalities and step length.

Residual plots and variance inflation factors confirmed that assumptions were met for all stopover duration and mortality models (Kutner *et al.* 2005). However, we natural log transformed mean step length to meet assumptions of general linear models. In all regression analyses, we centred all continuous covariates on the mean and scaled with one standard deviation. Thus, parameter estimates for continuous variables represent the expected change in the response variable given a change of one standard deviation in the predictor variable. We also monitored mean lipid reserves for birds on the model landscape as a function of time, which included birds that were censored. We also monitored patch depletion to examine temporal patterns in food consumption.

Foraging and metabolic sensitivity analyses indicated *food-max* had a substantially greater effect on spring migration stopover duration compared to *roost-rate* and *forage-rate* based on standardized parameter estimates (Appendix S3). Consequently, we varied *food-max* but held *roost-rate* and *forage-rate* at intermediate values in scenario analyses (Table 3). In addition, flooding parameters influenced migration stopover duration. Thus, we varied *wetland-flood-prop* and *crop-flood-prop* in all scenarios to account for variation in wetland habitat availability due to precipitation patterns. We varied *food-max* (two levels), *wetland-flood-prop* (nine levels) and *crop-flood-prop* (seven levels) for a total of 126 parameter combinations for each scenario. We ran 20 simulations for each parameter combination to generate 2520 simulations for each scenario and a total of 10 080 simulations across all four scenarios (present day, A1B, A2 and B1). We regressed mean spring migration stopover duration on *food-max*, *wetland-flood-prop*, *crop-flood-prop*, *wetland-flood-prop* × *crop-flood-prop* and scenario with present day as the reference category.

Censoring birds may have resulted in underestimation of stopover duration. Thus, we performed a set of simulations to examine the effects of our parameters on the number of censored birds. In these simulations, we set *roost-rate* and *forage-rate* to median values and varied food-max (100, 120), *crop-flood-prop* (0·05, 0·25, 0·45) and *wetland-flood-prop* (0·025, 0·1, 0·175). We ran 20 simulations for each parameter. We ran these simulations on all four scenarios (present day, A1B, A2 and B1) and performed regression with the number of censored birds as the dependent variable and *food-max*, *crop-flood-prop*, *wetland-flood-prop* and emission scenario as independent variables.

Results

Parameter estimates indicated all three future scenarios increased spring migration stopover duration compared to present conditions (A1B: $\hat{\beta} = 0.68$, SE < 0·01; A2: $\hat{\beta} = 0.48$, SE < 0·01; B1: $\hat{\beta} = 0.83$, SE < 0·01). In addition, *food-max*

Table 3. Intermediate values of state variables used for sensitivity analyses in an individual-based model to examine effects of climate scenarios on mallard spring migration stop over duration

Variable	Formula	Value	Units	Source
RMR	–	4·90	kcal h^{-1}	Miller & Eadie (2006)
Flight-cost	$(1 \text{ km}/v_f) \times (\text{RMR} \times 14)$	0.78	kcal km^{-1}	Norberg (1996); Bruderer & Boldt (2001); Miller & Eadie (2006)
Forage-rate	RMR × 2·5	12·24*	kcal h^{-1}	Prange & Schmidt-Nielsen (1970)
Roost-rate	RMR × 2·0	9·79	kcal h^{-1}	Wooley & Owen (1978)
Food-max	–	100	g	Sugden (1971)
Attack	–	0·016	m^2 s^{-1}	Fritz, Durant & Guillemain (2001)
Handling-time	–	0·001	h	Fritz, Durant & Guillemain (2001)
Crop-flood-prop	–	0·10	See text	
Wetland-flood-prop	–	0·25	See text	Bishop & Vrtiska (2008)

RMR, resting metabolic rate; v_f, flight velocity.
Forage-rate set at 14·69 for *roost-rate* analysis based on assumption that *forage-rate* > *roost-rate*.

($\hat{\beta} = -4·88$, SE < 0·01) had an effect on stopover duration, whereas *wetland-flood-prop*, *crop-flood-prop* and the *wetland-flood-prop × crop-flood-prop* interaction did not impact mallard spring migration stopover duration. Thus, scenarios A1B, A2 and B1 all increased stopover duration, but the increase was <1 day compared to present conditions.

Emission scenarios also significantly increased mean step length (i.e. movement distance) compared to present conditions in model simulations. Specifically, scenario A1B ($\hat{\beta} = 0·09$, SE < 0·01), scenario A2 ($\hat{\beta} = 0·09$, SE < 0·01) and scenario B1 ($\hat{\beta} = 0·07$, SE < 0·01) had similar effects on mean step length compared to present conditions. *Food-max* also influenced overall mean step length ($\hat{\beta} = -0·02$, SE < 0·01), whereas *wetland-flood-prop* did not have an impact. *Crop-flood-prop* ($\hat{\beta} = -0·01$, SE < 0·01) and the *wetland-flood-prop × crop-flood-prop* interaction ($\hat{\beta} = -0·02$, SE < 0·01) did affect mallard mean step length. Increased step lengths in IPCC scenarios generated overall lower lipid reserves at the end of simulations in IPCC scenarios compared to lipid reserves for birds simulated under present conditions (Fig. 2). Thus, scenarios A1B, A2 and B1 increased movement distances by approximately 7–10% compared to present conditions. In contrast to migration stopover duration and mean step length, emission scenario did not have an effect on number of mortalities in model simulations.

Simulations and regression indicated that *food-max* ($\hat{\beta} = -650·67$, SE = 8·14) and scenario (A1B $\hat{\beta} = 311·89$, SE = 23·01; A2 $\hat{\beta} = 282·70$, SE = 23·01; B1 $\hat{\beta} = 321·66$, SE = 23·01) influenced the number of censored birds. Thus, the number of censored birds differed between present conditions ($\bar{x} = 421·4$) and future scenarios but not among future scenarios (A1B $\bar{x} = 733·3$; A2 $\bar{x} = 704·1$; B1 $\bar{x} = 743·0$). Furthermore, all simulations with *food-max* = 120 contained no censored birds, whereas simulations with *food-max* = 100 contained a mean of 1300·9 censored birds (out of 10 000). As a result, our conclusions about the effect size of alternative LULC scenarios on spring migration stopover duration may represent underestimates.

Discussion

Although North America contains a diverse network of protected wetlands, a considerable amount of uncertainty remains about the response of migratory waterfowl to changing climates and land-use trends (Johnson *et al.* 2010; Conroy *et al.* 2011). In this study, we used scenario planning to evaluate the possible effects of different IPCC scenarios on spring-migrating dabbling ducks in the midcontinent region of North America. Specifically, we evaluated the effects of each scenario on spring migration stopover duration, mean step length (i.e. movement distance) and mortality, and demonstrated that the three emission scenarios may have varying impacts on dabbling duck spring migration patterns. When compared to present conditions, IPCC scenarios increased mean migration stopover duration and increased mean step length. Although all IPCC scenarios included substantially more wetland habitat than present conditions, croplands were greatly reduced in scenario landscapes (Table 2), which likely caused agents to exhibit extended stopovers and longer step lengths due to net energy loss on the landscape. In addition, croplands in future scenarios were depleted at a higher rate than croplands in present-day simulations, further emphasizing the limited availability of crops in our simulations (Fig. 2). Consequently, we observed increased stopover durations in future scenarios that contained increased wetland habitat, in contrast to our prediction.

Although LULC scenarios project an overall increase in wetland habitat within our study area, these projections likely represent a conservative estimate. In LULC models, land cover types are spatially allocated based on an algorithm that accounts for protected areas such as National Wildlife Refuges, state conservation areas and other land protected through private conservation organizations (Sohl *et al.* 2007; Sohl & Sayler 2008). However, conservation easements are not considered protected lands in the spatial allocation algorithm, which increases the vulnerability of these areas to change in the model
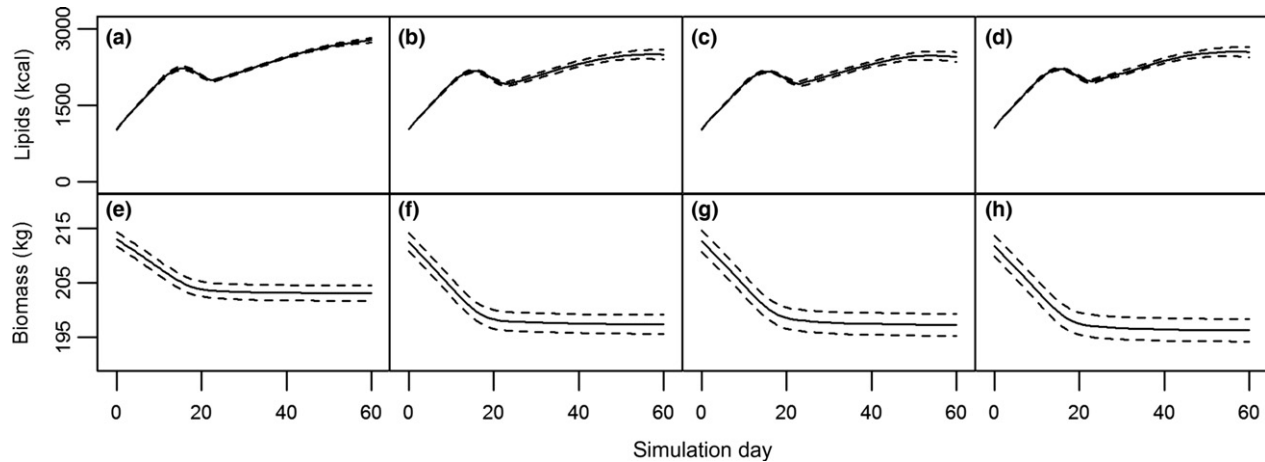
Fig. 2. Emergent properties of an individual-based model that examined dabbling duck spring migration ecology. Mean lipid reserves of virtual birds on the study area (a–d) and depletion patterns for flooded corn patches (e–h) are displayed for (a, e) present conditions and Intergovernmental Panel on Climate Changes scenarios (b, f) A1B, (c, g) A2 and (d, h) B1. Black lines represent mean and dashed lines represent 95% confidence intervals.

(Zhu *et al.* 2010). Provided that most conservation easements within the midcontinent region are permanent easements (Beatty *et al.* 2014a), substantial increases in conservation easement area could occur in future scenarios. Nevertheless, the LULC scenarios examined in this study do not account for conservation easements and any possible increase/decrease in enrolment in these programmes.

Crops are important food resources for dabbling ducks during autumn migration and winter (Reid *et al.* 1989; Reinecke *et al.* 1989; Pearse *et al.* 2012). However, over-winter depletion and decomposition limit availability of crops such as corn during spring migration, and space use patterns indicate crops are less important during spring migration than during autumn migration and winter (Beatty *et al.* 2014b). In our simulations, we modelled crop biomass based on estimates for spring migration (Foster, Gray & Kaminski 2010), and the limited availability of wetlands (compared to crops) within our simulations likely increased the importance of crops as food resources. Although IPCC scenarios project a slight increase in wetland habitat area within our study area, mallards and perhaps other dabbling ducks in the midcontinent region will likely have to adapt to altered agricultural practices and patterns. For example, increasing temperatures may lead to geographic shifts in corn and rice production areas throughout the world, challenging waterfowl populations to adapt to different dominant crops within an area or alter winter distributions (Wang *et al.* 2011; Lehikoinen *et al.* 2013; Tripathi *et al.* 2016).

Large-scale climate models predict increasing variability in interannual precipitation patterns within the midcontinent region, which may produce high uncertainty in wetland inundation patterns and availability from year to year. For example, increasing levels of hydrological drought have been predicted for much of the contiguous USA across all three scenarios examined in this study

(Strzepek *et al.* 2010; Singh *et al.* 2013). We modelled a range of flooding probabilities to account for this uncertainty locally, but we assumed the same mean and variance to initialize body condition values for all runs of the model (Appendix S1). However, mean body condition of birds may vary annually and, in dry years, birds may arrive on a stopover site in poorer body condition. Consequently, our results offer an overall perspective on the possible effects of future LULC and do not account for any cumulative effects on populations during prolonged droughts throughout the range of a species. Indeed, many waterfowl species may be able to adapt to changing land-use trends, but variation in annual precipitation patterns due to climate change may have a more prominent effect on spring migration ecology in the midcontinent region. Furthermore, changing precipitation patterns may alter nesting, migratory and winter distributions of waterfowl, and these changes across large spatial scales could increase or decrease the general biological relevance of stopover areas (Johnson *et al.* 2010). Thus, conservation planners may have to address reduced energetic carrying capacities due to altered crop cultivation patterns (e.g. corn cultivation shifting north) on spring migration stopover areas and increased uncertainty in yearly precipitation patterns due to climate change within the next 50 years.

Although our models predicted relatively small increases in spring migration stopover duration (<1 day) and movement distances (7–10%), the cumulative effects of increased stopover duration and step lengths at multiple stopover sites throughout the migration period could substantially alter spring migration ecology. Furthermore, our predicted increase in stopover duration likely represents a conservative estimate. For example, the number of stopovers may range from 1 to 3 during one migration cycle, which would correspond to an increase in migration time of approximately 1·5–2·0 days according to our model (Yamaguchi *et al.* 2008; Krementz, Asante & Naylor

2011). In an experimental manipulation of spring stopover duration among greater snow geese *Anser caerulescens atlanticus*, Legagneux *et al.* (2012) reported a negative relationship between number of days individuals were held in captivity (between 2–4 days) at stopover locations and subsequent reproductive success, although the authors attribute decreases in reproductive success to captivity-induced stress. Longer stopover duration may also delay arrival dates of dabbling ducks on the nesting grounds. Later arrival dates combined with predicted responses to earlier spring thaw dates and invertebrate emergence phenology could result in a temporal asynchrony or 'mismatch' between hatching date and period of peak duckling prey availability (Visser, te Marvelde & Lof 2012). In addition, step length increases represent the increase in movement distance each time a bird moves; thus, cumulative daily and weekly effects of an increased step length could have negative energetic consequences. Furthermore, step lengths could increase at all stopover areas, increasing energetic demand and promoting a positive feedback loop between increased movement distances and increased stopover duration. Alternatively, dabbling ducks may exhibit little to no changes in stopover duration, yet increased energetic demand from increased movement distances could cause individuals to arrive on nesting grounds in poor body condition (Anteau & Afton 2004).

Increased stopover duration and increased movement distances for spring-migrating dabbling ducks may also have important cross-seasonal effects (Sedinger & Alisauskas 2014). Cross-seasonal effects link processes and conditions in one season to reproductive success in a subsequent season (Harrison *et al.* 2011; Sedinger & Alisauskas 2014). According to the 'individual heterogeneity hypothesis' (Vaupel & Yashin 1985), individuals with poor body condition in a given year may skip breeding and allocate their limited energetic resources to survival to increase the probability of breeding in a subsequent year with better conditions (Caudill *et al.* 2014). In addition, the 'individual heterogeneity hypothesis' also predicts that individuals with superior body condition exhibit increased reproductive success and survival, whereas individuals with poor body condition exhibit decreased probabilities of reproduction and survival (Warren *et al.* 2014). For example, female mallards that arrived on nesting grounds with higher nutrient reserves had increased nesting propensity and clutch sizes, establishing a biological link between conditions on spring migration stopover sites and population-level parameters (Devries *et al.* 2008). In our simulations, ducks expended increased energy to move longer distances to obtain food, which required individuals to increase stopover duration to obtain the necessary energetic reserves to depart the study area. Although ducks in our model left the focal area when a specified level of energy reserves was obtained, the actual effects in a wild population will likely involve ducks arriving earlier on nesting grounds in poorer body condition and/or ducks arriving later on nesting grounds

in adequate body condition. As a result, our model demonstrates the potential for cross-seasonal effects in midcontinent dabbling duck populations based on LULC climate projections.

Climate change is one of the primary threats to biodiversity in the 21st century and numerous species have responded to altered environmental conditions with range shifts (Lenoir & Svenning 2015). For example, Lehikoinen *et al.* (2013) documented climate-driven range shifts for three diving duck species, including the common goldeneye *Bucephala clangula*, the tufted duck *Aythya fuligula* and the goosander *Mergus merganser*, at the flyway level in Europe. The effect of a wintering range shift in waterfowl could cascade through the annual cycle and increase/decrease the biological importance of specific stopover areas, which could impact conservation planning at large spatial scales (Hannah *et al.* 2007). Thus, the importance of any given protected area to waterfowl will be a function of a complex interaction of local land-use practices, local policies, precipitation patterns and other large-scale climate factors (Hansen & DeFries 2007; Cerdeira *et al.* 2010; Beatty *et al.* 2014a). Our study represents one example of the possible effects climate change may have on waterfowl in North America.

Acknowledgements

Data accessibility

NetLogo script uploaded as online supporting information (Appendix S2).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Detailed model description.

Appendix S2. NetLogo script.

Table S1. True metabolizable energy and Gamma distribution parameters.

Appendix S3. Sensitivity analyses and results.

Fig. S1. Mean number of virtual birds that departed from the focal site by simulation day.