Phenological and Geographical Shifts Have Interactive Effects on Migratory Bird Populations

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Abstract: For many taxa, ranges are shifting toward the poles and the timing of seasonal reproduction is advancing in response to climate change. For migratory birds, changes such as these could produce particularly strong impacts because of their potential to affect migratory timing and distance. Due to the relatively complex life histories of migratory species, however, it is difficult to intuit exactly what these impacts will be. Here, we develop a general population model for a long-distance migrant, introducing a framework for understanding the potential implications of changes in both phenology and migratory distance for bird abundances. We find that population sizes may increase with either shorter or longer migratory distances, depending on the nature of any concurrent phenological changes. This interaction between timing and distance suggests a need to consider multiple potential responses to climate change simultaneously in order to understand the overall impact of climate change on migratory populations. Our results reveal a degree of variability in the qualitative nature of this phenology-distance interaction, suggesting a possible explanation for observed variation in how migratory birds have already responded to climate change.

Keywords: bird population dynamics, migration, breeding phenology, range shift, climate change, network model.

Introduction

Many species of bird undertake long and costly roundtrip flights from wintering to breeding grounds every year, the logistics of which are complex and continual subjects of study. As we try to gauge how populations respond to a rapidly changing global climate, the plight of migratory birds has garnered special attention: they have not only one range to concern themselves with but two, and in two very different environments during two very different life-history phases. Due to these complexities, there remains great uncertainty about how these populations may react to climate change (Van Buskirk 2012). In order to study the fate of migratory bird populations as climate change progresses, we need to consider how responses to climate may carry forward to influence events in multiple seasons and perhaps even multiple environments.

Though overarching generalizations are hard to come by in the vast body of research on avian responses to climate change, there are unmistakable trends: ranges are shifting toward the poles (Root et al. 2003), and the timing of seasonal reproduction is advancing with warming (Brown et al. 1999; Crick and Sparks 1999; Dunn and Winkler 1999; Visser et al. 2009b). Studies documenting changes in the timing of migration and breeding are abundant in the climate change literature (Butler 2003; Crick 2004; Lehikoinen et al. 2004), as are studies showing geographical shifts of suitable habitat for migratory bird populations (Parmesan and Yohe 2003; Root et al. 2003), which may in turn cause range shifts in the birds themselves (Walther et al. 2002). Collectively, though, these studies are difficult to synthesize because specific effects vary across taxa and situations. Some populations have shifted their phenology (Root et al. 2003; Brommer 2004; Crick 2004; Miller-Rushing et al. 2008; Møller et al. 2008; Visser et al. 2009b; Smith and Paton 2011); others, their latitudinal ranges (Root et al. 2003; Brommer 2004; Crick 2004; Doswald et al. 2009). Still other populations seem to have not responded to climate change phenologically or latitudinally at all (Chambers and Keatley 2010; Goodenough et al. 2011; Smith and Paton 2011; Stanley et al. 2012).

Our current knowledge of these shifts is largely dependent on observational data, as experimental manipulations of phenology are often limited in application due to their necessarily small scale (Dingle 1996; Miller-Rushing et al. 2010). Accordingly, it is hard to tease apart exactly how each of these shifts affects populations and, further, whether multiple shifts will have interactive or additive effects at the population level. Without such an understanding, we can neither effectively explain the observed
variation in avian responses to climate nor predict how they will potentially be affected by a rapidly changing climate in the future.

Miller-Rushing et al. (2010) suggest that the development of population models that incorporate the timing of life-history events will help provide a theoretical framework for quantifying the role of phenology in shaping demographic consequences of climate change and generating testable hypotheses. Models permit direct manipulation of multiple possible responses to climate change and allow a means of investigating the potential for interactions. In this article, we use a network population dynamic model to generate such a framework, and we use our model to explore the potential implications of changes in both phenology and range for migratory avian population dynamics.

**Methods**

Our goal is to evaluate the separate effects and the potential for interaction of two consequences of climate change: (1) range shifts, resulting in altered migratory distance; and (2) phenological shifts, resulting in altered breeding season length. We do not model climate explicitly but rather impose shifts that represent likely responses to climate change and then study the consequences of those shifts. Advanced spring phenology and/or delayed fall phenology in response to climate change has been observed in a wide range of populations (Parmesan and Yohe 2003; Root et al. 2003) and so we explore the population-level effects of a longer breeding season. For completeness, we also consider breeding seasons that become shorter with climate change.

Our exploration of changes in migratory distance is grounded in emergent patterns showing that climate change can affect migration distance (Newton 2008, table 21.1). Changes in migratory direction may also be important, but for simplicity we focus below only on changes in migratory distance; this allows us to use a one-dimensional network model in which we can either lengthen or shorten migration and study the result. We consider post-climate-change migratory distances ranging from zero, representing a sedentary population, to twice the historical migratory distance; this allows us to use total population size (the sum of the abundances for all migration strategies) to measure how successful the population is as a whole under each set of conditions. Matlab code for performing these simulations is provided in the appendix, available online.1

**Population Dynamics.** We use \( A_i(t) \) to denote the population density at the end of the year \( t \) breeding season of birds that use the strategy of migrating between winter patch \( i \) and breeding patch \( j \). After southward migration at the onset of winter (assuming a species breeding in the Northern Hemisphere; for Southern Hemisphere birds, our use of “north” and “south” can simply be reversed throughout), the density of \( i,j \) birds is the product of this premigration density, \( A_i(t) \), and the probability of surviving migration between \( i \) and \( j \), \( M_{ij} \):

\[
A'_i(t) = A_i(t)M_{ij}. \tag{1}
\]

(The methods for calculating \( M_{ij} \) and the other survival and fecundity terms are described in the following section.) Next, the population size after overwintering but before spring migration is the product of the population density at the onset of winter and the probability of surviving winter, \( S_i(t) \),

\[
A^w_i(t) = S_i(t)A(t). \tag{2}
\]

At the beginning of the breeding season, the birds that survived winter and another migration arrive at the breeding grounds:

\[
A^b_i(t) = A^w_i(t)M_{ij}. \tag{3}
\]

Finally, the population size at the end of the year depends on the net fecundity, \( F_{ij}(t) \), of these surviving individuals:

\[
A_i(t + 1) = A^b_i(t)F_{ij}(t). \tag{4}
\]

At the end of each year, we calculate the global population size in time step \( t \) as the sum over all migration strategies,

\[
N(t + 1) = \sum_{i=1}^{N_i} \sum_{j=1}^{N_j} A_i(t + 1). \tag{5}
\]

High values of \( N(t) \) are taken as an indication that the

1 Code that appears in the American Naturalist is provided as a convenience to the readers. It has not necessarily been tested as part of the peer review.
environmental conditions imposed (i.e., the breeding season length and migration distances) are favorable at the population scale.

Spatial dynamics. Because migratory birds travel mainly on a north-south axis (Berthold 2001; Tankersly and Orvis 2003; Newton 2008), we define $N_w$ equidistant wintering sites and $N_b$ equidistant breeding sites along latitudinal gradients of habitat quality (fig. 1). Patch quality (here, carrying capacity and density-independent survival and fecundity) is set as highest in the patches furthest from the midpoint of the range, so the northernmost breeding patch and southernmost wintering patch each have the highest qualities in their respective ranges. This feature of the landscape gives birds incentive to migrate in the model, which is appropriate for what we are assuming is a historically migratory population, and reflects the probable ultimate mechanisms for annual migration: to take advantage of ephemeral resources (Levey and Stiles 1992; Bell 2000) or for temporary release from competition (Cox 1985) and predation (Fretwell 1980; Greenberg and Marra 2005). For example, increasing winter severity from the equator poleward limits year-round residency, creating a surplus in resources during the breeding season that migrants exploit increasingly along the latitudinal gradient (Herrera 1978; O’Connor 1985; Morse 1989; Newton and Dale 1996a, 1996b). Constructing our model as a network of discrete patches allows us to easily understand population dynamics at multiple scales: within patches, within ranges, and globally (Dunn and Majer 2007). It also pro-

Figure 1: Schematic representation of the model. The lower three boxes on the left represent an $N_w$-patch winter range, and the upper three boxes on the left represent an $N_b$-patch breeding range, separated by an inter-range distance, $D$. 

EXAMPLE: Dynamics within breeding patch $N_b$

$$F_{N_b}(t) = F_{N_b}B \exp \left( -\frac{z_{W_b} \sum_{h=1}^{N_w} A_{N_b}^w(t)}{K_{N_b}} \right)$$

EXAMPLE: Migration from breeding patch $N_B$ to wintering patch 1

$$M_{1N_b} = 1 - \frac{D_{1N_b}^2}{v + D_{1N_b}^2}$$

EXAMPLE: Dynamics within wintering patch 1

$$S_{1j}(t) = S_1 \exp \left( -\frac{p_{1j} \sum_{h=1}^{N_w} A_{1h}^w(t)}{K_1} \right)$$
vides a reasonable representation of how many avian species use space (Donovan et al. 1995; Sherry and Holmes 2000).

The minimum possible migration distance is the distance between the ranges, that is, the distance from the southernmost breeding patch to the northernmost wintering patch. We refer to this as the inter-range distance, $D$. The exact distance traveled by any individual depends on which breeding and which wintering patches it uses, but by increasing the inter-range distance we can lengthen the migration distance for all birds. Such a change would result from a range shift where, for example, the entire breeding range shifts northward with warming to a greater degree than in the wintering range. Our model also has the potential to be adapted for studying phenological shifts in resident populations by setting $D = 0$ and confining all individuals to a single patch ($N_w = N_b = 1$).

Individuals that arrive in breeding areas in the early part of the arrival period often take territories in the best habitat, begin breeding first, and show the highest nest success (e.g., Lanyon and Thompson 1986; Smallwood 1988; Bensch and Hasselquist 1991; Aebischer et al. 1996). Following Taylor and Norris (2010), we use this concept to model intraspecific competition such that competitive pressures are felt more intensely by later arriving individuals. Birds with migration strategy $ij$ will be the $i$th group to arrive into breeding patch $j$ (fig. 1); that is, birds wintering in northernmost patch $i = 1$ arrive first because they are the closest to the breeding range, and those in southernmost patch $i = N_w$ arrive last (Taylor and Norris 2010). The function $z_{ij}$ describes the strength of density dependence experienced by $i,j$-strategy birds, given their order arrival:

$$z_{ij} = \exp \left[ -q(N_w - i) \right].$$

(6)

This function increases with arrival order $i$, imposing stronger density dependence on later arriving birds. The parameter $q$ governs how severely this density dependence intensifies with later arrival. We use a similar function to describe a density-dependent penalty in the form of lower overwinter survival for birds arriving later in the wintering grounds:

$$p_{ij} = \exp \left[ a(j - 1) \right], \quad \text{see erratum}$$

(7)

where $a$ governs the strength of the effect of arrival order. In any wintering patch $i$, birds from southernmost breeding patch $j = N_b$ arrive first and those from northernmost breeding patch $j = 1$ arrive last; by decreasing with $j$, then, $p_{ij}$ imposes the strongest winter density dependence on birds from the northernmost breeding grounds. Below, we use $p_{ij}$ and $z_{ij}$ in the functions for survival and fecundity within the wintering and breeding patches, respectively.

### Survival and Fecundity Functions

**Migration Survival.** We model migration survival ($M_{ij}$) for birds wintering in patch $i$ and breeding in patch $j$ as a decreasing function of distance,

$$M_{ij} = 1 - \frac{D_{ij}^2}{v + D_{ij}^2},$$

(8)

where $D_{ij}$ is the distance between patches $i$ and $j$, and $v$ is a constant that determines how strongly increased distance decreases the survival of migrating individuals. The distance $D_{ij}$ that a bird must travel to get from patch $i$ to patch $j$ depends both on the distance between the breeding and wintering ranges ($D$) and the distances between patches within each range ($d$; see fig. 1 and table 1). For simplicity, we assume that climate change–induced range shifts affect $D$ but not $d$. Thus, any postclimate change shift in the inter-range distance $D$ will cause the same size shift in the distance between any pair of patches, $D_{ij}$.

Our function for $M_{ij}$ takes the shape of a negative sigmoid (fig. 1), such that there is high survival over short distances and lower survival for longer distances due to deterioration of the individuals’ conditions as migration progresses. If we instead assume migration survival declines exponentially with distance (as in Taylor and Norris 2010), our qualitative results are unchanged (A. James, unpublished results).

**Dynamics within Wintering Range.** In the wintering range, the quality of each patch is determined by its patch-specific carrying capacity ($K_i$) and intrinsic density-independent overwinter survival ($S_i$). The realized survival for birds using migration strategy $ij$ will additionally depend on density-dependent competition, determined by $p_{ij}$ (eq. [7]) and the current population density within the patch.

We specify a range of carrying capacities and intrinsic survival rates for the wintering range, then assign the highest $K_i$ and $S_i$ values to the southernmost patch and the lowest values to the northernmost, and impose a linear decline in patch quality between these extremes. This range of carrying capacities remains unchanged in the event of a change in migratory distance, because we assume that range shifts result from birds tracking favorable habitat. That is, we might suppose that the location of habitat of a particular quality will shift northward due to climate change. If birds also shift northward so as to remain in the same quality of habitat, this will not affect the values of the patch quality parameters, $K_i$ and $S_i$, that they experience.

Assuming Ricker-like density dependence (Taylor and Norris 2010), the realized winter survival of birds with migration strategy $ij$ is
Table 1: Model parameters and their corresponding values

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Definition</th>
<th>Value in baseline simulations</th>
<th>Range used in random simulations (values drawn from uniform distributions)</th>
</tr>
</thead>
<tbody>
<tr>
<td>N_w</td>
<td>No. winter patches</td>
<td>5</td>
<td>[3, 10]</td>
</tr>
<tr>
<td>N_p</td>
<td>No. breeding patches</td>
<td>5</td>
<td>[3, 10]</td>
</tr>
<tr>
<td>S_i</td>
<td>DI survival rate at winter site i</td>
<td>.9 (patch N_w)–.99 (patch 1)</td>
<td>Max. (patch 1): [.85, .99]; min. (patch N_w): [.75, 95% max]</td>
</tr>
<tr>
<td>F_j</td>
<td>DI net fecundity at breeding site j</td>
<td>1.7 (patch 1)–2 (patch N_p)</td>
<td>Max. (patch N_p): [1.5, 3]; min. (patch 1): [1, 95% max]</td>
</tr>
<tr>
<td>a</td>
<td>Governs effect of arrival order on DD survival in winter range</td>
<td>.08</td>
<td>[0, 1]</td>
</tr>
<tr>
<td>q</td>
<td>Governs effect of arrival order on DD fecundity in breeding range</td>
<td>.08</td>
<td>[0, 1]</td>
</tr>
<tr>
<td>v</td>
<td>Governs the decrease in migration survival with added distance</td>
<td>4.25 × 10^7 km^2</td>
<td>[4, 5] × 10^7 km^2</td>
</tr>
<tr>
<td>K_i</td>
<td>Carrying capacity at winter site i</td>
<td>3,000 (patch N_w)–4,500 (patch 1)</td>
<td>Max. (patch 1): [2,500, 10,000]; min. (patch N_w): [1,000, 95% max]</td>
</tr>
<tr>
<td>K_j</td>
<td>Carrying capacity at breeding site j</td>
<td>3,000 (patch 1)–4,500 (patch N_p)</td>
<td>Max. (patch N_p): [2,500, 10,000]; min. (patch 1): [1,000, 95% max]</td>
</tr>
<tr>
<td>T_h</td>
<td>Historical length of the breeding season</td>
<td>95 days</td>
<td>(Held at 95 days)</td>
</tr>
<tr>
<td>ΔT</td>
<td>Change in breeding season length</td>
<td>–10 to 30 days</td>
<td>(Held at –10 to 30 days)</td>
</tr>
<tr>
<td>D_h</td>
<td>Historical distance between ranges</td>
<td>2,000 km</td>
<td>(Held at 2,000 km)</td>
</tr>
<tr>
<td>D</td>
<td>Current distance between ranges</td>
<td>0–4,000 km</td>
<td>(Held at 0–4,000 km)</td>
</tr>
<tr>
<td>m</td>
<td>Migration rate</td>
<td>80 km/day</td>
<td>[25, 125] km/day</td>
</tr>
<tr>
<td>d</td>
<td>Interpatch distance in winter/breeding range</td>
<td>10 km</td>
<td>(Held at 10 km)</td>
</tr>
</tbody>
</table>

Note: Parameters, their corresponding values in the baseline simulations (figs. 2–4), and their ranges in the simulations with randomly chosen parameter values (table 2; fig. 5). For S_i, F_j, K_i, and K_j, values are given for the highest- and lowest-quality patches; values for other patches were even distributed between these values. DI = density independent, DD = density dependence.

\[ S_i(t) = S_i \exp \left( -\frac{p_i \sum_{i=1}^{N_w} A_{i,n}(t)}{K_i} \right) \]  

(9)

In the exponential term, the sum over all breeding patches yields the total density of birds occupying wintering patch i. As such, birds that breed in one location can influence the population dynamics in other breeding sites through density-dependent effects in their shared wintering patches.

**Dynamics within Breeding Range.** We model patch quality in the breeding range as a mirror of the wintering range, with quality determined by carrying capacity (K_i) and breeding success (F_j) that take their highest values in the northernmost patch. Net per capita fecundity in breeding patch j is

\[ F_j(t) = F_j B \exp \left( -\frac{p_j \sum_{j=1}^{N_p} A_{i,j}(t)}{K_j} \right) \]  

(10)

Term B represents the expected number of broods per year and allows us to consider the possibility that a change in the breeding season length could change the average number of broods produced. Empirical data suggest either an increase in the potential for multiple clutches during the breeding season (Lesley and Stutchbury 1996; Nagy and Holmes 2005; Monroe et al. 2008; Møller et al. 2008; Mulvihill et al. 2009) or an increase in the potential to produce a single brood successfully (Pease and Grzybowski 1995; Griebeler et al. 2010) with a longer breeding season. We therefore model the population average number of broods as

\[ B = \frac{T_h + ΔT - [(D - D_h)/m]}{T_h} \]  

(11)

where T_h is the historical breeding season length in days and ΔT is the number of days added to the breeding season due to phenological shifts. Term D is the current distance between winter and breeding ranges, whereas D_h is the historic distance; D − D_h, then, is the change due to range shifts in the inter-range distance. The parameter m is the rate of migration per day and allows us to account for any additional breeding days lost or gained by changes in migration distance. Although individual breeding pairs will have an integer number of broods, B is a population average number of broods and therefore need not take on integer values. That is, in our population-level model,
there is no threshold breeding season length at which all birds suddenly double brood but rather a gradual increase as the frequency of multiple nesting attempts increases with breeding season length (but see Schmidt and Whelan 2009).

**Model Simulation and Analysis**

The avian migration literature is replete with species-specific information on migratory distances, rates of migration, arrival times, and more (Crick 2004; Newton 2008). Because we are interested in generalized patterns, however, we set the values of our parameters with empirical realism in mind but without reference to any particular species. The approach emphasizes broad patterns and may even allow for application of the model beyond the avian clade (Dingle 1996).

For what we will refer to as our baseline simulations, we used the parameter values shown in table 1. The key parameters of interest are \( D \), the post-climate-change distance between breeding and wintering ranges, and \( \Delta T \), the phenological shift in the length of the breeding season. We considered inter-range distances spanning 0–4,000 km, compared to a historical distance of \( D_0 = 2,000 \) km (table 1). We assumed a historical breeding season length, \( T_{ih} \), of 95 days with \( \Delta T \) ranging from −10 to 30 days.

For each combination of \( D \) and \( \Delta T \), we ran simulations for 100 years and examined final population size \( (N_{100}) \) from eq. [5]) and spread of the final population among patches, summarized using Shannon’s equitability, \( E_{i1} \) (Shannon 1948). In the winter range, equitability among the \( N_w \) wintering patches is given by

\[
E_{i1}(W) = \frac{-\sum_{j=1}^{N_w} h_i \ln h_i}{\ln (N_w)},
\]

where \( h_i \) is the proportion of birds from the wintering range who are wintering in patch \( i \) in the final time step \( (t = 100) \). The numerator is Shannon’s evenness index and the denominator standardizes the metric by the maximum possible observed evenness, given by the natural log of the number of wintering patches. This bounds \( E_{i1}(W) \) between zero and one, making for easy comparison of simulation results with different numbers of patches. If \( E_{i1}(W) \) is high (close to one), then individuals are spread fairly evenly among wintering patches. We performed the same equitability calculation for the breeding range, \( E_{i1}(B) \), as well, substituting \( N_b \) for \( N_w \) in equation (12). With the parameter values we used, our model quickly settled on an equilibrium total population size and distribution, so analysis of the final time step provides meaningful information about the performance of a population that has experienced a particular combination of range and phenological shifts (Gatehouse 1987).

After examining the baseline simulations, we explored the generality of our results by generating 1,000 additional sets of simulations using different parameter values across all \( D-\Delta T \) combinations. Parameter values for each set were randomly chosen from uniform distributions over ranges shown in table 1. If a randomly selected parameter set resulted in peak bird densities at the extreme inter-range distance \( (D = 4,000 \) km) for every possible phenological shift, we eliminated that parameter set from the analysis because it did not allow us to conclude whether a phenology-distance interaction might exist outside the range of distances considered. Only 64 such cases were found and excluded in the course of accumulating 1,000 parameter sets lacking this issue.

All other randomly generated parameter sets produced one of a few distinct qualitative outcomes. For each of these parameter sets, we plotted the results and assigned them to one of three outcomes. We then performed a linear discriminant analysis using the MASS package in R to determine the extent to which each parameter explains its observed outcome. The independent variables in our discriminant analysis were the non-patch-specific parameters \( (a, q, v, and m) \) and additional quantities to summarize the effects of patch-specific parameters: the total carrying capacities of the entire breeding \( \left( \sum_{i=1}^{N_b} K_i \right) \) and wintering \( \left( \sum_{i=1}^{N_w} K_i \right) \) ranges, the average density-independent overwinter survival rate \( (1/N_{wi}) \sum_{i=1}^{N_w} S_i \) and the average density-independent fecundity \( (1/N_b) \sum_{i=1}^{N_b} F_i \).

**Results**

We plot \( N \) in the final time step, \( t = 100 \), in \( D-\Delta T \) parameter space to summarize the effect of each combination of shifts on overall population size (fig. 2). From the baseline simulations (those using values in table 1), we see a clear U-shaped pattern in population densities, with the largest populations occurring where the phenological shift is large and the inter-range distance is intermediate. We deliberately chose baseline parameter values such that the historical distance, \( D_0 \), is associated with the highest population densities possible when there is no phenology shift \( (\Delta T = 0) \). This choice corresponds to a biological assumption that the historical migration distance is adaptive under historical phenological conditions. Our results show, however, that this historical inter-range distance is no longer optimal when populations also experience a change in breeding season length. Instead, we see that populations with a shortened breeding season would in fact benefit from longer migrations (fig. 2). In contrast, when the breeding season is extended, the highest population sizes occur at shorter than historical inter-range
distances (figs. 2, 3). Populations that maintain the historical inter-range distance, or shift their ranges to increase that distance, will still benefit from longer breeding seasons, but they will do so to a lesser extent than if they shortened migration (fig. 2). This dependence of the effect of phenological shifts on the inter-range distance indicates that phenological and geographical shifts are expected to have interactive effects on overall population size.

The effect of breeding season length on population size is straightforward: a longer breeding season (higher $\Delta T$) increases the expected number of successful broods (eq. [11]) and thus increases mean per capita fecundity (fig. 4). The effect of inter-range distance is more complicated. Higher values of $D$ result in greater migration mortality (eq. [8]) and reduced time available for breeding (eq. [11]). We might then expect population sizes to decrease with $D$, but of course we only see this some of the time (right-hand side of the U-shaped pattern in fig. 2). The reason is that with higher migration mortality, fewer birds successfully arrive at the breeding grounds, and this decreases density dependence on those birds that do arrive to breed (fig. 4). With increasing values of $D$, then, it may be possible for the surviving birds to overcompensate for losses during migration and cause a net increase in population size (as on the left-hand side of the U in fig. 2). The balance between these direct negative and indirect positive effects of inter-range distance on total population size results in maximum population sizes at intermediate $D$ (see Rousset and Gandon 2002). The interaction between $\Delta T$ and $D$ shown in figure 2 arises because populations with shorter breeding seasons have lower density-independent fecundities (due to lower $B$ at lower $\Delta T$) and thus benefit proportionally more from the competitive release caused by greater migration mortality (due to higher $D$).

Within the combinations of shifts we considered, lengthening the breeding season had a stronger potential to increase total population size than shifting migratory distance. Even under the best conditions, the breeding range is well below capacity, suggesting that density dependence during the population growth phase is not severely restricting the impact of either type of shift. Instead, it appears that any benefits gained from changing migratory distance (e.g., competitive release with longer migrations) are always fairly close to being offset by the costs (lost breeding time and higher migration mortality). In contrast, lengthening the breeding season has a purely positive impact on fecundity and thus population growth.

Equitability ($E_H(W)$ and $E_H(B)$) at $t = 100$ was plotted for all combinations of $\Delta T$ and $D$ (fig. 5). Maximum equitabilities in both ranges followed a similar pattern to maximum population sizes (fig. 2), indicating that population sizes increase by adding individuals disproportionately to the less populous patches. Follow-up simulations (not

Figure 2: Our baseline model, with parameter values as given in table 1. Shading shows the total population size after 100 time steps, $N(100)$. The black lines indicate the historical inter-range distance ($D_h = 2,000$ km) and the historical breeding season length ($\Delta T = 0$; $T_b = 95$ days). Dots mark the inter-range distance that results in the highest population size for each $\Delta T$. 

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shown) confirm that when total population size increases due to changes in $D$ or $\Delta T$, it is the lower quality patches that grow the most. This trend is known as the buffer effect (e.g., Lanyon and Thompson 1986; Mearns and Newton 1988; Smallwood 1988; Ferrer and Donazar 1996; Currie et al. 2000): with lower total population sizes, equitability of patches is lower because there are simply not enough birds to fill the better patches to capacity.

The 1,000 simulations with randomly chosen parameter sets largely support the conclusions drawn from our baseline simulations. Of the 1,000 sets, 73.7% showed a pattern qualitatively identical to that of the baseline (fig. 2), with optimal inter-range distances decreasing monotonically with breeding season length. Including parameter sets that produced a nonmonotonic but otherwise similar pattern (where at least 80% of the total variability in optimal $D$ comprised decreases with longer breeding), a full 86.0% of parameter sets agreed with the baseline pattern. Only a single parameter set failed to show any interaction, such that the optimal inter-range distance was the same (within the same 10-km distance bin) regardless of breeding season length. The remaining simulations showed an interaction in a form different from the baseline. In 6.9% of the parameter sets, the direction of the interaction was reversed relative to our baseline result (fig. 6, top; in 5.8% of sets, this increase in optimal distance with $\Delta T$ was monotonic). The remaining parameter sets revealed more complex interactions, where the optimal inter-range distance neither primarily (>80% of the variation) increased nor primarily decreased with breeding season length (fig. 6, bottom).

Our discriminant analysis reveals that the most heavily weighted parameter in determining which of these four outcomes is produced is average fecundity $(\langle 1/N_B \rangle \sum_{j=1}^{N_B} F_j)$, followed by the effect of arrival order on winter ($a$) and summer ($q$) density dependence. The remaining parameters had minimal effects (table 2). Deviations from the baseline pattern typically occurred for higher fecundities and stronger effects of arrival order into the wintering grounds (table 2), although these two features alone were insufficient to cause a change away from the baseline pattern. What these results emphasize is that although there are some isolated regions of our high-dimensional parameter space in which other interactions can arise, our baseline simulation is a good representative of the model’s typical behavior in the vast majority of settings.

Discussion

Empirically, we know that some avian populations are modifying their patterns of migration. Many avian species are delaying migration in the autumn or advancing their migration time in the spring, resulting in longer breeding seasons (Balbontin et al. 2009; Van Buskirk et al. 2009). Simultaneously, ranges are consistently shifting poleward (Root et al. 2003; Brommer 2004; Doswald et al. 2009) resulting in longer or shorter migratory distances, even to

Figure 3: Population sizes ($t = 100$) across inter-range distances from the baseline simulations. Shown here is a horizontal “slice” through figure 2 at $\Delta T = 30$. The largest population, marked by a dot, occurs for shorter than the historical migratory distance, marked by a dashed line.
Figure 4: Average per capita fecundities, $F_{ij}(t)$, from the baseline simulations. A longer breeding season directly increases fecundity by increasing the expected number of successful broods ($B_i$; eq. [11]). A longer inter-range distance increases fecundity indirectly by reducing the density of birds that successfully arrive at the breeding grounds (due to lower $M_{ij}$; eq. [8]) and thus decreasing density dependence.

The point of populations switching from sedentary to migratory behaviors and vice versa (e.g., Root 1989; Able and Belthoff 1998; Berthold 1999; Wernam et al. 2002). Our results show that timing and range shifts can have interactive impacts on population size and suggest an explanation for why natural populations seem to exhibit the full range of geographical shifts with climate change as listed above: whether populations benefit from shortening, lengthening, or leaving their migration distances unchanged depends on phenology (fig. 2) and, to a lesser extent, on demography in both the breeding and wintering ranges (fig. 6; table 2).

Our model-generated results are corroborated by observed patterns in migratory bird populations. As breeding seasons lengthen, a long inter-range distance is increasingly suboptimal (fig. 2), which is consistent with the finding that birds with longer migratory distances have suffered the worst declines with climate change (Møller et al. 2008; Jones and Cresswell 2010; Saino et al. 2010). Additionally, a longer breeding season has been shown to increase population sizes in nature (Møller et al. 2008), as it does in our model (fig. 2). Although underlying mechanisms are difficult to discern empirically, observational data has also suggested an interaction between phenological shifts and migratory distance (Jones and Cresswell 2010; Gunnarsson and Tomassen 2011; Moussus et al. 2011), which is in agreement with our theoretical findings.

We have assumed in our simulations that under historical phenological conditions ($\Delta T = 0$), the historical inter-range migration distance ($D = D_h$) yields the maximum population size. We feel this is reasonable for a species with a sufficiently long evolutionary history in its breeding and wintering ranges, at least within the context of the very simple landscape we model. Inter-range distances following rapid climate change may not be adaptive, however, and bird populations may not adopt the strategies that maximize population size in our model. Depending on the degree to which a bird population has the flexibility to adjust its migratory behavior, our model generates two types of predictions. In the case of a highly flexible population, we can think of our model-derived combinations of $\Delta T$ and $D$ that maximize population size as predictions for how the population will adjust to climatic changes (they should move toward the dots in fig. 2). For inflexible species, however, the values of $\Delta T$ and $D$ they experience may be determined entirely by the environment; in these cases, our model instead predicts how total population size is likely to change in response to these environmentally imposed shifts. Flexibility in migration response is typically found in those species with higher behavioral plasticity in response to climate in general (Jones and Cresswell 2010; Van Buskirk 2012; but see Van Buskirk et al. 2012), oftentimes a trait exhibited in short-distance migrants (sensu Coppack and Both 2002; Butler
Figure 5: Equitabilities, $E_H$, at all combinations of $D$ and $\Delta T$ at baseline parameter values (see table 1). Points indicate highest values of $E_H$. **Top**, equitability of wintering patches, $E_H(W)$, increases with shorter migration distance $D$ and longer breeding seasons, $\Delta T$. All equitabilities are high, indicating that birds are fairly evenly distributed among wintering patches for all $D$ and $\Delta T$ combinations. **Bottom**, equitability of patches in the breeding range, $E_H(B)$, also increases with shorter migration distance $D$ and longer breeding season $\Delta T$ but are lower than equitabilities in the winter range.

2003; Visser et al. 2009b; Moussus et al. 2011) who may rely more heavily on environmental conditions to calibrate the timing of their migration. Conversely, the inflexible species are those generally long-distance migrants who rely more heavily on endogenous rhythms in the timing of their migration (Berthold 1996; Both and Visser 2001; Coppack and Both 2002; Butler 2003; Gordo et al. 2005).

In our model, we have assumed that range shifts affect migratory distance ($D$) but not breeding season length ($\Delta T$). This is reasonable in situations where breeding season length is determined largely by environmental factors like food availability and temperature (Visser et al. 2004, 2009a; Visser and Both 2005) that populations track when they shift their ranges. By modeling species whose phenology is influenced by climate change, our model does not apply to cases where photoperiod alone governs breed-
Figure 6: Examples of results that differ from the baseline pattern in figure 2. Top, reverse interaction ($N_w = 6$, $N_b = 8$, $a = 0.83$, $q = 0.11$, $v = 3.97 \times 10^3$, $K_w = 6,321–8,125$, $K_b = 5,260–6,962$, $F_w = 2.09–2.98$, $S_b = 0.90–0.97$, and $m = 113.1$). Bottom, complex interaction ($N_w = 5$, $N_b = 8$, $a = 0.48$, $q = 0.88$, $v = 4.39 \times 10^3$, $K_w = 2,217–2,542$, $K_b = 4,312–5,760$, $F_w = 2.69–2.96$, $S_b = 0.80–0.95$, and $m = 100.5$). These examples are a subset of our 1,000 simulations with randomly chosen values, except that we tuned the parameter $v$ so that the highest population size at $\Delta T = 0$ occurs at the historical inter-range distance ($D = 2,000$ km), in accordance with our expectation for biologically realistic systems; this adjustment merely shifted the patterns right or left and did not alter their qualitative appearance.

If it does play a role, then birds that shift far enough to breed may consequently experience a decrease in $\Delta T$ due to this decrease in photoperiod. Examining this effect in our model is not straightforward because changes in $D$ result from the net effect of shifts in both ranges. However, if we momentarily suppose that a population maintains its historical wintering grounds but shifts to breed farther north, larger shifts may then be accompanied by more modest increases in breeding season length. This could work to constrain the combi-
Table 2: Results of the linear discriminant analysis

<table>
<thead>
<tr>
<th>Parameter</th>
<th>First linear discriminant coefficient</th>
<th>Baseline mean value</th>
<th>Reverse interaction mean value</th>
<th>Complex interaction mean value</th>
</tr>
</thead>
<tbody>
<tr>
<td>((1/N_B) \sum_{i=1}^{N_B} F_i)</td>
<td>.73</td>
<td>1.8</td>
<td>2.3</td>
<td>2.1</td>
</tr>
<tr>
<td>a</td>
<td>.70</td>
<td>.46</td>
<td>.72</td>
<td>.72</td>
</tr>
<tr>
<td>q</td>
<td>-.52</td>
<td>.53</td>
<td>.28</td>
<td>.43</td>
</tr>
<tr>
<td>((1/N_W) \sum_{i=1}^{N_W} S_i)</td>
<td>.15</td>
<td>.86</td>
<td>.87</td>
<td>.87</td>
</tr>
<tr>
<td>m</td>
<td>.11</td>
<td>.76</td>
<td>82</td>
<td>86</td>
</tr>
<tr>
<td>(\sum_{i=1}^{N_W} K_i)</td>
<td>.05</td>
<td>32,000</td>
<td>30,400</td>
<td>34,500</td>
</tr>
<tr>
<td>(\nu)</td>
<td>-.04</td>
<td>(4.5 \times 10^7)</td>
<td>(4.5 \times 10^7)</td>
<td>(4.5 \times 10^7)</td>
</tr>
<tr>
<td>(\sum_{i=1}^{N_W} K_i)</td>
<td>.03</td>
<td>32,500</td>
<td>33,600</td>
<td>31,200</td>
</tr>
</tbody>
</table>

Note: Results of the linear discriminant analysis of simulations from 1,000 randomly generated parameter sets. Standardized coefficients are given for the first linear discriminant, which explained 96% of the variation in the simulation results. Examples of each pattern can be seen in figures 2 (baseline) and 5 (others).

nations of \(D\) and \(\Delta T\) that are available to populations, potentially pushing them toward the diagonal that also yields the highest population sizes in the model (fig. 2). This idea warrants further study.

We make four key assumptions in our model to reduce complexity and aid interpretation of our results. First, we make the simplifying assumption that the new ranges have the same qualities as the historical ones, which requires migrants to have the behavioral plasticity to track the movement of suitable habitat with climate change. Though such plasticity has been documented (Møller et al. 2008), it is unlikely that range shifts result exactly in the maintenance of pre-climate-change habitat conditions. In order to isolate the general effects of changes to migratory distance and timing, we deliberately omitted climate-driven changes to habitat quality. For more detailed species-specific predictions, such considerations could be easily incorporated into the model by altering the patch-quality parameter values following climate change.

Our second assumption is that patches are best the furthest from the midpoint between ranges. Without this, we would need to include some other assumption to provide an incentive for migration in the model. It is interesting to note that if climate change should cause this assumption to no longer hold, a population could potentially shift completely from migratory to sedentary (Coppack and Both 2002). Third, we assume that stopover ecology remains constant, implying that the change in inter-range distance gives us full information on changes to migration survival. Violations to this assumption exist in nature (Both 2010), and understanding their effects on how migratory populations respond to climate change would be a fruitful avenue for future research. Some effects of stopover ecology could potentially be accounted for in a more complex migration mortality function. Finally, a full consideration of other potential impacts of climate change, such as possible temporal mismatches with food sources (Stenseth and Mysterud 2002; Both et al. 2009), is beyond the scope of this study but would likely yield insights in future work. Despite our simplifying assumptions, our model serves as a conceptual framework for understanding migratory bird populations in the face of several interacting effects of climate change.

In sum, our model encompasses two types of responses to the question of how avian populations may respond to climate change. In terms of application, our model may be used with system-specific parameter estimates to make predictions about how particular migratory species may be affected by climate-driven shifts. It can also be applied to questions about migratory patterns, rather than population dynamics, within networks (Lundberg and Alerstam 1986; A. R. M. James, C. Taylor, and K. Abbott, unpublished manuscript). In a broader sense, we have provided a response to the call for a theoretical framework for the role of phenology in shaping demographic consequences of climate change (Miller-Rushing et al. 2010). Empirical evidence for an interaction between phenology and geographical shifts exists (Jones and Cresswell 2010; Gunnarsson and Tomassen 2011; Moussus et al. 2011), and a major contribution of our work is to propose a theoretical explanation for this observation.

Acknowledgments

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Erratum

In “Phenological and geographical shifts have interactive effects on migratory bird populations” (American Naturalist 183:40–53), there was an error in equation (7), which appears on page 43. The correct equation appears below:

\[ p_i = \exp[-a(j - 1)] \]  

(7)

The publisher regrets the error.

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