DISPERSAL AND DISTRIBUTIONS IN THE ERA OF GLOBAL CHANGE: PATTERNS AND MECHANISMS OF INDIVIDUAL DISPERSAL AND DISTRIBUTIONAL SHIFTS IN NORTH AMERICAN BIRDS

by

Hanna Marie McCaslin

A thesis
submitted in partial fulfillment
of the requirements for the degree of
Master of Science in Raptor Biology
Boise State University

May 2019

BOISE STATE UNIVERSITY GRADUATE COLLEGE

DEFENSE COMMITTEE AND FINAL READING APPROVALS

of the thesis submitted by

Hanna Marie McCaslin

Thesis Title: Dispersal and Distributions in The Era of Global Change: Patterns and Mechanisms of Individual Dispersal and Distributional Shifts in North American Birds

Date of Final Oral Examination: 08 March 2019

The following individuals read and discussed the thesis submitted by student Hanna Marie McCaslin, and they evaluated the student's presentation and response to questions during the final oral examination. They found that the student passed the final oral examination.

Julie Heath, Ph.D.	Chair, Supervisory Committee
Jesse R. Barber, Ph.D.	Member, Supervisory Committee
Jodi Brandt, Ph.D.	Member, Supervisory Committee
Christopher J. McClure, Ph.D.	Member, Supervisory Committee

The final reading approval of the thesis was granted by Julie Heath, Ph.D., Chair of the Supervisory Committee. The thesis was approved by the Graduate College.

DEDICATION

To my mom, for her unconditional friendship, support, and belief in me, and for making it possible for me to pursue everything I’ve dreamed of.

ACKNOWLEDGEMENTS

I am extremely grateful for the community of family, friends, and mentors without whom this project would not have been possible. I would first like to thank my major advisor and chair of my supervisory committee Dr. Julie Heath. I consider myself very lucky to have had her mentorship and guidance throughout this process, and she has helped me develop the skills that I have needed to complete this project and continue to pursue a career in ecology. Julie has offered me the support, advice, and little bit of a push I have needed throughout this project, and I am inspired by her example of how to successfully balance research and life outside of the lab. I am also grateful to the other members of my supervisory committee, Dr. Jesse Barber, Dr. Jodi Brandt, and Dr. Chris McClure for their help and input developing the concept for this project, and for help with statistics and spatial analysis. Additionally, I would have not been able to complete my analyses without the help of Dr. Trevor Caughlin, who was always available for help with Bayesian statistics and to answer computational questions, and has been an excellent mentor with great perspective as an early-career quantitative ecologist. I am also very appreciative of the Boise State University Research Computing team for their support with cluster computing and spatial analysis.

I am grateful to the Boise State University Department of Biological Sciences and Raptor Research Center for the Michael W. Butler Ecological Research Award, two Trustee Fellowships in Raptor Biology, and the Teaching Assistantship that supported me financially so that I could focus on research, attend short courses, and present my research at several conferences. Additional funding for the American kestrel chapter of this thesis came from the Department of Defense Strategic Environmental Research and Development Program (RC 2702).

I could not have finished this thesis without my friends and fellow Boise State Biology graduate students, who were always available for research input, advice, or an escape from stats and writing, and who I have enjoyed collaborating with and learning alongside these past three years. Thanks especially to my fellow Heath lab members Caitlin Davis, Mikki Brinkmeyer, Anjolene Hunt, Jay Winiarski, Ben Dudek, Katie Callery, and Casey Pozzanghera for lab meetings that made me laugh until I cried, feedback on research and presentations, and great field and travel camaraderie. Thanks also to Bryce Robinson for his willingness to discuss songbirds and distributions, and helpful feedback on the second chapter of this thesis.

Finally, I am so incredibly grateful to my family for their support and for encouraging me to pursue the things, both academically and in life, that I love to do. I feel so lucky to have been able to complete this project in my hometown, close to family moral support, meals, and perspective whenever I needed them. I am especially grateful to my mom, who has always put me and my sister, and our educations, first, and has worked and sacrificed so that we may pursue the careers and lives we dream of. Her support, patience, and belief in me means everything.

ABSTRACT

Dispersal is a critical process influencing population dynamics, and patterns of dispersal movement impact species distribution and abundance and have important evolutionary and ecological consequences. In particular, long-distance dispersal (LDD) can be especially important for gene flow and adaptability, although little is known about the mechanisms of LDD because of the challenges of studying large-scale animal movement. Global change is driving selection for new movement patterns in animals by stressing physiological tolerances and affecting the dynamics of biotic interactions. This is resulting in shifts in species distributions that are widespread across taxa. The distributions of migratory bird species are shifting heterogeneously, and multidirectional shifts are inconsistent with unidirectional climate niche tracking hypotheses. We studied correlates of natal LDD using bird banding data for American kestrels (*Falco sparverius*) in the United States and Canada from 1960-2015. We used Bayesian hierarchical models to investigate temporal trends and the effects of sex, migration strategy, weather, and landcover on LDD frequency and distance and understand potential sampling bias. We also studied the directions and correlates of shifts in breeding distributions for 73 avian species and subspecies from 1994-2017 using the North American Breeding Bird Survey. We modeled regional changes over time in breeding abundance centroid and investigated the effects of abundance trends and migratory, habitat, and dietary traits on these shifts.

Nearly half of all natal dispersal (48.7%) in kestrels was LDD (> 30 km), and the likelihood of LDD was positively associated with agriculture at natal sites. LDD distance was positively correlated with latitude, a proxy for migration strategy, indicating that migratory individuals disperse farther than residents. For male kestrels, LDD was positively associated with maximum summer temperature. Unlike previous studies of short-distance dispersal (SDD), we did not find female-bias in either LDD frequency or distance. Sampling affected frequency and magnitude of LDD, likely because local studies more frequently capture SDD within study areas.

In our study of breeding distributions, we found that 44% of regional shifts were equatorward, 55% were poleward, and several species shifted in different directions in different regions. We did not find any life history traits that explained southward shifts, but diet, migratory strategy, and tolerance to humans predicted northward shifts. Our results clearly indicate the prevalence of multidirectional breeding distribution shifts, and suggest that life history is one component in a likely complex set of interacting mechanisms acting at many scales to drive shifts.

Our results show that patterns of dispersal and distributions are complex, and shaped by interactions between environmental factors and life history. Our results that LDD frequency and distance are influenced by different intrinsic and proximate environmental factors from SDD suggest LDD and SDD may be distinct processes rather than originating from a single dispersal distribution. While the drivers of equatorward distribution shifts are still unclear, multidirectional shifts do not support the hypothesis that tracking climate warming is the primary driver of shifts, and investigation into drivers of equatorward shifts is necessary for understanding the heterogeneous effects of climate change on distributions. The feedback between dispersal and distributions is a critical piece of species' response to global change, and it is important we strive to

understand their causes and consequences to further develop our concept of adaptation and persistence in the current era.

TABLE OF CONTENTS

DEDICATION iv

ACKNOWLEDGEMENTS v

ABSTRACT vii

LIST OF TABLES xii

LIST OF FIGURES xviii

LIST OF ABBREVIATIONS xxi

INTRODUCTION 1

REFERENCES 4

LONG-DISTANCE NATAL DISPERSAL IS RELATIVELY FREQUENT AND CORRELATED WITH ENVIRONMENTAL FACTORS IN A WIDESPREAD RAPTOR 6

- Abstract 6
- Introduction 7
- Methods 11
- Results 16
- Discussion 18
- Acknowledgements 25

REFERENCES 26

SUPPLEMENTAL MATERIAL 41

- Additional Model Information and Diagnostics 50

Note on possible scenarios for the effects of landscape matrix on dispersal distribution....54

PATTERNS AND MECHANISMS OF HETEROGENEOUS BREEDING DISTRIBUTION SHIFTS IN NORTH AMERICAN MIGRATORY BIRDS....56

Abstract....56

Introduction....57

Methods....62

Results....69

Discussion....71

Acknowledgements....78

REFERENCES....79

Supplemental Material....104

CONCLUSION....122

REFERENCES....124

APPENDIX A....125

Model selection for Chapter 2 life history traits analysis....125

Model Selection Results....128

East Region....128

West Region....136

Central Region....144

LIST OF TABLES

Table 1.1. Summary of American kestrel natal dispersal studies conducted within study areas with nest boxes and this study based on banding and encounter data. In previous studies, the majority of kestrel individuals dispersed short distances, but these studies have limited potential to detect long-distance movements resulting in settlement outside of the study area. 34

Table S1.1 Correlation matrix for temperature variables across all months. We tested for correlations using Pearson correlation tests. Minimum and maximum temperature anomalies in May were correlated with each other ($r = 0.796$), but temperature anomalies were not correlated across months. 42

Table S1.2 Correlation matrix for all covariates used to model long-distance dispersal frequency and distance. We tested for correlations between variables using Pearson correlation tests. Percentage of agriculture metrics were weakly correlated with one another ($0.5 < r < 0.8$). No environmental correlates (temperature or agriculture metrics) were correlated with year. Who encountered a bird was somewhat correlated with whether the bird was encountered alive or dead ($r = 0.54$), so we did not include multiple sampling variables within a single model. 43

Table S1.3. Candidate models and model selection results using Log Pseudo Marginal Likelihoods (LPML) for logistic regression for the likelihood of long distance natal dispersal (> 30km) by American kestrels in North America based on banding and encounter data from 1960-2015. The model with the lowest LPML is considered the best fitting model. All models contain a spatial random effect, except for the model designated as *.nsp*. All models with a spatial random effect outperformed all other non-spatial models. .45

Table S1.4. Candidate models and model selection results for long-distance dispersal distance in American kestrels in the United States and Canada 1960-2015, with intrinsic and environmental covariates. The best fitting model is selected using the Expected Log Pointwise Posterior Density (ELPD). Comparing models with a spatial random effect using LPML indicated no spatial autocorrelation and spatial random effects were omitted from this model. 47

Table S1.5 Diagnostic statistics for top gamma regression model. Number of effective parameters is high for all parameters, and all Rhat values < 1.1, indicating model convergence. 51

Table 2.1. Summary of eastern region breeding distribution centroid abundance shift results, 1994-2017. Bold type indicates significant shift velocities, inferred by 95% of posterior samples positive (north shift) or negative (south shift). Population status was computed at the regional level by regressing the sum of all stratum abundance weights by year. (Increasing: 95% of posterior samples for regression slope > 0; decreasing: 95% of posterior samples < 0) 88

Table 2.2. Summary of western region breeding distribution centroid shift results, 1994-2017. Bold type indicates significant shift velocities, inferred by 95% of posterior samples positive (north shift) or negative (south shift). Population status was computed at the regional level by regressing the sum of all stratum abundance weights by year. (Increasing: 95% of posterior samples for regression slope > 0; decreasing: 95% of posterior samples < 0) 91

Table 2.3. Summary of central region breeding distribution centroid shift results, 1994-2017. Bold type indicates significant shift velocities, inferred by 95% of posterior samples positive (north shift) or negative (south shift). Population status was computed at the regional level by regressing the sum of all stratum abundance weights by year. (Increasing: 95% of posterior samples for regression slope > 0; decreasing: 95% of posterior samples < 0) 94

Table 2.4. Ninety-five percent (95%) credible intervals for breeding distribution centroid shift velocity (km per year) by regional population status for East, West, and Central regions from 1994-2017. Population status did not predict shift velocity, except in the east region, where species with no change or an increase in abundance index were slightly more likely than species with a decreasing population abundance to shift north. 97

Table S2.1. List of species for which we calculated breeding season abundance centroids to estimate shifts in distribution centroid from 1994-2017. Each species was analyzed in the region(s) listed (East, Central, West) and diet and habitat traits used to model distribution shifts were compiled from each species' Birds of North America Online account (Rodewald 2015, ed.). 104

Table S2.2. Species for which we estimated breeding distribution abundance centroid shifts from 1994-2017 and migratory traits used to model shifts in centroid abundance. Migratory traits were compiled from each species' Birds of North America Online account (Rodewald 2015, ed.). 114

Table A1.1 Model selection results for model set including migration type (Mig), habitat specialization (Hab), and human association (Human) in the east region, from leave-one-out cross validation and Bayesian model stacking (BMS) weights. All models include a random effect of taxonomic family. Models are in ordered most-supported to least-supported based on Expected Log Pointwise Posterior Density (ELPD) from LOO-CV, although model weights were also considered to determine most-supported model because LOO-CV can cause overfitting with small sample sizes. The models used to determine the most-supported model across the three hypotheses is indicated in bold. ………………………………………..128

Table A1.2 Model selection results for model set including primary diet type (Diet), foraging strategy (For), migration time (Time), and wintering latitude (Wint) in the east region, from leave-one-out cross validation and Bayesian model stacking (BMS) weights. All models include a random effect of taxonomic family. Models are in ordered most-supported to least-supported based on Expected Log Pointwise Posterior Density (ELPD) from LOO-CV, although model weights were also considered to determine most-supported model because LOO-CV can cause overfitting with small sample sizes. The models used to determine the most-supported model across the three hypotheses is indicated in bold………………………..130

Table A1.3 Model selection results for model set including migration distance (Dist1 with levels short, mid, long, very long; or Dist2 with levels short, long), whether breeding and wintering distributions (Overlap), whether species are territorial (Terr), presence of differential migration by sex (Sex), and migratory group size (Group) in the east region, from leave-one-out cross validation and Bayesian model stacking (BMS) weights. All models include a random effect of taxonomic family. Models are in ordered most-supported to least-supported based on Expected Log Pointwise Posterior Density (ELPD) from LOO-CV, although model weights were also considered to determine most-supported model because LOO-CV can cause overfitting with small sample sizes. The models used to determine the most-supported model across the three hypotheses is indicated in bold……………………………………………………………………..132

Table A1.4 Bayesian model stacking weights for single covariates in the east region, for each set of covariates corresponding to the three hypotheses: (A) migration type (Mig), habitat specialization (Hab), and human association (Human); (B) primary diet type (Diet), foraging strategy (For), migration time (Time), and wintering latitude (Wint); and (C) migration distance (Dist2), whether breeding and wintering distributions (Overlap), whether species are territorial (Terr), presence of differential migration by sex (Sex), and migratory group size (Group)..134

Table A1.5 Model selection results for model set including covariates from most-supported model from each single-hypothesis model set (Tables A1.1-3) and combinations of these covariates in the east region, from leave-one-out cross validation and Bayesian model stacking (BMS) weights. All models include a random effect of taxonomic family. Models are in ordered most-supported to least-supported based on Expected Log Pointwise Posterior Density (ELPD) from LOO-CV, although model weights were also considered to determine most-supported model because LOO-CV can cause overfitting with small sample sizes. The most-supported model used for inference is indicated in bold. 135

Table A1.6 Model selection results for model set including migration type (Mig), habitat specialization (Hab), and human association (Human) in the west region, from leave-one-out cross validation and Bayesian model stacking (BMS) weights. All models include a random effect of taxonomic family. Models are in ordered most-supported to least-supported based on Expected Log Pointwise Posterior Density (ELPD) from LOO-CV, although model weights were also considered to determine most-supported model because LOO-CV can cause overfitting with small sample sizes. The models used to determine the most-supported model across the three hypotheses is indicated in bold…………………………………………137

Table A1.7 Model selection results for model set including primary diet type (Diet), foraging strategy (For), migration time (Time), and wintering latitude (Wint) in the west region, from leave-one-out cross validation and Bayesian model stacking (BMS) weights. All models include a random effect of taxonomic family. Models are in ordered most-supported to least-supported based on Expected Log Pointwise Posterior Density (ELPD) from LOO-CV, although model weights were also considered to determine most-supported model because LOO-CV can cause overfitting with small sample sizes. The models used to determine the most-supported model across the three hypotheses is indicated in bold………………………..138

Table A1.8 Model selection results for model set including migration distance (Dist1 with levels short, mid, long, very long; or Dist2 with levels short, long), whether breeding and wintering distributions (Overlap), whether species are territorial (Terr), presence of differential migration by sex (Sex), and migratory group size (Group) in the west region, from leave-one-out cross validation and Bayesian model stacking (BMS) weights. All models include a random effect of taxonomic family. Models are in ordered most-supported to least-supported based on Expected Log Pointwise Posterior Density (ELPD) from LOO-CV, although model weights were also considered to determine most-supported model because LOO-CV can cause overfitting with small sample sizes. The models used to determine the most-supported model across the three hypotheses is indicated in bold……………………………………………………………………..140

Table A1.9 Bayesian model stacking weights for single covariates in the west region, for each set of covariates corresponding to the three hypotheses: (A) migration type (Mig), habitat specialization (Hab), and human association (Human); (B) primary diet type (Diet), foraging strategy (For), migration time (Time), and wintering latitude (Wint); and (C) migration distance (Dist2), whether breeding and wintering distributions (Overlap), whether species are territorial (Terr), presence of differential migration by sex (Sex), and migratory group size (Group)..142

Table A1.10 Model selection results for model set including covariates from most-supported model from each single-hypothesis model set (Tables A1.6-8) and combinations of these covariates in the west region, from leave-one-out cross validation and Bayesian model stacking (BMS) weights. All models include a random effect of taxonomic family. Models are in ordered most-supported to least-supported based on Expected Log Pointwise Posterior Density (ELPD) from LOO-CV, although model weights were also considered to determine most-supported model because LOO-CV can cause overfitting with small sample sizes. The most-supported model used for inference is indicated in bold. 143

Table A1.11 Model selection results for model set including migration type (Mig), habitat specialization (Hab), and human association (Human) in the central region, from leave-one-out cross validation and Bayesian model stacking (BMS) weights. All models include a random effect of taxonomic family. Models are in ordered most-supported to least-supported based on Expected Log Pointwise Posterior Density (ELPD) from LOO-CV, although model weights were also considered to determine most-supported model because LOO-CV can cause overfitting with small sample sizes. The models used to determine the most-supported model across the three hypotheses is indicated in bold…………………………………………145

Table A1.12 Model selection results for model set including primary diet type (Diet), foraging strategy (For), migration time (Time), and wintering latitude (Wint) in the central region, from leave-one-out cross validation and Bayesian model stacking (BMS) weights. All models include a random effect of taxonomic family. Models are in ordered most-supported to least-supported based on Expected Log Pointwise Posterior Density (ELPD) from LOO-CV, although model weights were also considered to determine most-supported model because LOO-CV can cause overfitting with small sample sizes. The models used to determine the most-supported model across the three hypotheses is indicated in bold………………………..146

Table A1.13 Model selection results for model set including migration distance (Dist1 with levels short, mid, long, very long; or Dist2 with levels short, long), whether breeding and wintering distributions (Overlap), whether species are territorial (Terr), presence of differential migration by sex (Sex), and migratory group size (Group) in the central region, from leave-one-out cross validation and Bayesian model stacking (BMS) weights. All models include a random effect of taxonomic family. Models are in ordered most-supported to least-supported based on Expected Log Pointwise Posterior Density (ELPD) from LOO-CV, although model weights were also considered to determine most-supported model because LOO-CV can cause overfitting with small sample sizes. The models used to determine the most-supported model across the three hypotheses is indicated in bold……………………………………………………………………..148

Table A1.14 Bayesian model stacking weights for single covariates in the central region, for each set of covariates corresponding to the three hypotheses: (A) migration type (Mig) and human association (Human); (B) primary diet type (Diet), foraging strategy (For), migration time (Time), and wintering latitude (Wint); and (C) migration distance (Dist2), whether breeding and wintering distributions (Overlap), whether species are territorial (Terr), presence of differential migration by sex (Sex), and migratory group size (Group). 150

Table A1.15 Model selection results for model set including covariates from most-supported model from each single-hypothesis model set (Tables A1.11-13) and combinations of these covariates in the central region, from leave-one-out cross validation and Bayesian model stacking (BMS) weights. All models include a random effect of taxonomic family. Models are in ordered most-supported to least-supported based on Expected Log Pointwise Posterior Density (ELPD) from LOO-CV, although model weights were also considered to determine most-supported model because LOO-CV can cause overfitting with small sample sizes. The most-supported model used for inference is indicated in bold. 151

LIST OF FIGURES

Figure 1.1. Frequency of natal dispersal distances of American kestrels from North American banding and encounter data, 1960-2015. Of 311 total individuals (161 F, 105 M, 45 unk), 152 (86 F, 49 M, 17 unk) dispersed a distance greater than 30 km, indicated by the dashed line........................35

Figure 1.2. Frequency of natal dispersal directions of American kestrels from North American banding and encounter data, 1960-2015. Length of bar corresponds to frequency of direction. Dispersal direction was not uniformly distributed across (A) all distances ($p < 0.001$), (C) short-distance ($p < 0.01$), or (D) long-distance ($p < 0.01$), but there was no difference between sexes ($p > 0.1$). There was no difference in dispersal direction between birds (B) encountered alive or dead ($p > 0.1$). 36

Figure 1.3A. Coefficient plot for predictors of long-distance dispersal frequency in American kestrels in the US and Canada from 1960-2015 from banding and encounter data. Dots are median parameter estimates and bars represent 95% credible intervals for parameter estimates. Percentage of agriculture at the banding site (Ag_B) is positively correlated with the likelihood of long-distance dispersal, and the positive effect of encounter condition ($Enc_{condition}$) indicates that birds encountered dead are more likely to be LDD and suggests an effect of sampling on dispersal tendency. Latitude had no effect on the likelihood of an individual being a long-distance disperser. 37

Figure 1.3B. Effect of the percentage of agriculture in natal territory on long-distance dispersal frequency in American kestrels in the US and Canada from 1960-2015 from banding and encounter data. The solid line shows mean effect of agriculture on frequency and dashed lines represent 95% credible intervals for parameter estimate. Percentage of agriculture at the banding site is positively correlated with the likelihood of long-distance dispersal. 38

Figure 1.4A. Coefficient plot of effects of covariates on LDD distance in American kestrels in the US and Canada 1960-2015 from banding and encounter data. Dots are median parameter estimates and bars represent 95% credible intervals for parameter estimates. Latitude is positively correlated with LDD distance, the difference between the percentage of agriculture at the encounter and banding sites (Ag_{Diff}) is negatively correlated with dispersal distance, and maximum August temperature is positively correlated with distance in males (Male x Temp_{Aug}) but not females (Female x Temp_{Aug}). The positive effect of encounter condition ($\text{Enc}_{\text{condition}}$) indicates that birds encountered dead have longer LDD than those encountered alive, suggesting an effect of sampling on distances observed. Year did not affect dispersal distance. 39

Figure 1.4B-C. Effects of latitude (B) and agriculture (C) on LDD distance in American kestrels in the US and Canada 1960-2015 from banding and encounter data. Solid lines are mean effect sizes and dashed lines represent 95% credible intervals for model predictions. Latitude is positively correlated with LDD distance, and the difference between the percentage of agriculture at the encounter and banding sites is negatively correlated with dispersal distance. 40

Figure S1.1. Frequency of long-distance (> 30 km) natal dispersal distances of American kestrels from North American banding and encounter data, 1960-2015. One hundred fifty-two individuals (86 F, 49 M, 17 unk) of 311 total individuals (48.7%) dispersed long-distance. 41

Figure S1.2 Spatial autocorrelation in frequency of long-distance dispersal. 50

Figure S1.3. Effect of space on likelihood of long-distance dispersal for American kestrel banding data. Areas of strong spatial effect tend to be near kestrel nest box study areas. 51

Figure S1.4 Markov chain Monte Carlo trace plots for post-warmup iterations for top LDD distance gamma regression model. For all parameters, chains appear well-blended. 53

Figure S1.5. Conceptual diagram illustrating the observed relationship between percentage of agriculture in the natal (N) and encounter (E) territories and LDD distance in American kestrels in the US and Canada, 1960-2015, from banding and encounter data, and potential mechanisms. In scenario 1, individuals (A) disperse a mid-distance to a similar landcover type, or (B) experience an area of much higher agricultural cover and do not continue to disperse farther. In scenario 2, individuals (D) disperse a mid-distance to a similar landcover type or (C) continue to disperse a greater distance and must stop due to an environmental or intrinsic threshold, despite not locating higher quality habitat. 55

Figure 2.1. (A) Conceptual diagram reprinted from Cox (1968), illustrating the influence of seasonality on the transition of a partial migrant to a migrant with disjunct breeding and wintering ranges. (B) Reversal of panel A, schematic illustrating how under current climate change, as seasonality becomes less pronounced throughout part of the temperate region (warming winter temperatures), Cox's theory can also explain a shift of a

migrant to a less migratory strategy via the shortening of the fall and spring legs of migration. 98

Figure 2.2. Map illustrating regions, strata, and centroids for 73 species and subspecies of North American migratory birds. Strata, outlined in black, are the intersections between Bird Conservation Region boundaries and state or province boundaries. Dots are regional species centroids in 1994 and color represents whether regional species abundance, estimated using a hierarchical model to account for stratum, route, and observer sampling bias, decreased (orange), increased (green), or did not change (yellow) from 1994-2017. Fifty-four regional species centroids shifted over the 23-year period, and black arrows illustrate the projected latitudinal shift of the species centroid, based on the average shift velocity (km per year) for the species over the 23 years. Note that these arrows do not illustrate longitudinal shift in centroid, which is outside the scope of this study.....99

Figure 2.3. Significant shifts in breeding distribution centroids for North American migratory bird species by region from 1994 – 2017. 100

Figure 2.4. Relationship between primary diet and species' breeding distribution shift velocities in the (A) western, (B) central, and (C) eastern regions from 1994-2017 based on predictions for simulated data from the posterior distributions of the best performing model for each region. Vertebrate-eating species shifted northward with average velocities of 2.5, 3.6 and 7.5 km per year in the west, central, and east regions respectively. Species with primarily invertebrate diets did not shift in either direction, and plant-eating species were slightly more likely to shift southward than northward. 101

Figure 2.5. Relationship between (A) presence of differential migration in the eastern region, (B) human tolerance, and (C) migratory strategy in the central region and species' breeding distribution shift velocities from 1994-2017 based on predictions for simulated data from the posterior distributions of the best performing model for each region. (A) In the eastern region, species with differential migration were slightly more likely to shift northward than those that do not display differential migration. (B) In the central region, species that are negatively affected by humans and those with positive associations with humans shifted northward over the 23-year period, while species that are not affected by humans showed a slight tendency to shift southward. (C) In the central region, partial migrants were more likely to shift northward and complete migrants were more likely to shift southward, although neither group shifted substantially in either direction..102

LIST OF ABBREVIATIONS

BSU	Boise State University
KM	Kilometer
C	Celsius
LDD	Long-distance dispersal
SDD	Short-distance dispersal
USGS	United States Geological Survey
BBL	Bird Banding Laboratory
NLCD	National Land Cover Database
MCMC	Markov Chain Monte Carlo
LOO-CV	Leave-one-out cross validation
SPDE	Spatial partial differential equation
INLA	Integrated nested Laplacian approximation
LPML	Log-pseudo marginal likelihood
CPO	Conditional predictive ordinate
CI	Credible interval
BBS	Breeding Bird Survey
BCR	Bird Conservation Region

INTRODUCTION

Dispersal occurs in nearly all organisms and is the primary mechanism of gene flow between populations (Clobert et al. 2001). Dispersal influences individual fitness and population genetic structuring and diversity, and is a key factor in determining distributions and species' abilities to adapt to global change (Hanski and Gilpin 1997, Kokko and López-Sepulchre 2006). Additionally, dispersal is determined by interactions between intrinsic and environmental factors and tends to be highly plastic in response to environmental conditions (Clobert et al. 2001). Therefore, it has both the potential to be strongly influenced by global change, and to significantly constrain or promote responses and adaptation (Kokko and López-Sepulchre 2006).

Global change, both in climate and land use, is having widespread effects on organisms in every region of the world, impacting phenology, distributions, and species interactions. Global average temperatures have increased 0.85 degrees C from 1880-2012 (IPCC 2014), and shifts in anthropogenic land use have urbanized or fragmented many natural or agricultural habitats. As a result, patterns of seasonality are shifting and animals are constantly experiencing novel environments. Warming temperatures have caused spring vegetation emergence to advance by an average of 2.5 days per decade, shifting spring phenology forward and evening it out across elevations (Körner and Basler 2010, Vitasse et al. 2018), with widespread ramifications for animals including advancing spring migration and laying dates in birds, calling and breeding activities in amphibians, and first appearance of butterflies (Parmesan 2006). Additionally, distributions across a wide range of animal species including arthropods, fish, birds, and mammals have shifted northward at an average of 16.9 km per decade and upslope at an average of 11 meters per decade, although within these groups, specific responses vary widely in direction and magnitude (Chen et al. 2011).

In migratory birds, climate change is causing shifts in both breeding and wintering distributions, but shifts in the two distributions may not follow the same pattern (Potvin et al 2016). In the Northern hemisphere, winter distributions of migratory bird species are consistently shifting poleward at rates of over 10 km per decade (La Sorte and Thompson 2007). On the other hand, breeding distribution responses to global change are more variable, and up to 40% of species distributions may be shifting towards the equator, despite most research being aimed at explaining northward shifts (Huang et al. 2017, Zuckerberg et al. 2009, VanDerWal et al. 2012). Because multidirectional shifts cannot entirely be explained by warming temperatures (Lenoir et al. 2010), the factors driving breeding distribution shifts are largely unresolved but likely reflect complex interactions between climate, land use change, and dispersal ability (Barbet-Massin et al. 2011).

The chapters in this thesis aim to investigate drivers of avian dispersal and distributions to further understand their interactions and how they may facilitate adaptation and responses to global change. The first chapter investigates the frequency and drivers of long-distance dispersal in American kestrels. While dispersal has received prolific research attention, LDD is typically viewed as a stochastic event occurring in the tail of a distribution centered on short-distance movements (Paradis 1998, Lowe and McPeek 2011). Given LDD’s potential importance for adaptation and shaping distributions, understanding its frequency and underlying mechanisms is critical for a complete picture of dispersal ecology. The second chapter describes breeding distributions shifts for a suite of migratory species in the era of anthropogenic climate change, and tests possible life history mechanisms underlying these shifts. This chapter introduces a hypothesis for a mechanism underlying southward shifts in breeding distributions considering interactions between migration and environment from an evolutionary perspective. The chapters in this thesis are written in the format of scientific papers for publishing in specific peer-reviewed journals: chapter one, “Long-distance dispersal is relatively frequent and correlated with environmental factors in a widespread raptor”, is formatted for submission to *Oikos* and chapter two, “Patterns and mechanisms of heterogenous breeding distribution shifts in North American migratory birds”, is written for submission to *Proceedings of the Royal Society B: Biological Sciences.* For the purposes of this thesis, coauthors of each are identified in the corresponding acknowledgements.

REFERENCES

Barbet-Massin, M., W. Thuiller, and F. Jiguet. 2011. The fate of European breeding birds under climate, land-use and dispersal scenarios. *Global Change Biology* 18:881-890.

Chen, I., J.K. Hill, R. Ohlemüller, D.B. Roy, and C.D. Thomas. 2011. Rapid range shifts of species associated with high levels of climate warming. *Science* 333:1024-1026.

Clobert, J., E. Danchin, A. A. Dhondt, and J.D. Nichols, *eds.* 2001. *Dispersal.* Oxford University Press, Oxford, UK.

Hanski, I. and M. E. Gilpin, *eds*. 1997. *Metapopulation biology: ecology, genetics, and evolution.* Academic Press, San Diego, CA.

Huang, Q., J. R. Sauer, R. O. Dubayah. 2017. Multidirectional abundance shifts among North American birds and the relative influence of multifaceted climate factors. *Global Change Biology* 23: 3610-3622.

Intergovernmental Panel on Climate Change. 2014. *Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* [Core Writing Team, R.K. Pachauri and L.A. Meyer (eds.)]. IPCC, Geneva, Switzerland, 151 pp.

Kokko, H. and A. López-Sepulchre. 2006. From individual dispersal to species ranges: perspectives for a changing world. *Science* 313: 789-791.

Körner, C. and D. Basler. 2010. Phenology under global warming. *Science* 327: 1461-1642.

La Sorte, F. A. and F. R. Thompson. 2007. Poleward shifts in winter ranges of North American birds. *Ecology* 88: 1803-1812.

Lenoir, J., J-.C. Gégout, A. Guisan, P. Vittoz, T. Wohlgemuth, N.E. Zimmerman, S. Dullinger, H. Pauli, W. Willner, and J-.C. Svenning. 2010. Going against the flow: potential mechanisms for unexpected downslope range shifts in a warming climate. *Ecography* 33:295-303.

Lowe, W. H. and M. A. McPeek. 2011. Can natural selection maintain long-distance dispersal? Insight from a stream salamander population. *Evolutionary Ecology* 26: 11-24.

Paradis, E., S. R. Baillie, W. J. Sutherland, and R. D. Gregory. 1998. Patterns of natal and breeding dispersal in birds. *Journal of Animal Ecology* 67: 518-536.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics* 37: 637-669.

Potvin, D. A., K. Välimäki, and A. Lehikoinen. 2016. Differences in shifts of wintering and breeding ranges lead to changing migration distances in European birds. *Journal of Avian Biology* 47: 619-628.

VanDerWal, J., H.T. Murphy, A.S. Kutt, G.C. Perkins, B.L. Bateman, J.J. Perry, and A.E. Reside. 2012. Focus on poleward shifts in species' distribution underestimates the fingerprint of climate change. *Nature Climate Change* 3: 239-243.

Vitasse, Y., C. Signarbieux, and Y.H. Fu. 2018. Global warming leads to more uniform spring phenology across elevations. *Proceedings of the National Academy of Sciences* 115: 1004-1008.

Zuckerberg, B., A. M. Woods, and W. F. Porter. 2009. Poleward shifts in breeding bird distributions in New York State. *Global Change Biology* 15: 1866-83.

LONG-DISTANCE NATAL DISPERSAL IS RELATIVELY FREQUENT AND CORRELATED WITH ENVIRONMENTAL FACTORS IN A WIDESPREAD RAPTOR

Abstract

Dispersal is a critical process influencing population dynamics, and long-distance dispersal (LDD) can be especially important for gene flow and adaptability. However, little is known about the mechanisms of LDD because of the challenges of studying large-scale animal movements. We studied correlates of natal LDD using North American bird banding data for American kestrels (*Falco sparverius*) from 1960-2015. We used Bayesian hierarchical and spatial models to investigate temporal trends and the effects of sex, migration strategy, weather, and landcover type on LDD frequency and distance and understand potential sampling bias. Nearly half of all natal dispersal (48.7%) was LDD (> 30km), and the likelihood of LDD was positively associated with agricultural landcover at natal sites. LDD distance was positively correlated with latitude (*median effect 1.08, 95% CI 1.04-1.11*), a proxy for migration strategy, indicating that migratory individuals disperse farther than residents. For male kestrels, LDD was positively associated with maximum summer temperature (*median effect 1.37, 95% CI 1.17-1.59*). Unlike previous studies of short-distance dispersal (SDD), we did not find sex-bias in dispersal distance or frequency. However, in warm summers males but not females tended to disperse farther than in other years. Sampling affected frequency and magnitude of LDD, likely because local studies more frequently capture short-distance

dispersal within study areas. We suggest that LDD and SDD may be distinct processes rather than two outcomes originating from a single dispersal distribution. Long-distance dispersal and SDD have different ultimate effects, and the results presented here suggest that LDD frequency and distance are influenced by different proximate intrinsic and environmental factors compared to SDD.

Introduction

Dispersal occurs in nearly all organisms and is the primary mechanism of gene migration between populations (Clobert et al. 2001). Dispersal influences individual fitness, population genetic structuring and diversity, and is a key factor in species' abilities to adapt to global change (Hanski and Gilpin 1997, Kokko and López-Sepulchre 2006). Thus, understanding how individuals integrate and respond to the intrinsic and environmental factors underlying dispersal is important for understanding population dynamics and potential species' responses to global change.

Natal dispersal, defined as the movement between natal area and the area where first breeding takes place (Clobert et al. 2001), is common and tends to occur over greater distances than dispersal between breeding locations by adults (Greenwood and Harvey 1982). The majority of natal dispersal movements occur at relatively short distances with some movements reaching longer distances, so that the distributions of natal dispersal tend to be right-skewed and heavier-tailed than normal distributions (Nathan 2006). Long-distance dispersal (LDD) movements are often viewed as stochastic outliers (Nathan 2006) and this, coupled with the logistical challenges of studying long-distance animal movements (Koenig et al. 1996), has led most animal dispersal studies to occur at scales smaller than the full dispersal distribution. However, small-scale studies can result in biases towards short-distance dispersal (SDD) movements and often underestimate or fail to detect LDD (Morton et al. 2018). Bias towards SDD events may lead to a poor understanding of the causes and consequences of natal dispersal. For example, compared to SDD, LDD can have disproportionate effects on gene flow, connectivity, and species persistence (Goldwasser et al. 1994, Tittler et al. 2006). It is also unclear whether the ultimate causes of dispersal, inbreeding avoidance and competition for food or breeding resources (Bowler and Benton 2005, Clobert et al. 2001), affect SDD and LDD equally. Therefore, a better understanding of the frequency and drivers of LDD is needed, along with whether proximate causes of LDD may differ from short-distance dispersal.

Intrinsic factors influence animal dispersal patterns within and among taxa, affecting both tendency and magnitude of dispersal movements (Clobert et al. 2012). In a meta-analysis of 145 terrestrial bird and mammal species, Sutherland et al. (2000) found that body size and diet type are important correlates of natal dispersal distance across taxa. Additionally, sex-biased dispersal is common in animals, with males dispersing farther than females in many mammal species and females dispersing farther than males in most bird species (Greenwood 1980). Dispersal distance is also correlated with migratory strategy. For example, within a single population of song sparrows (*Melospiza melodia*), migration and dispersal distances were positively correlated (Kelly et al. 2016), and across species, migratory songbirds tend to disperse farther than non-migratory species (Paradis et al. 1998).

Environmental factors throughout the annual cycle also can influence dispersal distances and rates, directly by affecting landscape permeability and the energetic costs of movement, and indirectly by influencing body condition and population structure that affects density-dependent dispersal. A study of genetic structuring in grand skinks (*Oligosoma grande*) found that habitat type and patchiness influenced dispersal rate, likely because some matrix vegetation acted as greater movement barriers than others (Berry et al. 2005). In common buzzards (*Buteo buteo*), warmer temperatures during the post-fledging period in late summer and early fall are associated with greater natal dispersal distances, perhaps because warm temperatures create favorable conditions for soaring and flight dynamics (Walls et al. 2005). Similarly, natal dispersal distance in arctic terns (*Sterna paradisaea*) is positively correlated with temperatures during dispersal, but also with temperatures in the prior breeding season, suggesting that both direct temperature effects on movement and indirect temperature effects on maternal care and provisioning influence dispersal (Møller et al. 2006). In contrast, in stream salamanders (*Gyrinophilus porphyriticus*), LDD frequency increased during periods of low habitat quality when body condition was lower than when LDD was less frequent (Lowe 2009). Environmental conditions interact with density-dependence to influence dispersal in white-throated dippers (*Cinclus cinclus*), because warm winters increase overwintering survival and conspecific densities leading to a higher rate of LDD (Sæther et al. 2000). Similarly, in house sparrows (*Passer domesticus*), dispersal rate increases with spring temperature and population size in low quality but not high quality habitats, suggesting that low quality habitats cannot support high population densities, causing higher dispersal rates (Pärn and Sæther 2012).

The American kestrel (*Falco sparverius*) is a widespread species that breeds throughout Canada and the United States, and populations display continuous variation in migratory strategies along a latitudinal cline, from fully resident southern populations to fully migratory northern populations (Smallwood and Bird 2002, Smallwood et al. 2009a). Recent genetic work on kestrels suggests that migratory strategy and dispersal tendency may be correlated, because populations in which most individuals migrate display less genetic structuring than populations with fewer migrants, indicating more dispersal-mediated mixing between these populations (Miller et al. 2012). Kestrels frequently select nesting sites in agricultural areas, which often have high prey abundance and are open landscapes for foraging, and agriculture is associated with high reproductive rates in kestrels, suggesting that agriculture may be high quality habitat for kestrels (Shave and Lindell 2017, Smallwood 1987, Smallwood et al. 2009b).

For several decades, American kestrels have been captured and marked via nest box projects and numerous studies have addressed short-distance kestrel dispersal within project areas (Table 1). These studies show kestrels display female-biased dispersal, and females may disperse nearly twice as far as males (Smallwood and Bird 2002, Steenhof and Heath 2013). However, studies of kestrel dispersal (Steenhof and Heath 2013) and demography (Brown and Collopy 2013, McClure et al 2018, *in review*) suggest extensive external recruitment and indicate that long-distance dispersal contributes to stable populations, perhaps to a greater extent in more migratory populations (Miller and Smallwood 1997). However, given the limitations of local nest box studies, the frequency and magnitude of LDD in kestrel populations are unknown.

Our objective was to describe long distance dispersal frequency, distance, and direction and examine possible correlates of frequency and distance to investigate the mechanisms underlying dispersal in American kestrels. We hypothesized that long-distance natal dispersal frequency and distance in kestrels could be explained by a combination of intrinsic and environmental factors. We predicted that frequency and distance of long-distance dispersal would be female-biased, and migratory individuals would disperse farther than non-migratory individuals. Also, we predicted that temperatures during key phases of the annual cycle would correlate with dispersal distance, specifically that maximum temperatures during hatching and post-fledging exploration would be positively correlated with distance if nestling physical condition affects dispersal distance, and if dispersal occurs during the exploratory post-fledging phase, respectively, and that minimum temperatures during either winter or nest establishment would be negatively correlated with dispersal distance if migration and dispersal distance phenotypes are correlated or if natal dispersal occurs in the spring following birds' first winter. We expected that percentage of agriculture would be negatively correlated with dispersal distance, because agriculture may be high quality habitat for kestrels, and that temperature and agricultural changes over time would lead to temporal trends in dispersal distance. Finally, we expected that migratory strategy and temperature would interact to cause individuals from higher latitudes to increase dispersal distance more over time than those at lower latitudes.

Methods

We obtained band and encounter data from the U.S. Geological Survey's Bird Banding Laboratory (BBL) for all kestrels banded in the United States or Canada from 1960 – 2017. As of 11 May 2017, 329,987 kestrels were reported banded during this timeframe, and 5,329 (1.6%) of those birds were subsequently encountered (alive or dead) and reported by scientists or the public. We defined natal dispersers as "local" (nestling) or "hatch year" birds banded during the breeding season (1 April – 15 August) and encountered during the breeding season one year later. We assumed that birds encountered during this period were within their breeding territory because kestrels can breed in their second year (Steenhof and Heath 2009). We removed all birds with any of the following in either the banding or encounter record: missing latitude or longitude, precision below the 10-minute block level, evidence of transport by humans (i.e. “transported”, “rehabbed”), or a recovery code indicating a long delay between death and discovery. We removed nine records from Alaska that were spatially disjunct from the rest of our study area. We included one banding record from Florida that may be an individual of subspecies *F. s. paulus* because dispersal distance of this bird fit within the statistical distribution of distance.

We used the sex and year reported with the banding record in all analyses. We used natal latitude as a proxy for migration strategy because more northern individuals migrate farther than more southern individuals (Heath et al. 2012). We calculated natal dispersal distance and direction from latitude and longitude with the package ‘geosphere’ (Hijmans 2016a) in the R programming language, version 3.4.1 (R Core Team 2017). We classified movements greater than 30 km as LDD because the maximum dispersal distance of philopatric kestrels is ~ 25 km (Shields 1982) and to be conservative with our designation of long-distance movements.

We used maximum and minimum temperature anomalies during different parts of the annual cycle to predict LDD frequency and distance. We included maximum temperatures from May and August when kestrels are provisioned by their parents and making post-fledging exploratory movements, respectively. We included minimum monthly temperatures from May, because cold springs can delay food availability;

January, because winter severity can affect migration distance; and March, to test if cold temperatures during spring migration influence dispersal. We used Berkeley Earth gridded 1°x 1° resolution modeled monthly temperature anomalies from a baseline period 1951-1980 and extracted values at the location and year of banding for all temperature variables (Berkeley Earth 2017). We tested the effect of agricultural land cover on dispersal using the percentage of agricultural land cover at the banding site, at the encounter site, and in the matrix between the banding and encounter site using average percentage between the sites and the difference in percentages between the sites. We calculated percentage of agricultural cover using the National Land Cover Databases (NLCD, Vogelmann et al. 2001, Homer et al. 2007, Fry et al. 2011, Homer et al. 2015) at 30m x 30m resolution with R packages ‘raster’ and ‘rgdal’ (Hijmans 2016b, Bivand et al. 2017). We considered all classifications in the “Planted/Cultivated” categories to be agricultural and all other classifications non-agricultural. Some areas utilized for grazing were not considered agricultural because unmanaged grasslands used for grazing and natural, un-grazed grasslands are designated as the same cover type in the NLCD classification system and aren’t distinguishable from one another (Homer et al. 2015). We computed percentage of agriculture in four square kilometer areas, corresponding to typical kestrel home range size (Bird and Palmer 1988). NLCD classifications exist for four discrete time periods (1992, 2001, 2006, 2011), so we used the database closest to the year of each banding record to assign values. For banding records in Canada (n = 26), we assigned period-appropriate median values for all land cover variables because the NLCD does not cover this region and so that we could use these records in analyses, and verified that this did not affect parameter estimates by running models with agriculture predictors with and without the Canadian records.

We described the distribution of dispersal distances using wind rose diagrams and tested for uniformity of dispersal direction for SDD-only, LDD-only, and all distances combined using Rao spacing tests, and for differences in direction between males and females and between birds encountered alive and dead using Watson two sample tests for homogeneity in the 'circular' package in R (Jammalamadaka and SenGupta 2001, Lund and Agostinelli 2007).

We modeled the relationship between intrinsic and environmental factors and natal dispersal using a hurdle model structure (Eq. 1.1) and Bayesian regression in R with Stan via rstan and rstanarm (Carpenter et al. 2017, Stan Development Team 2017).

$$dist_{LDD} \sim \begin{cases} 0 \; if \; LDD = 0 \\ \text{Gamma}\left(\alpha, \frac{\alpha}{\mu}\right) \; if \; LDD = 1 \end{cases} \quad (1.1)$$

$$LDD \sim \text{Bernoulli}(p) \quad (1.2)$$

$$p_i = \text{logit}^{-1}(a_0 + A_1 + A_2 + \cdots + A_j + S_a) \; (1.3)$$

$$\mu_i = \exp(b_0 + B_1 + B_2 + \cdots + B_k + S_b) \; (1.4)$$

We estimated the frequency of LDD by modeling the binomial outcome of short- or long-distance disperser (Eq. 1.2) with biological predictors sex, latitude, percent of agricultural land cover at the natal location, and banding year ($A_{1,\ldots,j}$, Table S1.3) and included a variable (S_a) to account for possible sampling bias (Eq. 1.3). We ran models for four MCMC chains with 1000 iterations per chain (plus 1000 iterations burn-in), and used weakly informative, normally distributed priors with mean 0 for all parameters. We diagnosed Markov Chain convergence using R-hat < 1.1 and by visually checking chain blending. We tested for correlation between covariates using Pearson correlation tests to ensure that variables appearing together in models were not correlated (Tables S1.1, S1.2).

We modeled the dispersal distance of LDD individuals with a gamma distribution and fit Bayesian generalized linear models with the predictors. We included sex, latitude, temperature, percentage agriculture at the encounter location, percentage agriculture in the matrix between banding and encounter locations, banding year (B_{1-k}), and interactions sex*latitude, sex*temperature, sex*agriculture, and latitude*year, and included a sampling term (S_b) in models (Table S1.4, Eq. 1.4). We selected best models using efficient approximate leave-one-out cross validation (LOO-CV) with the R package loo (Vehtari et al. 2018).

We expected that the chance nature of band encounters, differences in the types of encounters reported by researchers and the public, and inconsistencies in encounter location reporting would influence the distributions of dispersal distance, so we included variables to account for sampling bias in our analysis. The sampling variables used were encounter condition (alive or dead) and who reported an encounter (researcher or public). We did not use more than one sampling variable per model because sampling variables were correlated with each other (Table S1.2). The BBL historically maintained data with the spatial precision of a ten-minute block of latitude and longitude and began accepting and saving records at this precision, one-minute block precision, or exact precision in the early 2000s. We ran all analyses at both the reported precision (exact, one-minute block, ten-minute block) and at the ten-minute block precision for all records to check that differences in precision between records did not cause bias in calculated distances. We used the original precision for each model in final models because running models at the ten-minute block precision did not influence model results.

We ran the most supported model for LDD frequency and the top model for LDD distance with the banding location as a spatial random effect using a stochastic partial differential equation (SPDE) approach in the R package INLA (Rue et al. 2009, Lindgren and Rue 2015) to test for spatial autocorrelation. We compared INLA models with and without the spatial random effect using the log pseudo-marginal likelihood (LPML), which is the sum of the log conditional predictive ordinates (CPO) to determine if spatial autocorrelation was present (Lindgren et al. 2011). If spatial autocorrelation was indicated, we re-ran the full set of possible covariates for that response with and without a spatial random effect with SPDE in INLA and used LPML to select the best model. If spatial autocorrelation was not present in the response, we used the best supported Stan model for inference.

Results

Our final dataset included banding and encounter records for 311 individuals (161 female, 105 male, 45 sex unknown) banded between 1960 and 2015. Median dispersal distance for all individuals was 28.2 km and within the categories SDD and LDD median distances were 16.4 km and 87.4 km, respectively (Fig. 1.1). Long-distance dispersal made up 48.9% of dispersal movements (86 female, 49 male, 17 sex unknown). Dispersal direction was not uniformly distributed for all individuals ($p < 0.001$), SDD-only ($p < 0.01$), or LDD-only ($p < 0.01$). Short-distance dispersal movements occurred more frequently in east and west directions, and LDD tended to be in southward directions

(Fig. 1.2). Dispersal directions did not differ significantly between males and females ($p > 0.1$) or alive and dead encounters ($p > 0.1$).

Occurrence of long-distance dispersal was best predicted by the percentage of agricultural coverage at the natal site, encounter condition, and a spatial random effect of banding location (Table 1.2). Percentage of agriculture was positively correlated with the likelihood of being a long-distance disperser, with a mean effect of a 1% increase in likelihood of LDD from the first to the third quartile of agricultural cover. The likelihood of an individual being a long-distance disperser increased slightly (*95% credible interval 0.8% - 2.5%*) if the bird was encountered dead, suggesting an effect of encounter sampling on patterns in the data. Banding latitude appeared in the most supported model but the 95% credible interval for the parameter crossed zero indicating that the effect was unreliable (Fig. 1.3). Occurrence of SDD was spatially autocorrelated in areas surrounding nest box study areas, indicating that short-distance dispersers are more frequently encountered in these areas, likely because of sampling in study areas (Supplemental Material).

The most supported model for LDD distance contained an interaction of sex and maximum August temperature, banding latitude, banding year, and agriculture in the matrix between sites. For long-distance dispersers, maximum August temperature was positively correlated with dispersal distance in males (*median effect size = 1.37, 95% credible interval 1.17-1.59,* Fig 1.4), but in females there was no relationship between dispersal distance and maximum August temperature. Latitude had a positive effect on LDD distance (*median effect size = 1.08, 95% CI 1.04-1.11*), suggesting that birds from higher latitudes disperse about one kilometer farther per degree latitude than birds from lower latitudes, and because fully migratory and resident populations are separated by approximately 10 degrees latitude, individuals from migratory populations may disperse up to 10 km farther than those from resident populations (Fig. 1.4). The difference in percentage of agriculture between the encounter and banding locations was negatively correlated with distance. Thus, individuals dispersing the shortest distances were moving from relatively lower to higher percentage agriculture, those dispersing mid distances were moving between relatively similar percentages of agriculture, and those dispersing the greatest distances were moving from relatively higher to lower percentage agriculture (Fig. S1.5). Year appeared as a covariate in the best fitting model, but did not have an effect because the parameter estimate was 0 (*95% CI -0.008 – 0.009)*. Encounter condition was an important variable for LDD distance. The probability of encountering a long-distance disperser dead rather than alive increased with distance from banding site (*median effect = 1.45, 95% CI 1.13 – 1.83*). There was no evidence of spatial autocorrelation in LDD distance.

Discussion

We studied long-distance natal dispersal in American kestrels over a large spatiotemporal scale using bird banding and encounter records. Our continental-scale approach indicates a higher frequency of LDD than previously reported using local-scale nest box studies of kestrel dispersal. The percentage of agricultural cover affected the frequency of LDD, suggesting that landcover type around the natal site influences post-fledging movement. Additionally, we found that the latitude of the natal site and the temperature during late summer affected the distance of LDD movements, indicating that LDD is affected by both intrinsic and environmental factors. However, we did not find sex-bias in either LDD frequency or distance as reported in intensive studies of SDD. Together, these results suggest that the same factors do not predict both LDD frequency and distance in kestrels, and that LDD is not driven by the same cues underlying SDD. This study provides evidence that short- and long-distance dispersal are distinct processes in kestrels and that LDD cannot be summarized as extreme events occurring in the tail of a single, mostly short-distance, dispersal distribution.

Long-distance movements made up nearly half of all natal dispersal movements within banding records. The relatively high frequency of LDD is supported by demographic studies that report a high proportion of immigration into study populations (Steenhof and Heath 2013, Brown and Collopy 2013, McClure et al *in review*) and analyses that show relatively low genetic structure in American kestrels even with the use of high-resolution approaches (Brinkmeyer 2018). We found no other studies comparing relative frequencies of short- and long-distance dispersal, and although large-scale banding data may overestimate the frequency of LDD because banders do not always report encounters of their own bands within the same ten-minute block, previous studies have shown that observed patterns of dispersal are scale dependent (Morton et al. 2018) and that local studies of avian dispersal can yield dispersal distances an order of magnitude smaller than those observed via other methods (Tittler et al. 2009). Thus, it is important to recognize that the true frequency of LDD probably lies somewhere between what has been reported via nest box studies and what is found across a large scale, and as our ability to track animals over large distances continues to improve and increases the possible scale of observation, we expect that empirical studies of dispersal may begin to detect higher frequencies of LDD.

The percentage of agriculture in the natal site positively affected an individual's likelihood of being a long-distance disperser. This could be because agricultural landcover is associated with high prey abundance and open landscapes for foraging (Smallwood et al. 2009b, Smallwood 1987), so nestlings were well-provisioned and capable of moving longer distances after fledging. This is similar to the relationship observed between body condition and dispersal distance in Spanish imperial eagles (*Aquila adalberti*, Ferrer 1993) and eagle owls (*Bubo bubo*, Delgado et al. 2010), in which better nourished juveniles dispersed earlier and moved farther than poorly fed juveniles. Additionally, because there is evidence that dispersal distance is correlated with parental dispersal distance in kestrels (Steenhof and Heath 2013), this pattern could arise because parents with greater dispersal ability select higher quality habitat than kestrels that disperse shorter distances.

We found a positive relationship between August temperature and dispersal distance in male kestrels, suggesting that environmental conditions during the post-fledging exploratory period in late summer are important for driving LDD. This result supports other studies that have found natal dispersal in raptors occurs during this period, when juvenile birds explore the area surrounding their natal site prior to settlement or fall migration (Walls and Kenward 1995, Soutullo et al. 2006). This relationship between temperature and dispersal could arise because individuals are responding to proximate environmental cues during dispersal movements, or because warmer temperatures create more favorable conditions for flight and allow for efficient long-distance movements. Walls et al. (2005) found that temperatures and wind directions during this time were strongly correlated with the onset and distance of dispersal in common buzzards, with southward winds predicting dispersal movements and dispersal distance positively correlated with winds to the west. We also found a southward trend in LDD movements, and a similar pattern has been found in Eurasian eagle owls, in which the majority of individuals dispersed in the west-southwest direction throughout the exploratory phase following fledging, apparently influenced by wind directions (Delgado et al. 2010). We did not find similar trends in SDD orientation, perhaps because either short- and long-distance dispersers are not dispersing simultaneously and therefore subject to different wind, or are the result of different phenotypes responding differently to proximate environmental cues.

The effect of sex depended on August maximum temperature, with differences between sexes only occurring at higher temperatures when males dispersed farther than females. This may be because warmer temperatures reduce the costs of LDD to a greater extent in males, either directly by allowing smaller-bodied individuals to more efficiently move greater distances because kestrels are sexually dimorphic and males are smaller than females (Smallwood and Bird 2002), or indirectly by influencing young males' ability to acquire a territory (Perrin and Mazalov 1999). It has been well-documented that female kestrels disperse farther than males in short distance dispersal studies (Steenhof and Heath 2013, Jacobs 1995, Smallwood and Bird 2002), and our finding that LDD does not appear female-biased suggests that SDD and LDD may be influenced by different mechanisms. Inbreeding avoidance is typically cited as the primary driver of sex-biased dispersal in vertebrates, with the mechanism being that if one sex regularly disperses farther than the other, siblings will not interbreed (Bowler and Benton 2005). Because we did not find sex-biased dispersal in kestrels at a large scale, independent of temperature effects, it is possible that inbreeding avoidance is not the ultimate cause of LDD in kestrels, and LDD may instead be driven by density-related factors. In American searocket (*Cakile edentula*), the density of individual plants in the maternal environment interacts with maternal phenotype and affects the phenotype of the fruits produced, subsequently affecting dispersal distance of progeny (Donohue 1998). If SDD and LDD are driven by different ultimate factors, there may also be distinct dispersal phenotypes in kestrels, similar to differences in behavioral boldness between 'movers' and 'stayers' in killifish (*Rivulus hartii*, Fraser et al. 2001) and phenotypic differences between dispersers and residents within several other vertebrate species (Clobert et al. 2009).

Long-distance dispersal was longer but not more frequent at higher latitudes. Therefore, long-distance dispersers from more migratory populations dispersed greater distances than those from less-migratory or resident populations, but LDD was maintained at similar frequencies in populations regardless of spatial location. This is consistent with Sutherland et al. (2000) who found that among species, migratory strategy is correlated with maximum dispersal distance but not median distance, which is determined by relative frequencies of SDD and LDD, and with studies that have found correlation between migration distance and dispersal distance in song sparrows (Kelly et al. 2016). Thus, there may be spatial variation in ability to adapt to global change if the ability to move long distances is important for adaptation, as suggested by Barbet-Massin et al. (2011) who showed that predicted future breeding range for several European bird species under predicted climate change is strongly influenced by mean natal dispersal distance. Lowe (2010) suggested that LDD is likely maintained at a certain frequency within populations of stream salamanders because LDD has predictable benefits for individual fitness and there is likely selection for phenotypes allowing for LDD, because survival and growth rate increased with dispersal distance independent of starting body condition.

We found that LDD was shortest for individuals moving from low to relatively higher percentage of agricultural cover, in which case landcover variability around the natal site was high and allowed individuals to locate areas likely to have high quality foraging at relatively short distances within the matrix. Individuals that dispersed to areas of similar extent of agriculture relative to their natal site dispersed farther, in agreement with theory that predicts that dispersal distance should increase as spatial variation in habitat quality decreases because individuals must move farther to find substantially higher quality habitat (Lowe 2009). We found that individuals dispersing from relatively high to relatively low percentage of agriculture moved the greatest distances, which is not explained by theory, but could be due to these individuals searching for better quality habitat and ultimately reaching a threshold associated with the energetic costs of dispersal that forces them to accept lower quality habitat (Bonte et al 2012).

Encounter condition affected both frequency and distance of LDD, with individuals encountered dead more likely to be long-distance dispersers and dispersing greater distances. The higher frequency of live recaptures occurring at short distances occurs because birds that disperse short distances may remain within study areas where there is effort to capture and band birds so they are more likely to be recaptured alive in a nest box than those who disperse out of study areas. Additionally, the uneven spatial distribution of nest box studies increases the likelihood of capturing SDD in these areas, but because long-distance movements exceed the size of study areas, observed distances are not affected by their distribution, which is likely the reason that frequency of LDD was spatially autocorrelated while LDD distance was not. Similar sampling effects have been found in previous studies using bird banding data to infer movement patterns (Thorup et al. 2014; Royle and Dubovsky 2001). Paradis et al. (1998) demonstrated the potential for bird banding data to be applied over large scales to study avian dispersal, but heterogeneity of encounter probability is a concern with using banding data in large-scale studies (van Noordwijk 1995; Thorup et al. 2014). While existing banding data is a cost-effective and powerful tool, it is important that future work with these data incorporate models that can account for this heterogeneity, and it would be worthwhile to collect small-scale data on encounter probability with future bird banding analyses to parameterize models.

We found a high frequency of LDD and a response of LDD to intrinsic and environmental factors that together suggest that long-distance dispersal in American kestrels is a distinct process from short-distance dispersal. We illustrate that studies at different scales capture different frequencies of LDD in kestrels and show that dispersal mechanisms vary between LDD and SDD. To our knowledge, this is the first evidence that long-distance and short-distance dispersal are different phenotypes in an avian species, and highlights the need for more research designed with long-distance movements in mind, to improve our understanding of the frequency of LDD and the drivers and dynamics of dispersal overall. Because LDD ability is an important factor for adaptation to global change (Barbet-Massin et al. 2011) via connecting populations and increasing gene flow (Greenwood 1980), it is plausible that LDD becomes more frequent with selective pressure for individuals to move greater distances (Kokko and López-

Sepulchre 2006; Lowe and McPeek 2012). Thus, it is important that ecologists conducting field studies more widely adopt the perspective of long-distance dispersal as a phenotypic process distinct from short-distance dispersal. Given the potential implications of long-distance dispersal on population dynamics, it is important we strive to better understand its causes and consequences to further develop our concept of adaptation and response to global change.

Acknowledgements

We thank the Bird Banding Laboratory staff at the USGS Patuxent Wildlife Research Center for maintaining and coordinating bird banding data. We are also grateful to researchers and members of the public who have contributed to BBL data by banding or reporting band encounters. This work was supported by the Michael W. Butler Ecological Research Award, the Department of Biological Sciences and Raptor Research Center at Boise State University, and the Department of Defense Strategic Environmental Research and Development Program (RC 2702). Coauthors on this manuscript are Trevor Caughlin and Julie Heath of Boise State University.

REFERENCES

Barbet-Massin, M., W. Thuiller, and F. Jiguet. 2011. The fate of European breeding birds under climate, land-use and dispersal scenarios. *Global Change Biology* doi: 10.1111/j.1365-2486.2011.02552.x

Berkeley Earth. 2017. Gridded Data: Monthly Land (1833 – Recent). Berkeley Earth, http://berkeleyearth.lbl.gov/auto/Global/Gridded/Gridded_README.txt.

Berry, O., M. D. Tocher, D. M. Gleeson, and S. D. Sarre. 2005. Effect of vegetation matrix on animal dispersal: genetic evidence from a study of endangered skinks. *Conservation Biology* 19: 855-864.

Bird, D. M. and R. S. Palmer. 1988. American Kestrel. *Handbook of North American birds* 5: 253-290. Yale University Press, New Haven, CT.

Bivand, R. T. Keitt, and B. Rowlingson. 2017. rgdal: Bindings for the Geospatial Data Abstraction Library. R package version 1.2-8. https://CRAN.R-project.org/package=rgdal

Bonte, D., H. Van Dyck, J. M. Bullock, A. Coulon, M. Delgado, M. Gibbs, V. Lehouck, E. Matthysen, K. Mustin, M. Saastamoinen, N. Sctickzelle, V. M. Stevens, S. Vandewoestijne, M. Baguette, K. Barton, T. G. Benton, A Chaput-Bardy, J. Clobert, C. Dytham, T. Hovestadt, C. M. Meier, S. C. F. Palmer, C. Turlure, and J. M. J. Travis. 2012. Costs of Dispersal. *Biological Reviews* 87: 290-312.

Bowler, D. E. and T. G. Benton. 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biological Reviews* 80: 205-225.

Brinkmeyer, M. 2018. Patterns of genetic structure in the American kestrel (*Falco sparverius*): the influence of distance and migration and implications for monitoring and management. *Boise State University Theses and Dissertations.* Boise State University, Boise, ID.

Brown JL, Collopy MW. 2013. Immigration stabilizes a population of threatened cavity-nesting raptors despite possibility of nest box imprinting. *Journal of Avian Biology* 44: 141–148.

Carpenter, B., A. Gelman, M. D. Hoffman, D. Lee, B. Goodrich, M. Betancourt, M. Brubaker, J. Guo, P. Li, and A. Riddell. 2017. Stan: A probabilistic programming language. *Journal of Statistical Software* 76. DOI 10.18637/jss.v076.i01

Clobert, J., E. Danchin, A. A. Dhondt, and J.D. Nichols, *eds.* 2001. *Dispersal.* Oxford University Press, Oxford, UK.

Clobert, J., J.-F. Le Galliard, J. Cote, S. Meylan, and M. Massot. 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecology Letters* 12: 197-209.

Clobert, J., M. Baguette, T. G. Benton, and J. M. Bullock, *eds.* 2012. *Dispersal Ecology and Evolution.* Oxford University Press, Oxford, UK.

del Mar Delgado, M., V. Penteriani, E. Revilla, and V. O. Nams. 2010. The effect of phenotypic traits and external cues on natal dispersal movements. *Journal of Animal Ecology* 79: 620-632.

Donohue, K. 1998. Maternal determinants of seed dispersal in *Cakile edentula*: fruit, plant, and site traits. *Ecology* 79: 2771-2788.

Ferrer, M. 1993. Ontogeny of dispersal distance in young Spanish imperial eagles. *Behavioral Ecology and Sociobiology* 32: 259-263.

Fraser, D. F., J. F. Gilliam, M. J. Daley, A. N. le, and G. T. Skalski. 2001. Explaining Leptokurtic Movement Distributions: Intrapopulation Variation in Boldness and Exploration. *The American Naturalist* 158: 124-135.

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

Goldwasser, L., J. Cook, and E. D. Silverman. 1994. The effects of variability on metapopulation dynamics and rates of invasion. *Ecology* 75: 40-47.

Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Animal Behavior* 28: 1140-1162.

Greenwood, P. J. and P. H. Harvey. 1982. The natal and breeding dispersal of birds. *Annual Review of Ecology and Systematics* 13: 1-21.

Hanski, I. and M. E. Gilpin, *eds*. 1997. *Metapopulation biology: ecology, genetics, and evolution.* Academic Press, San Diego, CA.

Heath, J. A., K. Steenhof, and M. A. Foster. 2012. Shorter migration distances associated with higher winter temperatures suggest a mechanism for advancing nesting phenology of American kestrels *Falco sparverius*. *Journal of Avian Biology* 43: 376-384.

Hijmans, R. J. 2016a. geosphere: Spherical Trigonometry. R package version 1.5-5. https://CRAN.R-project.org/package=geosphere

Hijmans, R. J. 2016b. raster: Geographic analysis and modeling with raster data. R package version 2.5-8. http://CRAN.R-project.org/package=raster

Homer, C. G., J. A. Dewitz, L. Yang, S. Jin, P. Danielson, G. Xian, J. Coulston, N. D. Herold, J. D. Wickham and K. Megown. 2015. Completion of the 2011 National Land Cover Database for the conterminous United States – Representing a decade of land cover change information. *Photogrammetric Engineering and Remote Sensing* 81: 345-354.

Homer, C., J. Dewitz, J. Fry, M. Coan, N. Hossain, C. Larson, N. Herold, A. McKerrow, J. N. Van Driel and J. Wickham. 2007. Completion of the 2001 National Land Cover Database for the conterminous United States. *Photogrammetric Engineering and Remote Sensing* 73: 337-341.

Jacobs, E. A. 1995. American kestrel reproduction and dispersal in central Wisconsin. *Journal of Raptor Research* 29: 135-137.

Kelly, T., H. MacGillivray, Y. Saquis-Adamson, M. J. Watson, K. A. Hobson, and E. A. MacDougall-Shackleton. 2016. Seasonal migration distance varies with natal dispersal and predicts parasitic infection in song sparrows. *Behavioral Ecology and Sociobiology* 70: 1857-1866.

Koenig, W. D., D. Van Vuren, and P. N. Hooge. 1996. Detectability, philopatry and the distribution of dispersal distances in vertebrates. *Trends in Ecology and Evolution* 11: 514-517.

Kokko, H. and A. López-Sepulchre. 2006. From individual dispersal to species ranges: perspectives for a changing world. *Science* 313: 789-791.

Jammalamadaka, S.R. and A. SenGupta. 2001. Topics in Circular Statistics, Section 7.5, World Scientific Press, Singapore.

Lindgren, F. and H. Rue. 2015. Bayesian Spatial Modelling with R-INLA. *Journal of Statistical Software* 63: 1-25.

Lindgren, F., H. Rue, and J. Lindstrom. 2011. An explicit link between Gaussian fields and Gaussian Markov random fields: The SPDE approach (with discussion). *Journal of the Royal Statistical Society, Series B* 73: 423-498.

Lowe, W. H. 2009. What drives long-distance dispersal? A test of theoretical predictions. *Ecology* 90: 1456-1462.

Lowe, W. H. 2010. Explaining long-distance dispersal: Effects of dispersal distance on survival and growth in a stream salamander. *Ecology* 91: 3008-3015.

Lowe, W. H. and M. A. McPeek. 2012. Can natural selection maintain long-distance dispersal? Insight from a stream salamander system. *Evolutionary Ecology* 26: 11-24.

Lund, U., and C. Agostinelli. 2007. Circular: circular statistics. Rpackage version 0.3–8. https://CRAN.R-project.org/package=circular

McClure, C. J. W., J. Brown, S. E. Schulwitz, J. Smallwood, K. E. Farley, J.-F. Therrien, K. Miller, K. Steenhof, and J. A. Heath. 2018. Demography of a widespread raptor varies across disparate regions. *In review.*

Miller, K. E., & J. A. Smallwood. 1997. Natal dispersal and philopatry of southeastern American Kestrels in Florida. *Wilson Bulletin* 109: 226–232.

Miller, M. P., T. D. Mullins, J. W. Parrish, J. R. Walters, and S. M. Haig. 2012. Variation in migratory behavior influences regional genetic diversity and structure among American Kestrel populations (Falco sparverius) in North America. *Journal of Heredity* 103: 503–514.

Møller, A. P., E. F. Flensted-Jensen, and W. Mardal. 2006. Dispersal and climate change: a case study of the Arctic tern *Sterna paradisaea*. *Global Change Biology* 12: 2005-2013.

Morton, E. R., M. J. McGrady, I. Newton, C. J. Rollie, G. D. Smith, R. Mearns, and M. K. Oli. 2018. Dispersal: a matter of scale. *Ecology* 98: 938-946.

Nathan, R. 2006. Long-distance dispersal of plants. *Science* 313: 786-788.

Paradis, E., S. R. Baillie, W. J. Sutherland, and R. D. Gregory. 1998. Patterns of natal and breeding dispersal in birds. *Journal of Animal Ecology* 67: 518-536.

Pärn, H. and B.- E. Sæther. 2012. Influence of temperature on dispersal in two bird species. *Dispersal Ecology and Evolution*. Oxford University Press, Oxford, UK.

Perrin, N. and V. Mazalov. 1999. Dispersal and inbreeding avoidance. *The American Naturalist* 154: 282-292.

R Development Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/**.**

Royle, J. A. and J. A. Dubovsky. 2001. Modeling spatial variation in waterfowl band-recovery data. *Journal of Wildlife Management* 65: 726-737.

Rue, H., S. Martino, and N. Chopin. 2009. Approximate Bayesian inference for latent Gaussian models using integrated nested Laplace approximations (with discussion). *Journal of the Royal Statistical Society, Series B* 71: 319-392.

Sæther, B.- E., J. Tufto, S. Engen, K. Jerstad, O. W. Røstad, and J. E. Skåtan. 2000. Population dynamical consequences of climate change for a small temperate songbird. *Science* 287: 854-856.

Shave, M. E. and C. A. Lindell. 2017. American kestrels occupying nest boxes in Michigan cherry orchards show high reproductive rates and tolerance fo monitoring. *Journal of Raptor Research* 51: 50-60.

Shields, W. M. 1982. *Philopatry, inbreeding, and the evolution of sex*. State University of New York Press, Albany, NY.

Smallwood, J. A. 1987. Sexual segregation by habitat in American kestrels wintering in southcentral Florida: vegetative structure and responses to differential prey availability. *The Condor* 89: 842-849.

Smallwood, J. A., M. F. Causey, D. H. Mossop, J. R. Klucsarits, B. Robertson, S. Robertson, J. Mason, M. J. Maurer, R. J. Melvin, R. D. Dawson, G. R. Bortolotti, J. W. Parrish Jr., T. F. Breen, and K. Boyd. 2009a. Why are American Kestrel (*Falco sparverius*) populations declining in North America? Evidence from nest-box programs. *Journal of Raptor Research* 43: 274-282.

Smallwood, J. A., P. Winkler, G. I. Fowles, and M. A. Craddock. 2009b. American Kestrel breeding habitat: the importance of patch size. *Journal of Raptor Research* 43: 308-318.

Smallwood, J. A. and D. M. Bird. 2002. American Kestrel (*Falco sparverius*). *In* P. G. Rodewald, editor. *The birds of North America.* Cornell Lab of Ornithology, Ithaca, New York, USA. http://dx.doi.org/10.2173/bna.602

Soutullo, A., V. Urios, M. Ferrer, S. G. Peñarrubia. 2006. Post-fledging behavior in Golden Eagles *Aquila chrysaetos*: onset of juvenile dispersal and progressive distancing from nest. *Ibis* 148: 307-312.

Stan Development Team. 2017. *RStan: the R interface to Stan*. R package version 2.16.2. http://mc-stan.org

Steenhof, K. and J. A. Heath. 2013. Local recruitment and natal dispersal distances of American Kestrels. *The Condor* 115: 584–592.

Steenhof, K. and J. A. Heath. 2009. American Kestrel reproduction: evidence for the selection hypothesis and the role of dispersal. *Ibis* 151: 493-501.

Sutherland, G. D., A. S. Harestad, K. Price, and K. P. Lertzman. 2000. Scaling of natal dispersal distances in terrestrial birds and mammals. *Conservation Ecology* 4: 16.

Tittler, R., L. Fahrig, and M-. A. Villard. 2006. Evidence of large-scale source-sink dynamics and long-distance dispersal among wood thrush populations. *Ecology* 87: 3029-3036.

Tittler, R., M.- A. Villard, and L. Fahrig. 2009. How far do songbirds disperse? *Ecography* 32: 1051-1061.

Thorup, K., F. Korner-Nievergelt, E. B. Cohen and S. R. Baillie. 2014. Large-scale spatial analysis of ringing and re-encounter data to infer movement patterns: A review including methodological perspectives. *Methods in Ecology and Evolution* 5: 1337-1350.

USGS Bird Banding Laboratory. 2017. North American bird banding and band encounter data set. Patuxent Wildlife Research Center, Laurel, MD. 11 May 2017.

Van Noordwijk, A. J. 1995. On bias due to observer distribution in the analysis of data on natal dispersal in birds. *Journal of Applied Statistics* 22: 683-694.

Vehtari, A., J. Gabry, Y. Yao, and A. Gelman. 2018. “loo: Efficient leave-one-out cross-validation and WAIC for Bayesian models.” R package version 2.0.0, <URL: https://CRAN.R-project.org/package=loo>.

Vogelmann, J. E., S. M. Howard, L. Yang, C. R. Larson, B. K. Wylie and J. N. Van Driel. 2001. Completion of the 1990’s National Land Cover Data set for the conterminous United States. *Photogrammetric Engineering and Remote Sensing* 67: 650-662.

Walls, S. S., R. E. Kenward and G. J. Holloway. 2005. Weather to disperse? Evidence that climatic conditions influence vertebrate dispersal. *Journal of Animal Ecology* 74: 190-197.

Walls, S. S. and R. E. Kenward. 1995. Movements of radio-tagged Common Buzzards *Buteo buteo* in their first year. *Ibis* 137: 177-182.

Table 1.1. Summary of American kestrel natal dispersal studies conducted within study areas with nest boxes and this study based on banding and encounter data. In previous studies, the majority of kestrel individuals dispersed short distances, but these studies have limited potential to detect long-distance movements resulting in settlement outside of the study area.

	Median dispersal distance (km)		**Maximum dispersal distance (km)**		**Sample size**	**Study area size (km^2)**
	Male	Female	Male	Female		
Jacobs 1995	16.0	30.0	--	--	10	75
Miller and Smallwood 1997*	4.4	5.1	32.4	38.8	34	1200
Steenhof and Heath 2013	3.5	8.1	24.1	42.9	81	1000
This study	23.5	33.7	938.3	772.6	311	Continental

* subspecies *F. s. paulus*

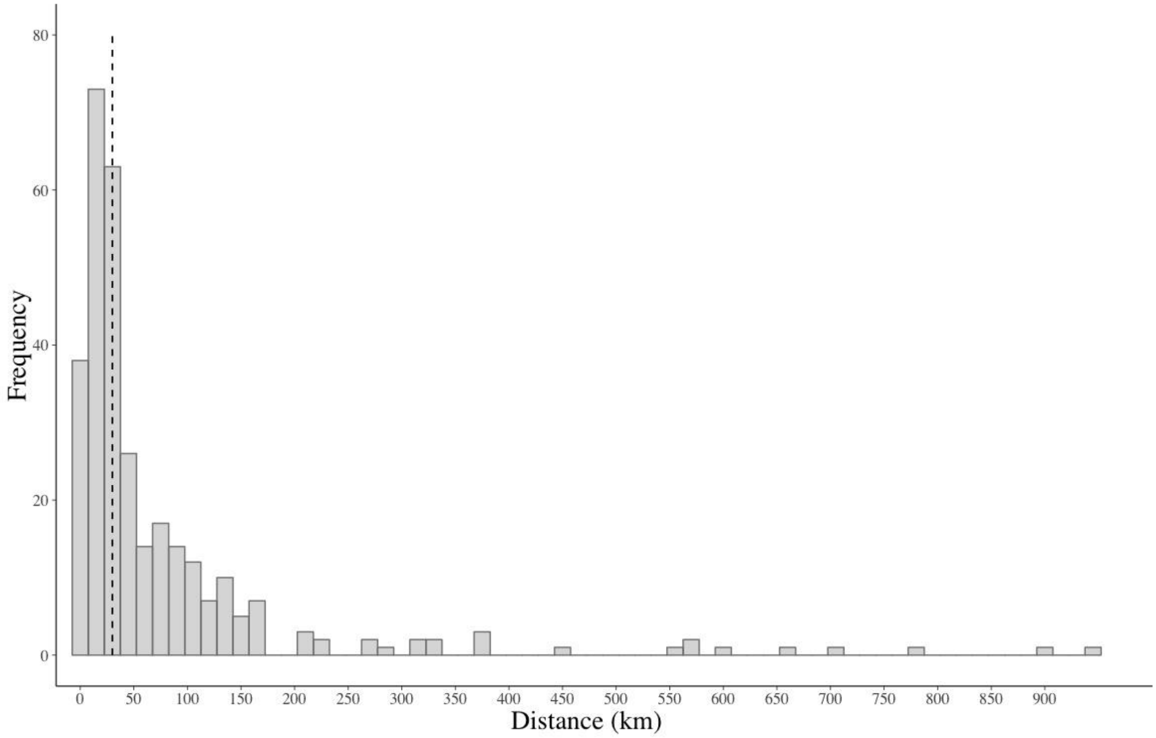

Figure 1.1. **Frequency of natal dispersal distances of American kestrels from North American banding and encounter data, 1960-2015. Of 311 total individuals (161 F, 105 M, 45 unk), 152 (86 F, 49 M, 17 unk) dispersed a distance greater than 30 km, indicated by the dashed line.**

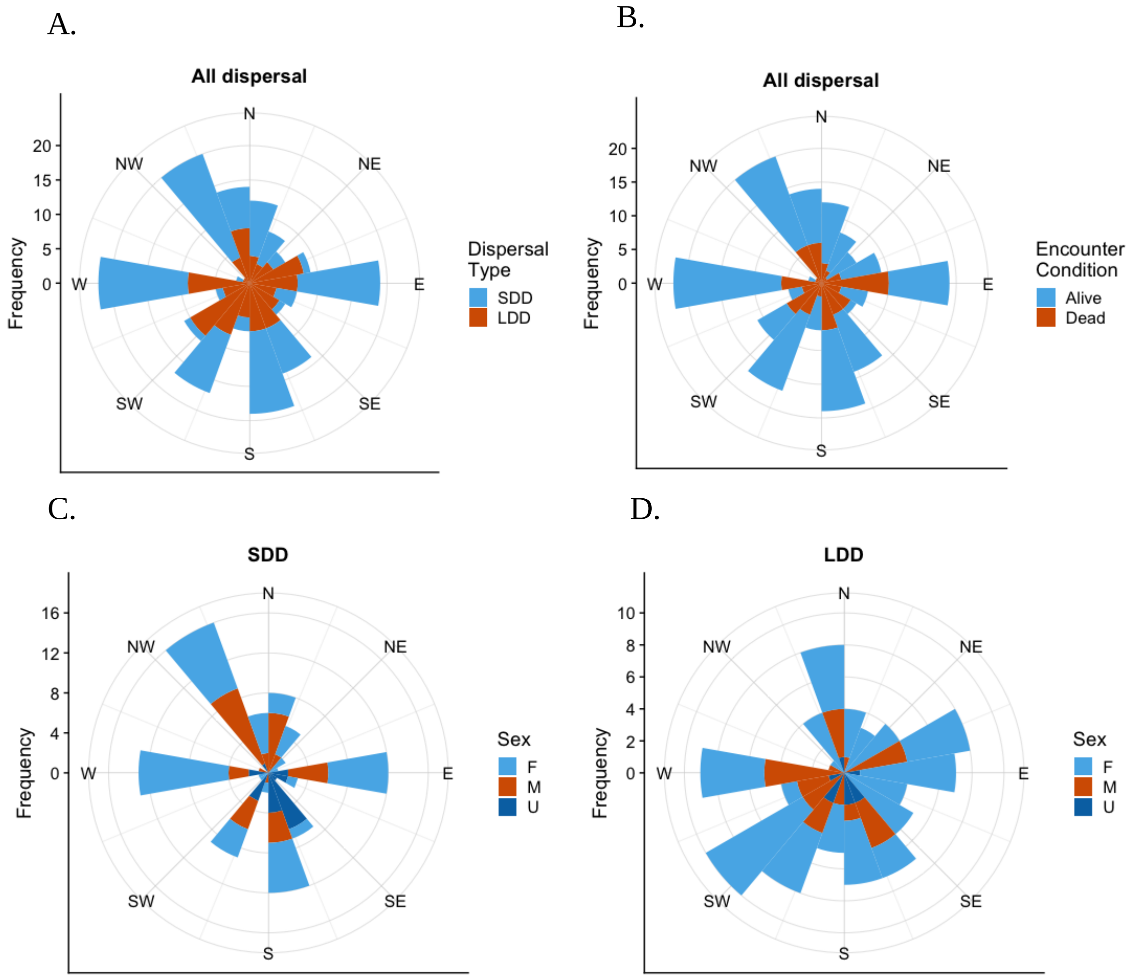

Figure 1.2. **Frequency of natal dispersal directions of American kestrels from North American banding and encounter data, 1960-2015. Length of bar corresponds to frequency of direction. Dispersal direction was not uniformly distributed across (A) all distances ($p < 0.001$), (C) short-distance ($p < 0.01$), or (D) long-distance ($p < 0.01$), but there was no difference between sexes ($p > 0.1$). There was no difference in dispersal direction between birds (B) encountered alive or dead ($p > 0.1$).**

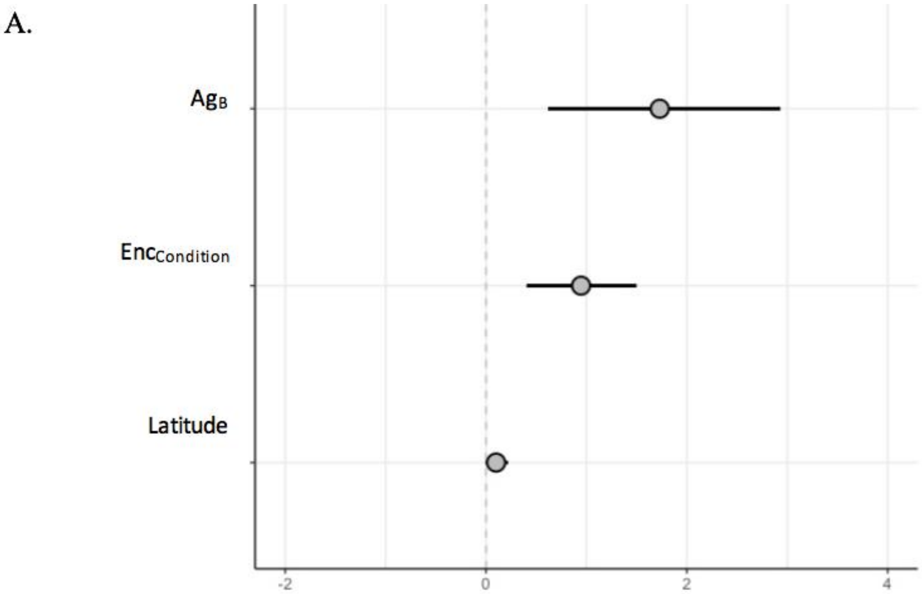

Figure 1.3A. **Coefficient plot for predictors of long-distance dispersal frequency in American kestrels in the US and Canada from 1960-2015 from banding and encounter data. Dots are median parameter estimates and bars represent 95% credible intervals for parameter estimates. Percentage of agriculture at the banding site (Ag_B) is positively correlated with the likelihood of long-distance dispersal, and the positive effect of encounter condition ($Enc_{condition}$) indicates that birds encountered dead are more likely to be LDD and suggests an effect of sampling on dispersal tendency. Latitude had no effect on the likelihood of an individual being a long-distance disperser.**

B.

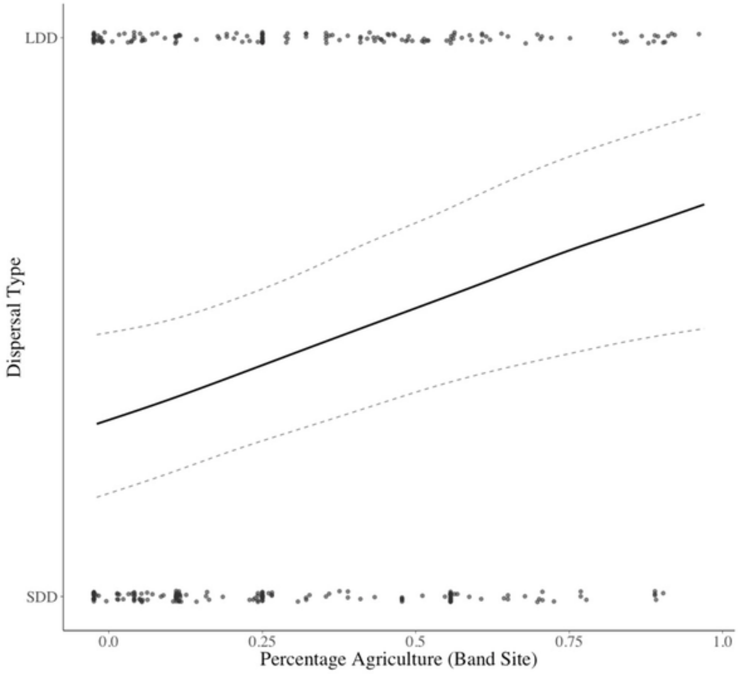

Figure 1.3B. Effect of the percentage of agriculture in natal territory on long-distance dispersal frequency in American kestrels in the US and Canada from 1960-2015 from banding and encounter data. The solid line shows mean effect of agriculture on frequency and dashed lines represent 95% credible intervals for parameter estimate. Percentage of agriculture at the banding site is positively correlated with the likelihood of long-distance dispersal.

A.

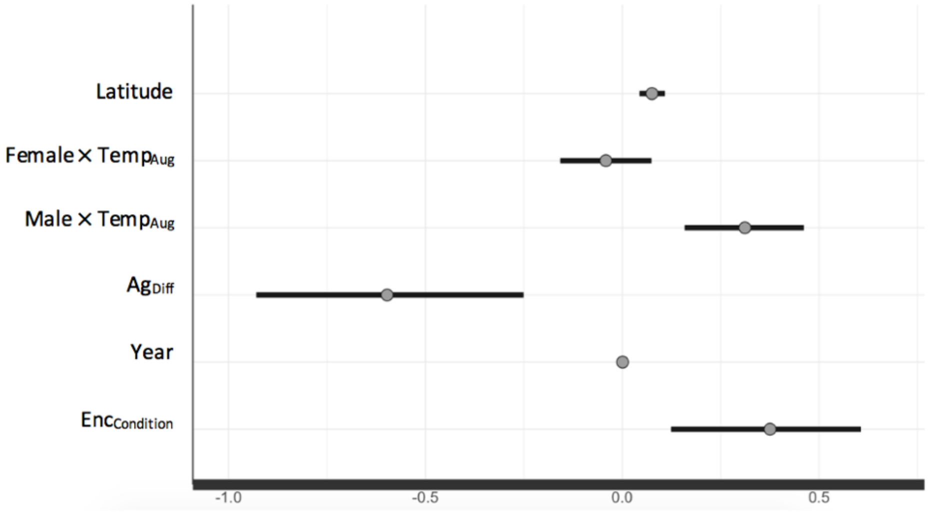

Figure 1.4A. Coefficient plot of effects of covariates on LDD distance in American kestrels in the US and Canada 1960-2015 from banding and encounter data. Dots are median parameter estimates and bars represent 95% credible intervals for parameter estimates. Latitude is positively correlated with LDD distance, the difference between the percentage of agriculture at the encounter and banding sites (Ag$_{Diff}$) is negatively correlated with dispersal distance, and maximum August temperature is positively correlated with distance in males (Male x Temp$_{Aug}$) but not females (Female x Temp$_{Aug}$). The positive effect of encounter condition (Enc$_{condition}$) indicates that birds encountered dead have longer LDD than those encountered alive, suggesting an effect of sampling on distances observed. Year did not affect dispersal distance.

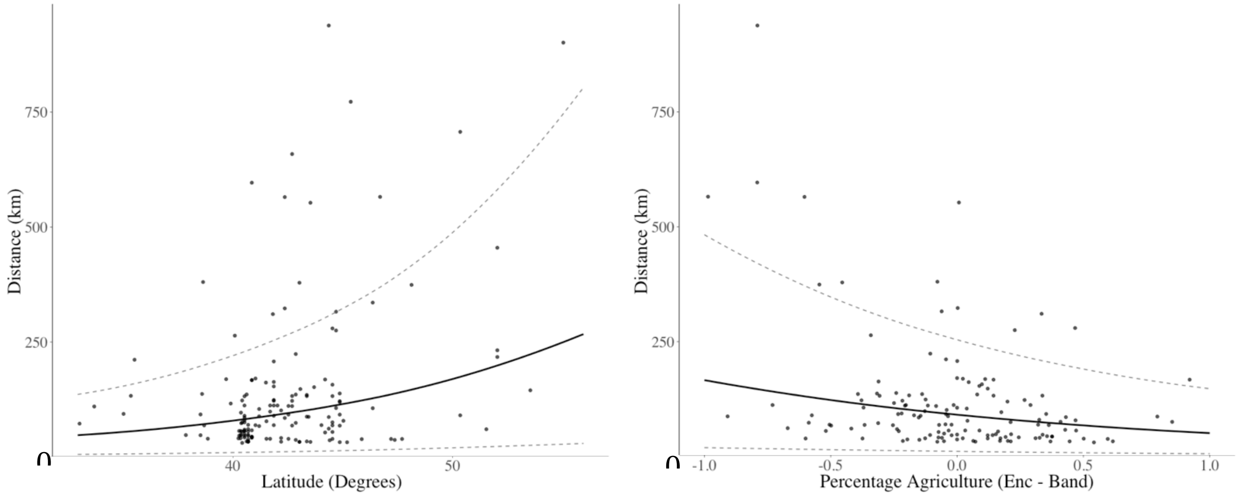

Figure 1.4B-C. **Effects of latitude (B) and agriculture (C) on LDD distance in American kestrels in the US and Canada 1960-2015 from banding and encounter data. Solid lines are mean effect sizes and dashed lines represent 95% credible intervals for model predictions. Latitude is positively correlated with LDD distance, and the difference between the percentage of agriculture at the encounter and banding sites is negatively correlated with dispersal distance.**

SUPPLEMENTAL MATERIAL

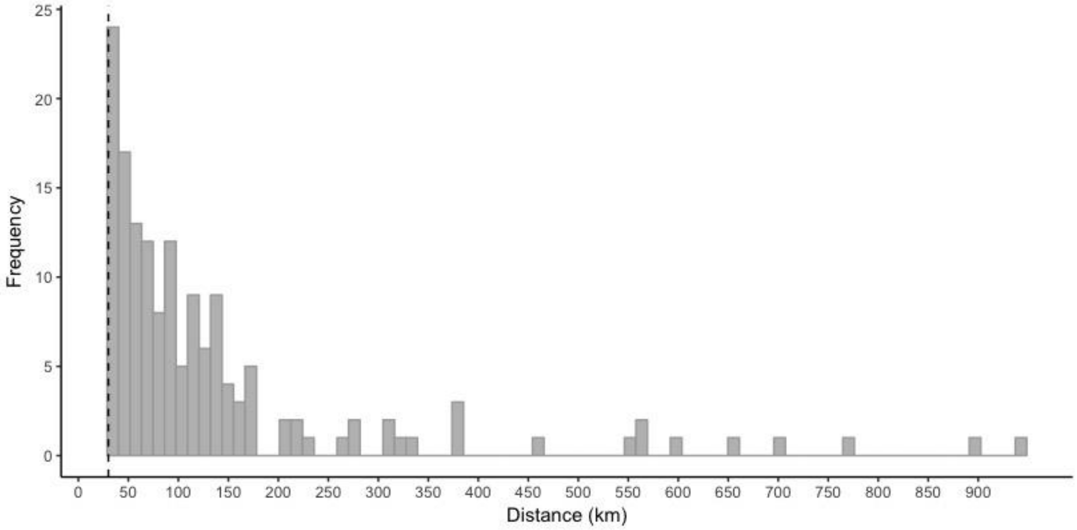

Figure S1.1. Frequency of long-distance (> 30 km) natal dispersal distances of American kestrels from North American banding and encounter data, 1960-2015. One hundred fifty-two individuals (86 F, 49 M, 17 unk) of 311 total individuals (48.7%) dispersed long-distance.

Table S1.1 Correlation matrix for temperature variables across all months. We tested for correlations using Pearson correlation tests. Minimum and maximum temperature anomalies in May were correlated with each other (r = 0.796), but temperature anomalies were not correlated across months.

	$\text{Temp}_{\text{MayMin}}$	$\text{Temp}_{\text{MayMax}}$	Temp_{Aug}	Temp_{Jan}	Temp_{Mar}
$\text{Temp}_{\text{MayMin}}$	1.000	0.796	0.088	0.190	0.073
$\text{Temp}_{\text{MayMax}}$		1.000	0.077	0.102	-0.101
Temp_{Aug}			1.000	0.073	0.043
Temp_{Jan}				1.000	0.404
Temp_{Mar}					1.000

Table S1.2 **Correlation matrix for all covariates used to model long-distance dispersal frequency and distance. We tested for correlations between variables using Pearson correlation tests. Percentage of agriculture metrics were weakly correlated with one another (0.5 < r < 0.8). No environmental correlates (temperature or agriculture metrics) were correlated with year. Who encountered a bird was somewhat correlated with whether the bird was encountered alive or dead (r = 0.54), so we did not include multiple sampling variables within a single model.**

	Sex	Latitude	Ag_B	Ag_E	Ag_Diff	Ag_Avg	Temp_Aug	Temp_Mar	Year	Precision	$\text{Enc}_\text{Condition}$	Enc_Who
Sex	1.000	0.056	-0.165	0.034	0.167	-0.032	0.018	0.018	-0.084	-0.006	0.135	0.046
Latitude		1.000	0.096	-0.050	-0.143	0.045	0.066	0.129	-0.166	0.107	0.015	-0.083
Ag_B			1.000	0.326	-0.575	0.656	-0.053	-0.009	0.055	0.049	0.030	-0.053
Ag_E				1.000	0.586	0.712	-0.177	0.065	0.149	-0.198	-0.099	-0.154
Ag_Diff					1.000	0.052	-0.109	0.060	0.085	-0.216	-0.116	-0.091
Ag_Avg						1.000	-0.177	0.057	0.058	0.019	-0.074	-0.145
Temp_Aug							1.000	0.058	0.086	0.053	0.042	0.111
Temp_Mar								1.000	-0.021	0.160	-0.144	-0.096

Year	1.000	-0.549	-0.282	-0.025
Precision		1.000	0.251	0.091
$\text{Enc}_{\text{Condition}}$			1.000	0.540
Enc_{Who}				1.000

Table S1.3. Candidate models and model selection results using Log Pseudo Marginal Likelihoods (LPML) for logistic regression for the likelihood of long distance natal dispersal (> 30km) by American kestrels in North America based on banding and encounter data from 1960-2015. The model with the lowest LPML is considered the best fitting model. All models contain a spatial random effect, except for the model designated as *.nsp*. All models with a spatial random effect outperformed all other non-spatial models.

Model	LPML
Ag_B + Latitude + $Enc_{Condition}$	191.24
Ag_B + $Enc_{Condition}$	191.94
Ag_B + Year + $Enc_{Condition}$	192.63
Ag_B + Latitude	193.84
Ag_B	194.23
Ag_B + Latitude + Year	194.81
Ag_B + Year	195.21
$Enc_{Condition}$	195.69
Latitude	195.69
Year + $Enc_{Condition}$	196.21
Sex × $Temp_{Aug}$+Ag_B	196.80
Enc_{Who}	197.44
Intercept-only	198.31
Sex	198.33
Ag_{Diff}	198.34
$Temp_{Aug}$	198.99
$Temp_{Mar}$	199.05
Year	199.20

Ag_B+Latitude+$Enc_{Condition}$.*nsp*	205.57
Precision	211.76

Notes: Sex = as reported by the bander (unknown sex is included and does not influence parameter estimates of males or females); $Temp_{Aug}$ = August maximum temperature deviation from 1950-1981 baseline for the banding location; $Temp_{Mar}$ = March minimum temperature deviation from 1950-1981 baseline for the banding location; Ag_B = percentage of agricultural land cover within 4 km^2 of the natal/banding site; Latitude = at natal site, at whatever precision (10-minute, 1-minute, or exact) reported by the bander; Year = at banding; $Enc_{Condition}$ = individual’s condition when it was encountered (alive or dead); Enc_{who} = Who encountered individual (public or researcher); Precision = precision of the encounter record (10-minute, 1-minute, or exact) used to calculate dispersal distance from the banding location; .nsp designates models without a spatial random effect.

Table S1.4. Candidate models and model selection results for long-distance dispersal distance in American kestrels in the United States and Canada 1960-2015, with intrinsic and environmental covariates. The best fitting model is selected using the Expected Log Pointwise Posterior Density (ELPD). Comparing models with a spatial random effect using LPML indicated no spatial autocorrelation and spatial random effects were omitted from this model.

MODEL	ELPD diff	ELPD LOO	SE ELPD LOO	Eff Pars LOO	LOOIC
Sex × Temp_{Aug} + Latitude + Ag_{Diff} + Year + $\text{Enc}_{\text{Condition}}$	0.00	-859.47	13.56	8.82	1718.94
Sex × Temp_{Aug} + Latitude + Year + Ag_{Diff} + Temp_{Mar} + $\text{Enc}_{\text{Condition}}$	-5.20	-864.67	14.19	10.93	1729.35
Sex × Temp_{Aug} + Latitude + Ag_{Diff} +Year	-5.75	-865.22	13.62	7.42	1730.45
Sex × Temp_{Aug} + Latitude + Ag_{Diff} + $\text{Enc}_{\text{Condition}}$	-10.52	-869.99	15.90	9.19	1739.99
Sex × Temp_{Mar} + Latitude + Year + $\text{Enc}_{\text{Condition}}$	-10.68	-870.15	13.71	7.84	1740.29
Sex × Temp_{Aug} + Latitude + Ag_{Diff}	-14.48	-873.95	15.60	8.41	1747.90
Sex × Temp_{Aug} + Latitude + $\text{Enc}_{\text{Condition}}$	-14.96	-874.43	16.66	8.26	1748.87
Sex × Latitude + Ag_{Diff}	-17.08	-876.55	15.80	6.26	1753.10
Latitude + Ag_{Diff}	-17.50	-876.97	15.15	3.89	1753.95

Sex × Temp$_{Aug}$ + Latitude	-19.24	-878.71	15.65	7.16	1757.42
Sex × Temp$_{Aug}$ + Latitude × Year	-19.38	-878.85	15.42	6.81	1757.70
Sex × Temp$_{Aug}$ + Latitude + Year	-19.99	-879.46	16.16	8.54	1758.93
Temp$_{Aug}$ + Latitude + Ag$_{Diff}$ + Year	-20.43	-879.90	15.36	7.47	1759.81
Sex × Temp$_{Aug}$ + Temp$_{Mar}$	-22.06	-881.53	14.11	6.27	1763.07
Temp$_{Aug}$ +Latitude	-25.44	-884.91	15.60	4.90	1769.82
Sex × Latitude+ Temp$_{Aug}$	-25.98	-885.45	15.95	7.40	1770.90
Temp$_{Aug}$ + Temp$_{Mar}$ +Latitude	-27.03	-886.50	15.97	6.96	1772.99
Sex+Latitude	-28.87	-888.34	15.96	6.26	1776.69
Latitude	-30.05	-889.52	16.09	3.96	1779.05
Temp$_{Aug}$ + Ag$_{Diff}$	-31.67	-891.14	16.20	5.60	1782.27
Temp$_{Aug}$ + Ag$_{Diff}$	-31.67	-891.14	16.20	5.60	1782.27
Sex × Ag$_{Diff}$	-32.76	-892.23	16.91	5.29	1784.46
Latitude × Ag$_{Diff}$	-33.76	-893.23	16.79	4.19	1786.46
Ag$_{Diff}$	-33.92	-893.39	16.89	4.31	1786.78
Sex + Temp$_{Aug}$	-34.61	-894.08	16.38	6.63	1788.16
Ag$_{E}$	-36.23	-895.70	16.74	3.87	1791.39
Temp$_{Aug}$	-36.24	-895.71	16.14	3.99	1791.42
Temp$_{Mar}$	-36.53	-896.00	15.93	4.04	1792.01

Sex	-37.43	-896.91	16.79	5.70	1793.81
$\text{Temp}_{\text{May,max}}$	-39.09	-898.56	16.97	4.42	1797.11
Year	-40.94	-900.41	17.28	4.71	1800.82
Intercept-only	-41.72	-901.20	17.17	2.92	1802.39
Temp_{Jan}	-42.27	-901.74	16.89	4.63	1803.48
Ag_{B}	-42.45	-901.92	17.09	5.21	1803.84
$\text{Temp}_{\text{May,min}}$	-43.22	-902.69	17.24	5.01	1805.38
Ag_{avg}	-43.29	-902.76	17.64	4.88	1805.53

Notes: Sex = reported by the bander (unknown sex is included and does not influence parameter estimates of males or females); Temp_{Aug} = August maximum temperature deviation in the banding year from 1950-1981 baseline for the natal/banding location; Temp_{Mar} = March minimum temperature deviation in the banding year from 1950-1981 baseline for the banding location; Temp_{Jan} = January minimum temperature deviation in the banding year from 1950-1981 baseline for the banding location; $\text{Temp}_{\text{May,max/min}}$ = May maximum and minimum, respectively, temperature deviations in the banding year from 1950-1981 baseline for the banding location; Ag_{B} = percentage of agricultural land cover within 4 km^2 of the banding site; Ag_{E} = percentage of agricultural land cover within 4 km^2 of the encounter site; Ag_{Diff} = difference between the percentage of agricultural landcover within 4 km^2 of the encounter site and within 4 km^2 of the banding site; Ag_{avg} = average percentage of agricultural land cover in the straight-line, 4 km-wide polygon between the banding and encounter location; Latitude = at natal site, at whatever precision (10-minute, 1-minute, or exact) reported by the bander; $\text{Enc}_{\text{Condition}}$ =

individual's condition when it was encountered (alive or dead); Year = at banding; Precision = precision of the encounter record (10-minute, 1-minute, or exact) used to calculate dispersal distance from the banding location.

Additional Model Information and Diagnostics

We modeled frequency of long-distance dispersal with a binomial distribution and the inclusion of a spatial random effect using a Spatial Partial Differential Equation (SPDE) approach in R- INLA. We included the spatial random effect because of the presence of spatial autocorrelation in our data. Likelihood of being a long-distance disperser was spatially autocorrelated to a distance of 136 km (Fig S2), and appears strongly related to the distribution of kestrel nest box studies across the continent, particularly in southern Idaho, Wisconsin, and along parts of the East Coast of the United States (Fig S3).

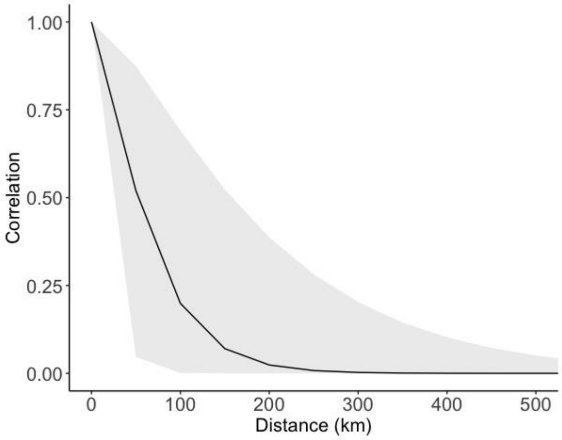

Figure S1.2 Spatial autocorrelation in frequency of long-distance dispersal.

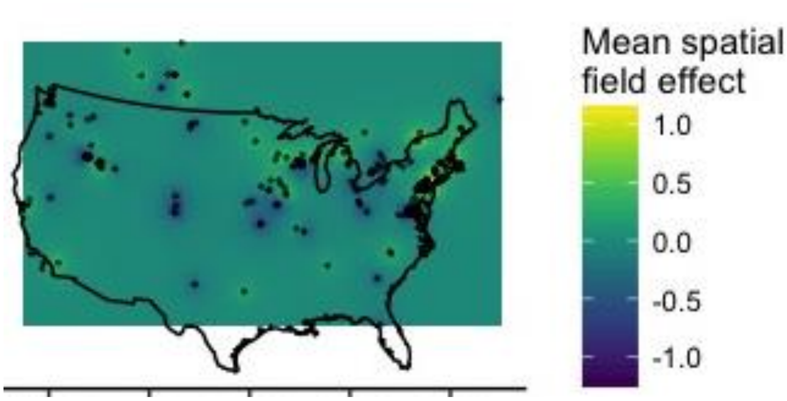

Figure S1.3. Effect of space on likelihood of long-distance dispersal for American kestrel banding data. Areas of strong spatial effect tend to be near kestrel nest box study areas.

We modeled long-distance dispersal distance with a gamma regression in RStan and rstanarm, because LDD was not spatially autocorrelated. We used the stan_glm( ) function in rstanarm with a gamma distribution and a log link, and the default weakly informative priors provided in rstanarm for all parameters. We ran all models for four chains with 2000 iterations, and assessed convergence using Rhat values for parameters and by visually checking chain blending (Table S5, Fig S4).

Table S1.5 Diagnostic statistics for top gamma regression model. Number of effective parameters is high for all parameters, and all Rhat values < 1.1, indicating model convergence.

Parameter	n_eff	Rhat
(Intercept)	2000	1.00
Latitude	1316	1.00
Ag_{Diff}	1425	1.00
Year	2000	1.00
$\text{Enc}_{\text{Condition}}$	1645	1.00
Sex F × Temp_{Aug}	2000	1.00
Sex M × Temp_{Aug}	2000	1.00
Sex U × Temp_{Aug}	2000	1.00
shape	2000	1.00
mean_PPD	2000	1.00
log-posterior	933	1.00

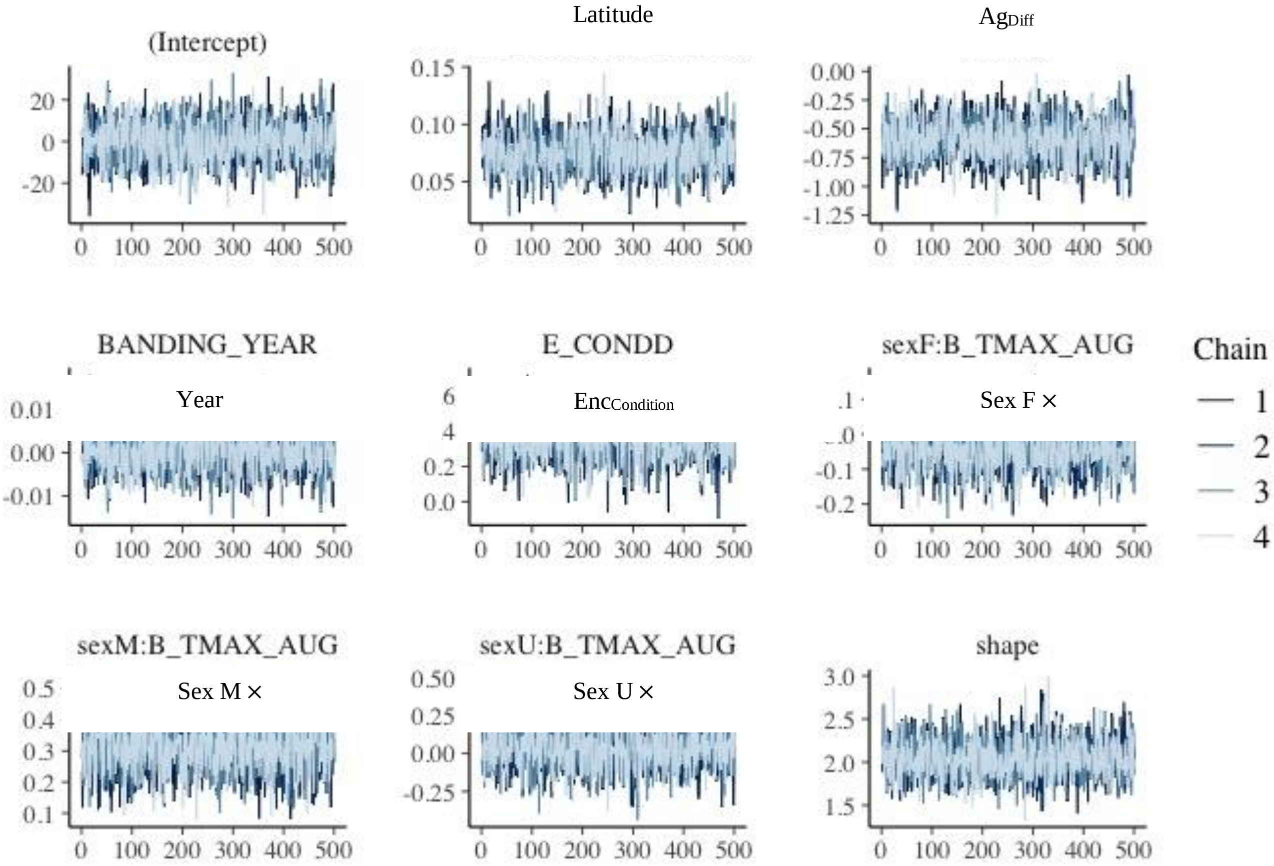

Figure S1.4 Markov chain Monte Carlo trace plots for post-warmup iterations for top LDD distance gamma regression model. For all parameters, chains appear well-blended.

Note on possible scenarios for the effects of landscape matrix on dispersal distribution

The difference in percentage of agriculture between the encounter and natal territories was negatively correlated with dispersal distance (*-0.59, 95% credible interval (-0.9, -0.25)*). This result is the opposite of our prediction, because we expected that high percentages of agriculture, which may be high quality habitat for kestrels (Shave and Lindell 2017, Smallwood 1987, Smallwood et al. 2009b), would lead to fewer individuals dispersing long distances from these areas. One hypothesis for the observed effect is that areas with high percentages of agriculture cannot support such high conspecific densities as occur in them, potentially because artificial nest boxes associated with these areas increase population densities (Shave and Lindell 2017). However, we do not have productivity data accompanying our set of banding data to investigate this hypothesis. An alternative hypothesis for this result is that highly agricultural areas may provide excellent food resources and facilitate good nestling provisioning (Shave and Lindell 2017, Smallwood 1987) so that natal dispersers from these areas are able to disperse greater distances during the exploratory period.

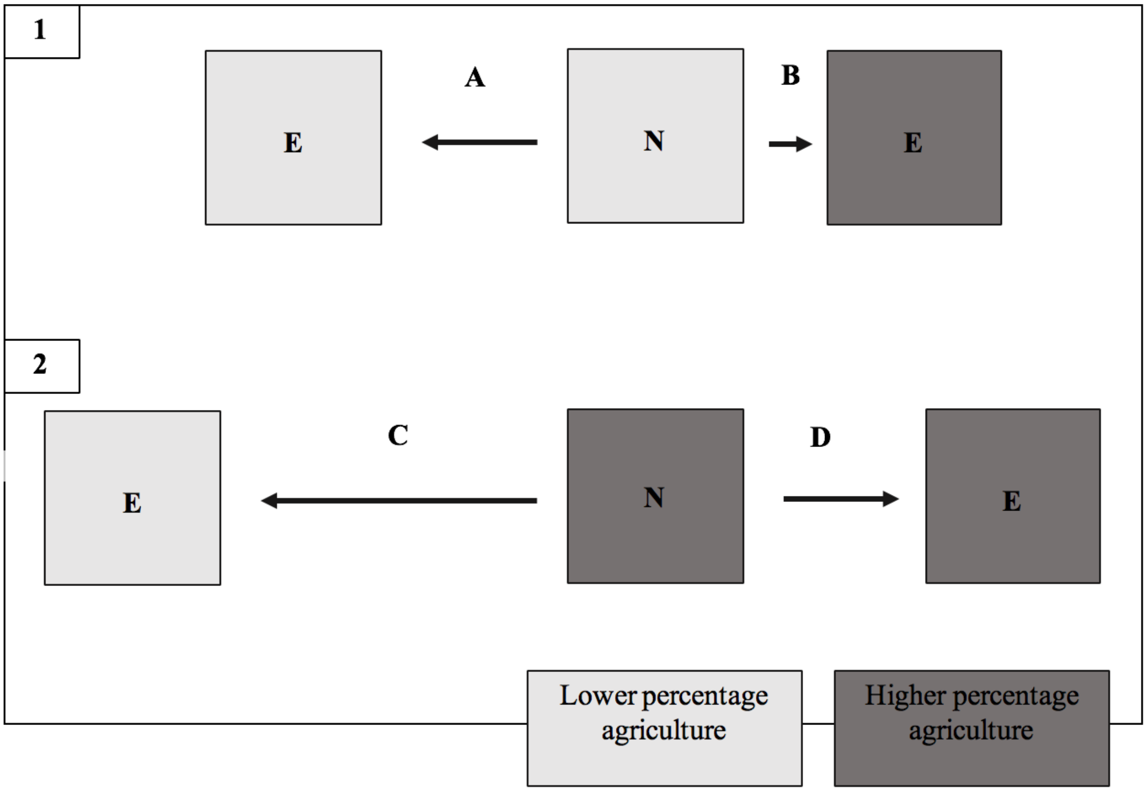

Figure S1.5. Conceptual diagram illustrating the observed relationship between percentage of agriculture in the natal (N) and encounter (E) territories and LDD distance in American kestrels in the US and Canada, 1960-2015, from banding and encounter data, and potential mechanisms. In scenario 1, individuals (A) disperse a mid-distance to a similar landcover type, or (B) experience an area of much higher agricultural cover and do not continue to disperse farther. In scenario 2, individuals (D) disperse a mid-distance to a similar landcover type or (C) continue to disperse a greater distance and must stop due to an environmental or intrinsic threshold, despite not locating higher quality habitat.

PATTERNS AND MECHANISMS OF HETEROGENEOUS BREEDING DISTRIBUTION SHIFTS IN NORTH AMERICAN MIGRATORY BIRDS

Abstract

There is widespread evidence that climate change is affecting species distributions. Warming temperatures and climate niche constraints are the most commonly hypothesized drivers of shifts in breeding distributions, but multidirectional shifts of migratory bird distributions are inconsistent with the climate niche hypothesis. We examined shifts in breeding distribution centroid for 73 species of North American migratory birds shifts from 1994-2017 across eastern, western, and central regions and tested whether life history characteristics were correlated with these shifts to identify potential mechanisms. We found that 44% of regional shifts were towards the equator, 55% were poleward, and several species shifted in different directions in different regions. Further, shifts in centroids were not explained by trends in abundance, suggesting that centroid shifts were not attributable to population declines or increases at distribution margins. We did not find any life history traits that explained southward shifts, but diet, migratory strategy, and tolerance to humans predicted northward shifts. Our results clearly indicate the prevalence of multidirectional breeding distribution shifts, and suggest that life history is one component in a likely complex set of interacting mechanisms acting at many scales to drive shifts.

Introduction

Why a species is present in one place but not another is a fundamental question in ecology. Species distributions are shaped by complex interactions between many factors, including physiology, the abiotic and biotic environment, competition, and dispersal capacity. Climate change is having widespread effects on species distributions, because changes in temperatures, precipitation, and extreme weather can directly stress physiological tolerances and energetics (Somero 2010). Additionally, climate change indirectly affects distributions by changing the dynamics of biotic interactions like resource competition and by altering the timing and distribution of resource seasonality in the temperate region (Parmesan 2006). Specifically, the emergence of spring vegetation is advancing (Richardson et al. 2013, Körner and Basler 2010), particularly at higher elevations, causing synchronization of spring onset at high and low elevations (Vitasse et al. 2018). To cope with changing conditions and shifting seasonal energy balance (Rapacciuolo et al. 2014), species distributions are shifting. Distributional responses vary widely in direction and magnitude across taxa, and many are not consistent with the hypothesis that warming temperatures are the primary driver of distribution shifts (Lenoir et al. 2010, Currie and Venne 2017).

Migratory species are interesting systems for studying distribution shifts in response to climate change because distributions of migratory animals change seasonally, migration is correlated to dispersal that shapes breeding distributions (Paradis et al. 1998), and migratory movement is an adaptive response to seasonal environments (Alerstam et al. 2003). Shifts in the breeding and wintering distributions of migratory birds may not follow the same pattern (Potvin et al 2016). In the Northern hemisphere, most wintering distributions of migratory birds have shifted poleward. An analysis of North American migratory birds found that range boundaries and winter centers of abundance for 254 species were shifting northward at a rate greater than 1 km per year, likely driven by climate and regional anthropogenic activities (La Sorte and Thompson 2007). Poleward shifts in wintering areas are associated with shorter migration distances between breeding and wintering areas, a pattern which has been termed “short-stopping” (Visser et al. 2009). These northward shifts in response to warmer winter temperatures likely have positive fitness implications, lowering energetic demands of migration and allowing individuals to better anticipate conditions on the breeding ground, and advance arrival date and breeding phenology (Visser et al. 2009, Heath et al. 2012).

Compared to winter distributions, the directionality of recent shifts in breeding distributions has been more heterogeneous. In New York state, 57% of avian species’ mean breeding latitude shifted northward, and 43% of species’ mean breeding latitude shifted southward from 1980 to 2005 (Zuckerberg et al. 2009). In the central United States, poleward shifts in breeding distributions were shown in 52% of studied avian species, and equatorward shifts were shown for 24% of species (Hovick et al. 2016). It is most commonly hypothesized that species are shifting distributions poleward to track suitable breeding temperatures (Hovick et al. 2016; Lenoir et al. 2010, Lawler et al. 2013), and several studies have addressed the degree to which species are able to track climatic niches poleward as a result of climate change (VanDerWal et al. 2012, Bateman et al. 2016, Lawler et al. 2013). However, climate niche hypotheses tend to predict poleward shifts, and multidirectional shifts in breeding distributions suggest there are more factors driving shifts (Lenoir et al. 2010, Currie and Venne 2017). Mechanisms underlying shifts towards the equator have not received much attention, with many hypotheses invoking stochasticity, error, or unusual local weather patterns (Hovick et al. 2016, Zuckerberg et al. 2009, Lenoir et al. 2010). Shifts in distributions other than northward shifts predicted by temperature warming have also been explained as the result of anthropogenic land use change constraining climate tracking (Chen et al. 2011, Hovick et al. 2016, Lawler et al 2013). Additionally, temporary competitive release at the southern range margin has been proposed as a possible mechanism underlying southward shifts (Lenoir et al. 2010, Hughes 2000).

The evolutionary ecology of migration in temperate North American birds may provide insight into equatorward breeding distribution shifts (Pulido 2007, Knudsen et al. 2011). In a foundational theory of the evolution of migration, Cox (1968) proposed that increasing seasonality at the breeding range is a driver of increased migratory tendency in avian species. Climate change has dampened the seasonal variation in temperature and altered phenology, potentially shifting the balance between the costs and benefits of migration for some species (Renner and Zohner 2018, Richardson et al. 2013). Specifically, warming is occurring fastest in the winter and previously costly cold environments with low winter resources are warmer with more resources, while the lengthening of the growing season throughout the year has altered the distribution of productivity throughout the year, so that seasonally abundant resources are less peaked (Austin and Rehfisch 2005, Peñuelas and Filella 2001). Migration enables species to breed in seasonal environments with high resources and avoid cold, low-resource conditions during the nonbreeding season, but migratory species must balance the benefits of separate breeding and wintering ranges with the costs of long-distance annual movement (Winger et al. 2018, Alerstam et al. 2003). As seasonality becomes less pronounced because of climate change, these benefits and costs may shift, and for species that may experience phenological mismatch because of late arrival on the breeding grounds, poor reproductive outcome may result in selection against returning to northern breeding areas. Thus, it is possible that species may respond to lessening seasonality by decreasing migratory tendency (Pulido and Berthold 2010, Knudsen et al. 2011; Figure 2.1), either by wintering at a higher latitude or breeding at a lower latitude. However, an adaptive or coping response would depend on phenotypic plasticity or variation within the population, dietary and habitat constraints, and the relative effects of predictive cues (e.g. photoperiod) and supplementary cues on migration.

In addition to changes in the ultimate costs and benefits of migration, changes in supplementary cues, like temperature and vegetation “green out” (Wingfield et al. 1992, Gwinner 1977), which influence migratory timing and the onset of reproductive readiness, may cause changes in spring migration distance similar to ‘short-stopping’ during fall migration. Earlier spring warming and warmer winters are associated with earlier spring arrivals of many bird species (Lehikoinen and Sparks 2010, Saino et al. 2004, 2010). Additionally, earlier spring temperatures and warmer winters with less freezing affect the phenology and extent of leaf emergence (Körner and Basler 2010, Fu et al. 2015), which influences spring migratory timing (Kelly et al. 2016, LaSorte et al. 2014). However, the impacts of earlier spring warming and fewer freezing days on leaf emergence may be additive or antagonistic (Fu et al. 2015), so changes to temperature and landcover cues are likely heterogeneous. Further, the effects of climate change on temperature and vegetation are not occurring uniformly across latitudes and elevations, so the temporal relationship between supplementary cues and conditions at the breeding grounds have shifted for some species (Visser et al. 2004). The resulting mismatch between cues and resources is a commonly cited driver of northward breeding distribution shifts (Visser et al. 2004, Parmesan 2006, Van Der Jeugd et al. 2009, Renner and Zohner 2018), but has not been considered as a possible driver of southward shifts.

We studied how migratory species' breeding distributions are shifting with global change, and assessed what life history characteristics correlate with these shifts to gain insight into possible underlying mechanisms. We hypothesized that species distributions would shift in a direction that most optimizes the balance between acquiring resources during the breeding season and the costs of migration, and we hypothesized that for species with certain life history traits, equatorward shifts in breeding distributions may be advantageous because they may reduce the costs of annual migration and maintain synchronization with resources for breeding. We examined shifts in the centroids of breeding distributions for a set of migratory birds over a 23-year period coinciding with the advancement of anthropogenic climate change using Breeding Bird Survey (BBS) data (Sauer et al. 2013), and tested relationships between changes to breeding distributions and diet, habitat, reproduction, and migration. We predicted that a species' breeding distribution may have shifted toward the equator if the species possess phenotypic variation and plasticity in migratory and reproductive traits, and if individuals of the species encounter and use supplementary cues for migration in the spring. Therefore, we predicted: (1) Dietary and habitat generalists and partial migrants, especially those that are also human tolerant, will be more likely to show equatorward shifts in breeding distributions because they can often adapt to different conditions and often display inter- and intra-population phenotypic variation. Conversely, specialists and obligate, long-distance migrants will be likely to shift poleward, because resource constraints and constrained annual schedules restrict the flexibility of specialists and obligate migrants. (2) Insectivorous species, particularly those foraging for larvae on vegetation and near the ground, will exhibit equatorward shifts because they will encounter abundant food resources earlier and farther south during migration with advancing start-of-spring. Additionally, diurnal migrants will be more likely to show equatorward shifts because they more easily perceive the early and rapid emergence of spring during migration. (3) Territorial species and those in which males use strategies to arrive earlier on the breeding grounds will be likely to shift towards the equator because of the competitive benefits of shorter migrations. Finally, short-distance migrants, species with overlapping breeding and wintering ranges, and species that migrate in conspecific groups will likely exhibit equatorward shifts in breeding distribution because they are most likely to encounter and settle in these areas consistently, increasing survival by reducing the risks of migration.

Methods

The North American Breeding Bird Survey (BBS) is a large scale avian monitoring project in which designated 40 km routes throughout the United States and Canada are sampled via a series of three-minute point counts each breeding season. Since its inception in 1966, the BBS has established over 5,200 unique routes, yielding counts for over 400 species (Sauer et al. 2013). Breeding Bird Survey routes are sampled by volunteer observers, who typically survey only a single route for several years. Link and Sauer (2002) showed that observers vary in their ability to detect species on routes, and that observers detect fewer birds their first year than in subsequent years. As a result, BBS counts are biased by combinations of observers and routes and the amount of experience of an observer, and because effort varies through space and time, BBS counts must be interpreted as indices of species trends, rather than as absolute population metrics. Therefore, BBS counts must be adjusted based on observer-route combinations, stratum, and year (Link and Sauer 2002). Despite these concerns, the BBS is nonetheless a useful dataset for addressing distribution questions over a large scale and is frequently used to assess patterns of distributions and distributional change in North America, using abundance centroid (Huang et al. 2017, Hovick et al. 2016) and range margins (Hitch and Leberg 2007). Centroid (center of mass, weighted latitudinal/longitudinal mean, or center of abundance) describes overall distribution patterns without being heavily influenced by changes at the range margins. Thus, it is a good metric to assess a distribution as a whole, and changes to the abundance centroid may not mirror behavior at the range margins (Huang et al. 2017, Virkkala and Lehikoinen 2014, Massimino et al. 2015).

We used BBS data to estimate shifts in centroid for 73 bird species and subspecies between 1994 and 2017 in the United States and Canada. We selected migratory species that had good BBS coverage and represented a range of broad life history traits. We then categorized each species in terms of diet, foraging type, migratory strategy and distance, degree of specialization and sensitivity to environmental change, and range characteristics which we compiled from the species records available on Birds of North America Online (Supplemental Material). We assigned traits missing from a species' Birds of North America record as 'no data' for that species. We obtained data from the BBS as ten-stop summaries for all years and species available at the BBS FTP site

(Pardieck et al. 2018). We filtered the data to include only surveys on which at least one of the 73 species included in our analysis was detected. We restricted our study to years between 1994 and 2017 because evidence of anthropogenic climate change and biological responses began to appear in the early 1990s (Hughes 2000, Easterling et al. 2000). We also restricted our study to the contiguous United States and Canada below 52 degrees North, because since the number of BBS routes sampled on a yearly basis leveled out around 1973, 97.5% of all unique route runs have occurred below 52 degrees North.

We followed Huang et al. (2017) and Link and Sauer (2002) in using strata as spatial units in our analyses to roughly homogenize sampling effort and habitat type within units (Huang et al. 2017), and calculated strata as the intersection of Bird Conservation Regions (BCRs, Bird Studies Canada 2016) and state or province boundaries, using the Albers Equal Area Conic projection for all spatial analyses in ArcGIS. Bird conservation regions represent areas with similar biogeographical characteristics and when intersected with political boundaries, also reflect management units for wildlife. We divided strata into three large regions (East, West, Central; Fig. 2.2) because many species that occur over a large area and in different habitats express different phenotypes and are exposed to different patterns of climate change across the continent. Therefore, species may exhibit different patterns of distribution shifts in different portions of their range. Also, BBS counts are relative metrics of population trends that are affected by sampling across time and space so region-specific estimates of centroid shifts may be more accurate than continent-wide estimates of centroid shifts (Link and Sauer 2002, Link and Sauer 1998). Our hierarchical model included terms to account for these sampling effects, but the ability of the model to describe trends over space decreases as the size of analysis unit increases from the stratum level to the full continental scale. We included data from 1973-2017 in this hierarchical model because including data for more years allowed us to better estimate sampling effects across years. For each region, we only included a species in the analysis if it was recorded in a minimum of 10 BBS strata within the region during the study period to ensure an adequate sample size for each species (Huang et al. 2017). Additionally, for each species, we removed records from any strata in which the species was detected on fewer than four routes to ensure enough samples per stratum (Huang et al. 2017). We maintained the distinction used by the BBS between subspecies of Northern flickers (*Colaptes auratus auratus* and *C. a. cafer*) and dark-eyed juncos (*Junco hyemalis hyemalis, J. h. oreganus,* and *J. h. caniceps*) throughout analyses, but combined one record of Harlan's hawk (*Buteo jamaicensis harlani*) with records for standard red-tailed hawks (*B. jamaicensis*).

$$\mathrm{Count} \sim \mathrm{neg\ binomial}(\lambda_{i,j,t}, \varepsilon_{i,j,t}) \tag{2.1}$$

$$\log(\lambda_{i,j,t}) = S_i + \beta_i t + \omega_j + \eta I(j,t) + \gamma_{i,t} \tag{2.2}$$

$$N_{i,t} = A_i z_i \exp(S_i + \beta_i \hat{t} + \gamma_{i,t}) \tag{2.3}$$

$$Y_t = \frac{\sum_i N_{i,t} y_i}{\sum_i N_{i,t}} \tag{2.4}$$

We used a modification of the hierarchical model presented by Link and Sauer (2002) to calculate adjusted stratum-specific annual abundance indices to adjust counts for route-, observer-, and stratum-level sampling effects (Eq. 2.2). In the model, i indexes stratum, j indexes unique observer-route combinations, and t indexes year; we modeled raw counts with a stratum-specific intercept (S_i), a stratum-specific slope (β_i) multiplied by centered year ($\hat{t}$) and to account for sampling effects, included a term for observer and route specific effects (ω_j), a binary term for first year sampling effects ($\eta I(j,t)$) and interactive year-stratum effects ($\gamma_{i,t}$). We modeled route abundance using a negative binomial distribution with overdispersion term $\varepsilon_{i,j,t}$, because BBS counts are overdispersed relative to a Poisson distribution, and a negative binomial offers an alternative that accounts for this dispersion, as long as the computational aspects of fitting models with this distribution and many parameters are not prohibitive (Link and Sauer 1998). All hyperparameters were given weakly informative priors of a normal distribution with mean zero, and variances for all hyperparameters were allowed to vary independently. We calculated abundance indices in R (R Core Team) using the Bayesian package INLA, which uses an integrated nested Laplacian transformation approach (INLA) to fit Bayesian models (Lindgren and Rue 2015). It is an alternative to Markov Chain Monte Carlo (MCMC) that is much less computationally expensive and can include georeferenced and spatial point data in models (Lindgren and Rue 2015, Rue et al. 2009*)*. We explored a set of hierarchical models that varied in their spatial and temporal structure (including spatial effects computed via stochastic partial differential equations and autoregressive order one models) to predict and adjust counts, using both in-sample and out-of-sample validation for a subset of our total species (Lindgren et al. 2011). However, the model structure that most closely resembled the hierarchical model from Link and Sauer (2002) and Huang et al. (2017) consistently performed as well or better than models with more complicated spatial structures, so we continued analysis with this model only, and calculated abundance indices per stratum per year ($N_{i,t}$, Eq. 2.3), for each species independently. In Equation 2.3, A_i is the area of stratum i divided by the total area of all the strata in the region that the species is present in, calculated independently for each region, and z_i is the number of routes in stratum i that the species was present on divided by the total number of routes in the stratum (Link and Sauer 2002). We used the posterior distributions of the $N_{i,t}$ and the centroids of the strata, calculated in ArcGIS, to calculate yearly regional centroids for each species that met the sample size requirements (Eq. 2.4).

We used the annual centroid estimates to analyze latitudinal shifts in regional center of abundance by modeling the locations of the annual centroids against year (centered) in a linear model for each species. We calculated these models under a Bayesian framework and therefore were able to extract full posterior distributions for the regression slopes to determine if shifts were significant. We categorized shifts as northward if 95% of posterior samples for the regression slope were positive, and shifts as southward shift if 95% of posterior samples were negative. We conducted the centroid regression analyses using Hamiltonian Monte Carlo sampling in Rstanarm (Carpenter et al. 2017, Stan Development Team 2017), running each model with four chains with 1000 burn-in and 1000 sampling iterations per chains and assessed model convergence with Rhat and by visually assessing chain blending.

We calculated population status in each region for each species over the 23-year period by regressing regional annual abundance indices ($\widetilde{N}_t$, Eq. 2.4) with year. We classified regional species status as “Increasing” if 95% of posterior samples for the regression slope were positive, “Decreasing” if 95% of posterior samples for the regression slope were negative, and “No change” otherwise. We used linear models with the estimated shift velocities (regression slopes) as the response and status as the predictor to assess if population abundance trends over the study period predicted shift magnitude and direction.

$$\widetilde{N_t} = \sum_i N_{i,t} \tag{2.4}$$

Within each region, we used the estimated shift velocities to test our hypotheses about drivers of shifts in breeding distribution by modeling the effect of life history characteristics on average yearly shift velocity for each species. We included all estimated shift velocities, including those for species for which the shifts were not significant, in these analyses because there were relatively equal nonsignificant shifts in both directions and because their inclusion did not affect interpretation. We used linear mixed models to determine the best model for each hypothesis (Appendix A) and then tested combinations of these hypothesis terms to determine the best model overall. We included a random effect of taxonomic family in all models to control for the effect of phylogeny (Sol et al. 2005, Acampora et al. 2016, Donald et al. 2018). We used a combination of efficient leave-one-out cross validation (LOO-CV) and Bayesian model stacking (Yao et al. 2018) via the R package loo (Vehtari et al. 2018) for model selection, because on its own, LOO-CV was not a reliable metric for selecting a single best model from a set of many models because of potential overfitting and small sample sizes (Piironen and Vehtari 2017). Our goal with analysis was inference rather than prediction, so we used LOO-CV and Bayesian stacking to guide variable selection rather than computing averaged models. We summarized shifts as mean velocity (km per year) of region-specific species estimates.

Results

We found shifts in breeding distribution centroid in at least one region for 54 of the 73 North American migratory bird species and subspecies we studied (Fig. 2.2). The average velocity of poleward centroid shifts was 3.67 km per year, suggesting an average northward shift over the 23-year period of approximately 84 km. The average velocity of equatorward centroid shifts was 2.72 km per year, suggesting that, on average, species that shifted southward shifted about 63 km over the 23-year period. Yellow-breasted chats (*Icteria virens*) and barn swallows (*Hirundo rustica*) exhibited the greatest southward shifts, moving an average of 10 km per year and 9 km per year, respectively, between 1994 and 2017, with projected total shifts of over 200 km over the 23-year period.

The occurrence and analysis of some species in multiple regions resulted in an analysis of 142 centroids across all regions. Of the region-specific centroid shifts, 44% percent (n = 38) were equatorward and 55% (n = 48) were poleward (Fig. 2.3). Twenty-two species were analyzed in all three regions, and 26 species occurred in only one region (East only 15, west 9, central 2; Tables 2.1-2.3). Thirty-five species shifted northward in at least one region, and 27 species shifted southward in at least one region. Of the 43 species analyzed in two or three regions, 14 species shifted the same direction across all regions, 25 species had a shift in one region and no shift in another region, and six species had shifts in opposite directions in different regions (Tables 2.1-2.3). Only three species showed shifts in the same direction across all three regions: barn swallows and yellow-breasted chats both shifted southward across all three regions, and purple martins shifted northward across all three regions. The direction of shifts was not correlated with whether a species was increasing, decreasing, or stable in regional population abundance over the study period (Table 2.4).

In the eastern region, diet (invertebrate, vertebrate, or plant) and the presence or absence of differential migration between sexes appeared in the model that best predicted centroid shift velocity. In the western region, diet was the only predictor in the best performing model of centroid shift velocity. In both regions, breeding distribution centroids of raptors and other species catching primarily vertebrate prey have shifted north more than those of species eating primarily plants or invertebrates. In the eastern region, species eating primarily vertebrate prey shifted north with an average velocity of 7.53 km per year (Fig. 2.4), and the probability that a vertebrate-eating species in this region shifting northward was over 99%. Invertebrate-eating and plant-eating species did not shift in either direction (*95% CIs [-4.52, 5.66] and [-5.10, 5.86], respectively*). Similarly, in the west, species with vertebrate diets shifted northward with an average velocity of 2.47 km per year, and the probability of a vertebrate-eating species shifting northward was 75%. Western invertebrate-eating species (*95% CI [-6.86, 6.65]*) and plant-eating species (*95% CI [-8.66, 6.35]*) did not shift in either direction, although it was slightly more likely that a plant-eating species shifted southward (*63%*) than northward.

In the eastern region, the best-performing model also included whether or not a species displayed differential migration between sexes, either in timing of spring migration or in wintering latitude. Species that display differential migration were about 15% more likely to shift northward than those that do not have differential migration (Fig. 2.5).

In the central region, the best performing model included diet; if a species associates negatively, neutrally, or positively with humans; and is partially or completely migratory (Fig. 2.4-2.5). As in the east and west regions, the probability that species with vertebrate diets shifted northward was 81%, with an average velocity of 3.57 km per year. Species with primarily invertebrate or plant diets did not shift in either direction (*95% CIs [-8.18, 9.89] and [-11.28, 8.37]*), but species with plant diets were more likely to shift southward (*61%)* than northward. Species with positive associations with humans and species that are negatively affected by humans both shifted northward with an average velocity of 2.55 km per year, and the probability of a species of either type shifting northward was 70%. Human-neutral species were 10% more likely to shift southward than northward, although they did not show a strong tendency to shift in one direction (*95% CI [-11.12, 8.36]*). Migratory strategy was a covariate in the top model for this region, and although partial migrants were 18% more likely to shift northward than complete migrants, neither group shifted substantially in either direction (*95% CIs: complete [-10.30, 9.76], partial [-8.09, 11.83]*).

Discussion

We found that shifts in breeding distributions of migratory bird species are not uniform in direction, nor are shifts of one species consistent across regions. Across all regions, the breeding distributions of species with vertebrate diets shifted northward while invertebrate-eating species did not shift and plant-eating species showed a tendency to shift southward. In the east and central regions, migratory traits (differential migration in the east and migration strategy in the central) influenced shifts, and in the central region, tolerance of humans also explained shifts. Interestingly, we did not identify life history traits that were strongly predictive of southward shifts in breeding distributions. Taken together, these results suggest that life history is an important component of shifts, particularly northward shifts, in distribution for migratory birds, and regional variation in the direction of centroid shifts for many species suggests that mechanisms of distributional change are complex and likely interactions between life history, local environment including weather and land use, and the ultimate determinates of distributions.

Population status did not predict direction of centroid shift indicating that southward shifts in abundance centroid cannot be attributed to declines in abundance in the northern portion of the range with steady populations throughout the rest of the range. Rather, the lack of a relationship between population trends and centroid shift, especially when considered with the regional variation in shift direction for many species, suggests that drivers of distributional change, including environmental factors like weather and landscape, act on species and populations across multiple scales.

Life history traits, like diet, explained northward shifts in some species. Vertebrate-eating species consistently exhibited greater northward shifts than species with primarily invertebrate or plant diets. This may be because this group consisted predominantly of raptors, which tend to have larger body sizes and longer lifespans, leading to tolerance to a wide range of temperatures (Stillwell 2010) and relatively longer nesting and brood-rearing periods than smaller species (Lack 1968). Thus, these species may benefit from breeding farther north when they also advance the timing of reproduction (Heath et al. 2012, Martin et al. 2014) in response to earlier springs at higher latitudes where short breeding seasons previously constrained reproduction. Also, these relatively long-lived species can have a high degree in phenotypic plasticity associated with migration (Ogonowski and Conway 2009), which may increase their adaptive potential to cope with climate change.

We predicted that species with primarily insect or plant diets would shift southward because they are likely to use emergence of vegetation as a supplementary cue for reproduction during a relatively short period of resource abundance, and earlier springs with less latitudinal gradient in onset would cause them to encounter these cues earlier during migration. This prediction was supported for some insectivorous species, like bobolinks, which shifted southward and have been shown to track primary productivity with migration movements (Renfrew et al. 2013), and yellow-breasted chats and swallows, which showed large southward shifts in distributions across all regions, but was not supported for invertebrate-eating species as a whole. Species that primarily feed on seeds or vegetation showed a higher tendency to shift southward. These species may use primary productivity to time migration because, as described by the ‘green wave hypothesis’, moving northward with the progression of spring enables them to accumulate body mass and prepare for reproduction during migration (Drent et al. 1978, Madsen and Klaassen 2006, Van der Jeugd et al. 2009). Thus, with climate change, they may be able to accumulate the necessary resources to initiate breeding prior to returning the full distance to their original breeding grounds.

We found some evidence that differential migration predicted northward breeding distribution shifts in the eastern region, where species with differential migration were slightly more likely to shift poleward than species without differential migration. This relationship was the opposite of our expectation, because we predicted shifting breeding distributions southward would give males the same advantage as beginning spring migration earlier or wintering farther north – allowing them to arrive on the breeding grounds earlier to be more competitive securing a territory and mate. There was a lot of variation within both the species with and without differential migration, suggesting that there are more factors interacting with differential migration to affect distribution shifts.

Different variables predicted shifts in the central region than in the eastern or western regions. This may be because the central United States tends to have more homogeneous topography, elevation, and landscape characteristics than the other regions, so there may be fewer potential interacting or confounding factors compared to the east or west regions (Hovick et al. 2016). Species that are neutral to human activities did not show a strong tendency to shift, while both species that have a positive association with humans or that are negatively affected by humans shifted northward. Human-neutral species did not shift, so it is possible that these species have been able to adapt to local change, including anthropogenic landscape change and climate, behaviorally or via plasticity in physiological tolerance as an alternative to shifting spatial distribution (Parmesan et al. 2005). It has been suggested that southward distribution shifts occur because anthropogenic land use change constrains temperature-driven northward shifts in species that are sensitive to humans (Lawler et al. 2013, Chen et al. 2011). However, our results do not support this hypothesis, because if this were the case, species negatively affected by humans and land use change would have shifted south while positively-associated and neutral species shifted north. Instead, species that are positively- and negatively-associated with humans both shifted north, and their different responses to anthropogenic land use change suggest that there are different mechanisms underlying shifts between these groups and more factors interacting with temperature and land use to drive shifts.

We found that partial migrants in the central region were more likely to shift northward, while complete migrants were more likely to shift southward. This is not consistent with our expectation that responses to supplementary cues drives shifts, which would predict that partial migrants possess more plasticity that would allow them to terminate migration early if they encountered suitable breeding conditions at lower latitudes. However, this result is consistent with the hypothesis that changes in the ultimate factors associated with migration costs and benefits may be influencing distributions. Partial migrants' plasticity may allow them to track resources farther north, but complete migrants cannot extend migration northward because they tend to migrate longer distances than partial migrants (Sullivan et al. 2016) and are constrained by more 'hard-wired' migratory schedules (Ramenofsky et al. 2012). Therefore, because complete migrants rely on predictive cues, such as photoperiod, more than partial or short-distance migrants that may integrate supplementary cues, complete migrants may not be able to adjust adequately to advancing spring phenology (Knudsen et al. 2011, Visser and Both 2005), and the selective pressures of mistimed reproduction at higher latitudes favor stopping short during spring migration. Our results are consistent with Hovick et al.'s (2016) analysis of bird species occurring in the central United States that showed short-distance migrants are shifting northward while neotropical migrants are not shifting.

Our results highlight that distributional responses to global change are highly variable, and that equatorward shifts are a possible strategy for coping with change, despite a lack of hypotheses in the literature that predict shifts towards the equator. We did not find strong predictors of southward shifts in breeding distributions, and more hypotheses about potential mechanisms underlying these shifts are needed. Other studies have also shown equatorward shifts in distributions without clear evidence of an effect of life history (e.g. Zuckerberg et al. 2009) and our results that 55% of shifts were poleward and 44% of shifts were equatorward are similar to other multispecies studies (Huang et al. 2017, VanDerWal et al. 2012, Currie and Venne 2017), but the predominant hypothesis to explain distribution shifts in response to climate change, that species will shift distributions to track climate niches, only predicts poleward shifts. Migratory distances and wintering distributions are also shifting with climate change (Visser et al. 2009, La Sorte and Thompson 2007, Paprocki et al. 2014) and placing breeding distribution shifts in the context of these other phenomena and applying an evolutionary perspective of migration to them together may yield new insight into potential drivers of these shifts.

We expect that the interaction between changes to seasonality and migration is a key factor underlying southward shifts in breeding distributions. Maximizing the benefits of reproducing in a seasonal environment and minimizing the costs of annual long-distance movement is a key determinant of distributions for temperate migratory animals (Winger et al. 2018, Alerstam et al. 2003, Cox 1985). Variation in migratory genes is likely maintained in nearly all avian species, including residents, allowing for changes in migratory tendency if the benefits of moving long-distances between seasons no longer outweigh the costs (Pulido 2007, Greenberg and Marra 2005). Selection for a shortening of migration distances as a result of warmer temperatures has already been documented in fall migrations as many species are short-stopping to winter closer to the breeding grounds (Visser et al. 2009, Heath et al. 2012), and it is generally acknowledged that the tendency to migrate can change over time (Knudsen et al. 2011). Shortening of migration in response to climate change has been hypothesized only in regards to wintering distributions because philopatry is expected to play a strong role in breeding distributions (Winger et al. 2018). However, there is clear evidence of southward shifts in breeding distributions, and such shifts have the potential to compound the fitness benefits of shortening migration via wintering distributions. Additionally, there have been several instances of migratory birds establishing breeding populations outside of their historical breeding ranges by not completing spring migration (Yeh 2004, Macias-Duarte 2011, Garcia-Perez et al. 2013, Winkler et al. 2017, Van der Jeugd et al. 2009), indicating environmental change can drive responses not predicted by philopatry. For example, a breeding population of dark-eyed juncos (*Junco hyemalis*) was established in southern California, outside of the species' typical range, in the 1980s (Yeh 2004). This population remains on its breeding grounds year round, and has a breeding season twice as long as its ancestral population, resulting in higher productivity and suggesting that phenotypic plasticity in breeding season length has allowed the population to benefit from a mild climate in the area (Yeh and Price 2004). Thus, we expect that as seasonality becomes less pronounced throughout the temperate region, species will shift to a more sedentary strategy to decrease the costs of movement, directly inverse to a mechanism commonly proposed as a driver of the evolution of migration (Cox 1968, Pulido 2007, Pulido and Berthold 2010; Fig. 2.1). If a species' breeding distribution shifts south while its wintering distribution shifts north, then the species can either drastically shorten its annual migration or, in extreme cases, cease annual migration altogether (Cox 1985).

Our results show that breeding distributions of North American migratory birds are have shifted both poleward and equatorward in the past 23 years, likely in response to global change. Inter- and intraspecific and regional variation in shift direction suggest the mechanisms of distributional shifts are complex and likely reflect interactions between environmental factors and life history. While the drivers of equatorward shifts are still largely unclear, the multidirectional nature of shifts is not consistent with the idea that tracking climate warming is the primary driver of shifts. Thus, focused investigation into drivers of equatorward shifts is critical for a more complete picture of the effects of global change on distributions. We propose that migratory traits interact with environment to influence distributional shifts, and that viewing responses to global change through an evolutionary perspective may allow us to parse out drivers of distributions and adaptation.

Acknowledgements

We thank the Breeding Bird Survey staff at the USGS Patuxent Wildlife Research Center for maintaining and coordinating survey efforts and data, and to the volunteers who conduct surveys for the BBS. We are also grateful to Bryce Robinson and Casey Lott for their feedback during the development of this project, and to Håvard Rue for his help with the INLA code. This work was supported by the Michael W. Butler Ecological Research Award, the Department of Biological Sciences and the Raptor Research Center at Boise State University. Julie Heath is a coauthor on this manuscript.

REFERENCES

Acampora, H., O. Lyashevska, J.A. Van Franeker, and I. O'Connor. 2016. The use of beached bird surveys for marine plastic litter monitoring in Ireland. *Marine Environmental research* 120: 122-129.

Alerstam, T., A. Hedenström, and S. Åkesson. 2003. Long-distance migration: evolution and determinants. *Oikos* 103: 247-260.

Austin, G.E. and M.M. Rehfisch. 2005. Shifting nonbreeding distributions of migratory fauna in relation to climatic change. *Global Change Biology* 11: 31-38.

Bateman, B.L., A.M. Pidgeon, V.C. Radeloff, J. VanDerWal, W.E. Thogmartin, S.J. Vavrus, and P.J. Heglund. 2016. The pace of past climate change vs. potential bird distributions and land use in the United States. *Global Change Biology* 22: 1130-1144.

Bird Studies Canada and NABCI. 2016. Bird Conservation Regions. Published by Bird Studies Canada on behalf of the North American Bird Conservation Initiative. http://www.birdscanada.org/research/gislab/index.jsp?targetpg=bcr

Carpenter, B., A. Gelman, M. D. Hoffman, D. Lee, B. Goodrich, M. Betancourt, M. Brubaker, J. Guo, P. Li, and A. Riddell. 2017. Stan: A probabilistic programming language. *Journal of Statistical Software* 76. DOI 10.18637/jss.v076.i01

Chen, I., J.K. Hill, R. Ohlemüller, D.B. Roy, and C.D. Thomas. 2011. Rapid range shifts of species associated with high levels of climate warming. *Science* 333:1024-1026.

Cox, G. W. 1985. The evolution of avian migration systems between temperature and tropical regions of the New World. *The American Naturalist* 126: 451-474.

Cox, G. W. 1968. The role of competition in the evolution of migration. *Evolution* 22: 180-192.

Currie, D. J. and S. Venne. 2017. Climate change is not a major driver of shifts in the geographical distributions of North American birds. *Global Ecology and Biogeography* 26: 333-346.

Donald, P.F., B. Arendarczyk, F. Spooner, and G.M. Buchanan. 2018. Loss of forest intactness elevates global extinction risk in birds. *Animal Conservation* doi:10.1111/acv.12469

Drent, R., B. Weijand, and B. Ebbings. 1978. Balancing the energy budget of arctic breeding geese throughout the annual cycle: a progress report. *Verhandlungen der Ornithologischen Gesellschaft in Bayern* 23: 239-264.

Easterling, D. R., G. A. Meehl, C. Parmesan, S. A. Changnon, T. R. Karl, and L. O. Mearns. 2000. Climate extremes: Observations, modeling, and impacts. *Science* 289: 2068-2074.

Fu, Y. H., H.F. Zhao, S. Piao, M. Peaucelle, S. Peng, G. Zhou, P. Ciais, M. Huang, A. Menzel, J. Peñuelas, Y. Song, Y. Vitasse, Z. Zeng, and I.A. Janssens. Declining global warming effects on the phenology of spring leaf unfolding. *Nature* 526: 104-107.

Garcia-Perez, B., K. A. Hobson, R. L. Powell, C. J. Still, and G. H. Huber. 2013. Switching hemispheres: a new migration strategy for the disjunct Argentinean breeding population of barn swallows (*Hirundo rustica*). *PLoS ONE* 8:e55654.

Greenberg, R.S. and P.P. Marra. 2005. *Birds of Two Worlds: The Ecology and Evolution of Migration*. Johns Hopkins University Press, Baltimore, MD, USA.

Gwinner, E. 1977. Circannual rhythms in bird migration. *Annual Review of Ecology and Systematics* 8: 381-405.

Heath, J.A., K. Steenhof, and M.A. Foster. 2012. Shorter migration distances associated with higher winter temperatures suggest a mechanism for advancing nesting phenology of American kestrels *Falco sparverius*. *Journal of Avian Biology* 43: 376-384.

Hitch, A. T. and P. L. Leberg. 2007. Breeding distributions of North American bird species moving north as a result of climate change. *Conservation Biology* 21: 534-539.

Hovick, T. J., B. W. Allred, D. A. McGranahan, M. W. Palmer, R. D. Elmore, and S. D. Fuhlendorf. 2016. Informing conservation by identifying range shift patterns across breeding habitats and migration strategies. *Biodiversity and Conservation* 25: 345-356.

Huang, Q., J. R. Sauer, R. O. Dubayah. 2017. Multidirectional abundance shifts among North American birds and the relative influence of multifaceted climate factors. *Global Change Biology* 23: 3610-3622.

Hughes, L. 2000. Biological consequences of global warming: is the signal already apparent? *Trends in Ecology and Evolution* 15: 286-287.

Kelly, J.F., K.G. Horton, P.M. Stepanian, K.M. de Beurs, T. Fagin, E.S. Bridge, and P.B. Chison. 2016. Novel measures of continental-scale avian migration phenology related to proximate environmental cues. *Ecosphere* 7: :e01434. 10.1002/ecs2.1434

Knudsen, E., A. Lindén, C. Both, N. Jonzén, F. Pulido, N. Saino, W.J. Sutherland, L.A. Bach, T. Coppack, T. Ergon, P. Gienapp, J.A. Gill, O. Gordo, A. Hedenström, E. Lehikoinen, P.P. Marra, A.P. Møller, A.L.K. Nilsson, G. Péron, E. Ranta, D. Rubolini, T.H. Sparks, F. Spina, C.E. Studds, S.A. Sæther, P. Tryjanowski, and N.C. Stenseth. 2011. Challenging claims in the study of migratory birds and climate change. *Biological Reviews* 86: 928-946.

Körner, C. and D. Basler. 2010. Phenology under global warming. *Science* 327: 1461-1642.

La Sorte, F. A., D. Fink, W.M. Hochachka, J.P. DeLong and S. Kelling. 2014. Spring phenology of ecological productivity contributes to the use of looped migration strategies by birds. *Proceedings of the Royal Society B* 281: 20140984.

La Sorte, F. A. and F. R. Thompson. 2007. Poleward shifts in winter ranges of North American birds. *Ecology* 88: 1803-1812.

Lack, D. L. 1968. Ecological adaptations for breeding in birds. London: Methuen.

Lawler, J. J., A. S. Ruesch, J. D. Olden, and B. H. McRae. 2013. Projected climate-driven faunal movement routes. *Ecology Letters* 16: 1014-1022.

Lehikoinen, E. and T.H. Sparks. 2010. Changes in migration. In *Effects of Climate Change on Birds* (eds. A. P. Møller, W. Fiedler, and P. Berthold). Oxford University Press, Oxford, UK, 89-112.

Lenoir, J., J-.C. Gégout, A. Guisan, P. Vittoz, T. Wohlgemuth, N.E. Zimmerman, S. Dullinger, H. Pauli, W. Willner, and J-.C. Svenning. 2010. Going against the flow: potential mechanisms for unexpected downslope range shifts in a warming climate. *Ecography* 33:295-303.

Lindgren, F. and H. Rue. 2015. Bayesian Spatial Modelling with R-INLA. *Journal of Statistical Software* 63: 1-25.

Lindgren, F., H. Rue, and J. Lindstrom. 2011. An explicit link between Gaussian fields and Gaussian Markov random fields: The SPDE approach (with discussion). *Journal of the Royal Statistical Society, Series B* 73: 423-498.

Link, W. A and J. R. Sauer. 1998. Estimating population change from count data: application to the North American Breeding Bird Survey. *Ecological Applications* 8: 258-268.

Link, W. A. and J. R. Sauer. 2002. A hierarchical analysis of population change with application to cerulean warblers. *Ecology* 83: 2832-2840.

Macias-Duarte, A. 2011. Change in migratory behavior as a possible explanation for Burrowing Owl population declines in northern latitudes. PhD Dissertation. The University of Arizona, Tucson, AZ, USA.

Madsen, J. and M. Klaassen. 2006. Assessing body condition and energy budget components by scoring abdominal profiles in free-ranging pink-footed geese *Anser brachyrhynchus. Journal of Avian Biology* 37: 283-287.

Martin, R. O., L. Sebele, A. Koeslag, O. Curtis, F. Abadi, and A. Amar. 2014. Phenological shifts assist colonization of a novel environment in a range-expanding raptor. *Oikos* 123: 1457-1468.

Massimino, D., A. Johnston, and J.W. Pearce-Higgins. 2015. The geographical range of British birds expands during 15 years of warming. *Bird Study* 62: 523-534.

Ogonowski, M.S. and C.J. Conway. 2009. Migratory decisions in birds: extent of genetic versus environmental control. *Oecologia* 161: 199-207.

Paprocki, N., J. A. Heath, and S. J. Novak. 2014. Regional distribution shifts help explain local changes in wintering raptor abundance: implications for interpreting population trends. *PLoS ONE* 9: e86814.

Paradis, E., S. R. Baillie, W. J. Sutherland, and R. D. Gregory. 1998. Patterns of natal and breeding dispersal in birds. *Journal of Animal Ecology* 67: 518-536.

Pardieck, K. L., D. J. Ziolkowski Jr., M. Lutmerding and M.-A. R. Hudson. 2018. North American Breeding Bird Survey Dataset 1966 - 2017, version 2017.0. U.S. Geological Survey, Patuxent Wildlife Research Center. https://doi.org/10.5066/F76972V8. Accessed 14 May 2018.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics* 37: 637-669.

Parmesan, C., S. Gaines, L. Gonzalez, D.M. Kaufman, J. Kingsolver, A.T. Peterson, and R. Sagarin. 2005. Empirical perspectives on species borders: from traditional biogeography to global change. *Oikos* 108: 58-75.

Peñuelas, J. and I. Filella. 2001. Responses to a warming world. *Science* 294: 793-795.

Piironen, J. and A. Vehtari. 2017. Comparison of Bayesian predictive methods for model selection. *Statistics and Computing* 27: 711-735.

Potvin, D. A., K. Välimäki, and A. Lehikoinen. 2016. Differences in shifts of wintering and breeding ranges lead to changing migration distances in European birds. *Journal of Avian Biology* 47: 619-628.

Pulido, F. 2007. The genetics and evolution of avian migration. *BioScience* 57:165-174.

Pulido, F. and P. Berthold. 2010. Current selection for lower migratory activity will drive the evolution of residency in a migratory bird population. *Proceedings of the National Academy of Sciences* 107: 7341-7346.

R Development Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/**.**

Ramenofsky, M., J.M. Cornelius, and B. Helm. 2012. Physiological and behavioral responses of migrants to environmental cues. *Journal of Ornithology* 153: 181-191.

Rapacciuolo, G., S. P. Maher, A. C. Schneider, T. T. Hammond, M. D. Jabis, R. E. Walsh, K. J. Iknayan, G. K. Walden, M. F. Oldfather, D. D. Ackerly, and S. R. Bessinger. 2014. Beyond a warming fingerprint: individualistic biogeographic responses to hereogeneous climate change in California. *Global Change Biology* 20: 2841-2855.

Renfrew, R. B., D. Kim, N. Perlut, J. Smith, J. Fox, and P. P. Marra. 2013. Phenological matching across hemispheres in a long-distance migratory bird. *Diversity and Distributions* 19: 1008-1019.

Renner, S.S. and C.M. Zohner. 2018. Climate change and phenological mismatch in trophic interactions among plants, insects, and vertebrates. *Annual Reviews* 49: 165-182.

Richardson, A.D., T.F. Keenan, M. Migliavacca, Y. Ryu, O. Sonnentag, and M. Toomey. 2013. Climate change, phenology, and phenological control of vegetation feedbacks to the climate system. *Agricultural and Forest Meteorology* 169: 156-173.

Rodewald, P. (Editor). 2015. The Birds of North America: https://birdsna.org. Cornell Laboratory of Ornithology, Ithaca, NY.

Rue, H., S. Martino, and N. Chopin. 2009. Approximate Bayesian inference for latent Gaussian models using integrated nested Laplace approximations (with discussion). *Journal of the Royal Statistical Society, Series B* 71: 319-392.

Saino, N., R. Ambrosini, D. Rubolini, J. von Hardenberg, A. Provenzale, K. Hüppop, O. Hüppop, A. Lehikoinen, E. Lehikoinen, K. Rainio, M. Romano, and L. Sokolov. 2010. Climate warming, ecological mismatch at arrival and population decline in migratory birds. *Proceedings of the Royal Society B* 278: 20101778.

Saino, N., T. Szep, M. Romano, D. Rubolini, F. Spina, and A.P. Møller. 2004. Ecological conditions during winter predict arrival date at the breeding quarters in a trans-Saharan migratory bird. *Ecological Letters* 7: 21-25.

Sauer, J. R., W. A. Link, J. E. Fallon, K. L. Pardieck, and D. J. Ziolkowski. 2013. The North American Breeding Bird Survey 1966-2011: Summary analysis and species accounts. *North American Fauna* 7: 1-32.

Sol, D., R. P. Duncan, T. M. Blackburn, P. Cassey, and L. Lefebvre. 2005. Big brains, enhanced cognition, and response of birds to novel environments. *Proceedings of the National Academy of Sciences of the United States of America* 102: 5460-5465.

Somero, G.N. 2010. The physiology of climate change: how potentials for acclimatization and genetic adaptation will determine 'winners' and 'losers'. *Journal of Experimental Biology* 213: 912-920.

Stan Development Team. 2017. *RStan: the R interface to Stan*. R package version 2.16.2. http://mc-stan.org

Stillwell, R.C. 2010. Are latitudinal clines in body size adaptive? *Oikos* 119: 1387-1390.

Sullivan, A. R., D. J. Flaspohler, R. E. Frose, and D. Ford. 2016. Climate variability and the timing of spring raptor migration in eastern North America. *Journal of Avian Biology* 47: 208-218.

Van der Jeugd, H.P., G. Eichhorn, K.E. Litvins, J. Stahl, K. Larsson, A.J. Van der Graaf, and R.H. Drent. 2009. Keeping up with early springs: rapid range expansion in an avian herbivore incurs a mismatch between reproductive timing and food supply. *Global Change Biology* 15: 1057-1071.

VanDerWal, J., H.T. Murphy, A.S. Kutt, G.C. Perkins, B.L. Bateman, J.J. Perry, and A.E. Reside. 2012. Focus on poleward shifts in species' distribution underestimates the fingerprint of climate change. *Nature Climate Change* 3: 239-243.

Vehtari, A., J. Gabry, Y. Yao, and A. Gelman. 2018. “loo: Efficient leave-one-out cross-validation and WAIC for Bayesian models.” R package version 2.0.0, <URL: https://CRAN.R-project.org/package=loo>.

Virkkala, R. and A. Lehikoinen. 2014. Patterns of climate-induced density shifts of species: Poleward shifts faster in northern boreal birds than in southern birds. *Global Change Biology* 20: 2995-3003.

Visser, M.E., A.C. Perdeck, J.H. van Balen, and C. Both. 2009. Climate change leads to decreasing bird migration distances. *Global Change Biology* 15: 1859-1865.

Visser, M.E., and C. Both. 2005. Shifts in phenology due to global climate change: the need for a yardstick. *Proceedings of the Royal Society B* 272: 2561-2569.

Visser, M.E., C. Both, and M.M. Lambrechts. 2004. Global climate change leads to mistimed avian reproduction. *Advances in Ecological Research* 35: 89-110.

Vitasse, Y., C. Signarbieux, and Y.H. Fu. 2018. Global warming leads to more uniform spring phenology across elevations. *Proceedings of the National Academy of Sciences* 115: 1004-1008.

Wingfield, J.C., T.P. Hahn, R. Levin, and P. Honey. 1992. Environmental predictability and control of gonadal cycles in birds. *Journal of Experimental Zoology* 261: 214-231.

Winger, B. M., G. G. Auteri, T. M. Pegan, and B. C. Weeks. 2018. A long winter for the Red Queen: rethinking the evolution of seasonal migration. *Biological Reviews* doi: 10.1111/brv.12476

Winkler, D.W., F.A. Gandoy, J.I. Areta, M.J. Iliff, E. Rakhimberdiev, K.J. Kardynal, and K.A. Hobson. 2017. Long-distance range expansion and rapid adjustment of migration in a newly established population of barn swallows breeding in Argentina. *Current Biology* 27: 1080-1084.

Yao, Y., A. Vehtari, D. Simpson, and A. Gelman. 2018. Using stacking to average Bayesian predictive distributions (with discussion). *Bayesian Analysis* 13: 917-1007.

Yeh, P.J. 2004. Rapid evolution of a sexually selected trait following population establishment in a novel habitat. *Evolution* 58: 166-174.

Yeh, P.J. and T.D. Price. 2004. Adaptive phenotypic plasticity and the successful colonization of a novel environment. *The American Naturalist* 164: 531-542.

Zuckerberg, B., A. M. Woods, and W. F. Porter. 2009. Poleward shifts in breeding bird distributions in New York State. *Global Change Biology* 15: 1866-83.

Table 2.1. Summary of eastern region breeding distribution centroid abundance shift results, 1994-2017. Bold type indicates significant shift velocities, inferred by 95% of posterior samples positive (north shift) or negative (south shift). Population status was computed at the regional level by regressing the sum of all stratum abundance weights by year. (Increasing: 95% of posterior samples for regression slope > 0; decreasing: 95% of posterior samples < 0)

Common Name	Shift Direction	Shift Velocity (km/yr)	Projected Total Shift (km)	Population Status
Osprey	North	**6.66**	153.24	Increasing
Red-tailed Hawk	North	**2.13**	48.88	Increasing
Northern Harrier	North	**11.67**	268.50	Increasing
Sharp-shinned Hawk	North	**9.67**	222.40	No change
Killdeer	South	**-3.81**	-87.56	Decreasing
Chimney Swift	North	**1.99**	45.68	Decreasing
Ruby-throated Hummingbird	North	**4.30**	98.92	Increasing
Northern Flicker (Yellow-shafted)	North	**4.91**	112.90	Decreasing
American Kestrel	North	**2.32**	53.46	Decreasing
Acadian Flycatcher	No shift	0.05	No shift	Increasing
Least Flycatcher	No shift	1.04	No shift	Decreasing
Eastern Phoebe	South	**-4.06**	-93.32	Increasing
Eastern Kingbird	South	**-1.32**	-30.32	Decreasing
Loggerhead Shrike	No shift	0.84	No shift	Decreasing
Red-eyed Vireo	North	**1.83**	42.06	Increasing
White-eyed Vireo	No shift	0.21	No shift	Increasing

Yellow-throated Vireo	No shift	0.17	No shift	Increasing
Warbling Vireo	South	**-0.64**	-14.69	Increasing
Bell's Vireo	No shift	0.98	No shift	Increasing
Purple Martin	North	**1.48**	34.14	Decreasing
Barn Swallow	South	**-4.02**	-92.48	Decreasing
Tree Swallow	South	**-5.43**	-124.94	Decreasing
Red-breasted Nuthatch	No shift	1.25	No shift	Increasing
Sedge Wren	North	**1.73**	39.69	Decreasing
Marsh Wren	No shift	-0.62	No shift	Decreasing
House Wren	No shift	0.16	No shift	Increasing
Blue-gray Gnatcatcher	No shift	0.19	No shift	No change
Ruby-crowned Kinglet	North	**2.33**	53.69	Increasing
Eastern Bluebird	No shift	0.00	No shift	Increasing
Wood Thrush	South	**-2.18**	-50.22	Decreasing
American Robin	South	**-1.64**	-37.80	Increasing
Cedar Waxwing	No shift	-1.23	No shift	Decreasing
Pine Warbler	North	**5.34**	122.83	Increasing
Yellow Warbler	North	**2.73**	62.74	Decreasing
Common Yellowthroat	North	**3.34**	76.72	Decreasing
Kentucky Warbler	No shift	0.17	No shift	Decreasing
Yellow-throated Warbler	North	**0.61**	13.94	Increasing
Black-and-white Warbler	No shift	0.26	No shift	Decreasing
Chestnut-sided Warbler	No shift	-0.99	No shift	Decreasing

Worm-eating Warbler	No shift	-0.22	No shift	Increasing
Hooded Warbler	North	**1.97**	45.34	Increasing
Prairie Warbler	South	**-1.72**	-39.50	Decreasing
American Redstart	No shift	0.77	No shift	Decreasing
Black-throated Blue Warbler	North	**2.13**	49.03	Increasing
Canada Warbler	North	**3.15**	72.38	Decreasing
Nashville Warbler	No shift	1.50	No shift	No change
Yellow-breasted Chat	South	**-0.65**	-14.91	Decreasing
Henslow's Sparrow	South	**-1.77**	-40.69	Increasing
Song Sparrow	North	**1.39**	32.05	Decreasing
Dark-eyed Junco (Slate-colored Junco)	North	**3.68**	84.60	No change
Bobolink	South	**-1.62**	-37.18	Decreasing
Baltimore Oriole	South	**-1.11**	-25.44	Decreasing
Purple Finch	No shift	1.57	No shift	Decreasing
American Goldfinch	No shift	0.18	No shift	No change

Table 2.2. Summary of western region breeding distribution centroid shift results, 1994-2017. Bold type indicates significant shift velocities, inferred by 95% of posterior samples positive (north shift) or negative (south shift). Population status was computed at the regional level by regressing the sum of all stratum abundance weights by year. (Increasing: 95% of posterior samples for regression slope > 0; decreasing: 95% of posterior samples < 0)

Common Name	Shift Direction	Shift Velocity (km/yr)	Projected Total Shift (km)	Population Status
Osprey	No shift	0.79	No shift	Increasing
Red-tailed Hawk	North	**0.83**	19.07	Increasing
Golden Eagle	No shift	1.47	No shift	Decreasing
Northern Harrier	No shift	1.80	No shift	Increasing
Swainson's Hawk	No shift	0.04	No shift	Increasing
Sharp-shinned Hawk	North	**11.35**	261.02	Decreasing
Killdeer	South	**-2.40**	-55.27	Decreasing
Long-billed Curlew	No shift	0.97	No shift	Increasing
Vaux's Swift	No shift	-2.76	No shift	Decreasing
Northern Flicker (Red-shafted)	No shift	-0.98	No shift	Decreasing
American Kestrel	South	**-2.31**	-53.21	Decreasing
Prairie Falcon	No shift	1.03	No shift	Increasing
Dusky Flycatcher	South	**-3.58**	-82.38	Decreasing
Gray Flycatcher	South	**-1.58**	-36.29	Increasing
Western Wood-Pewee	South	**-1.04**	-23.90	Decreasing
Say's Phoebe	No shift	0.81	No shift	Increasing

Eastern Kingbird	North	**0.77**	17.74	Increasing
Loggerhead Shrike	North	**3.07**	70.70	Decreasing
Red-eyed Vireo	No shift	-0.30	No shift	Decreasing
Warbling Vireo	North	**4.81**	110.70	Increasing
Purple Martin	North	**9.52**	219.05	Increasing
Barn Swallow	South	**-9.04**	-208.01	Decreasing
Tree Swallow	No shift	-0.60	No shift	Decreasing
Red-breasted Nuthatch	No shift	0.14	No shift	Decreasing
Marsh Wren	North	**2.37**	54.57	Increasing
House Wren	North	**2.42**	55.69	Increasing
Blue-gray Gnatcatcher	No shift	-0.60	No shift	Increasing
Ruby-crowned Kinglet	No shift	1.73	No shift	Decreasing
Western Bluebird	North	**2.54**	58.40	Increasing
Mountain Bluebird	North	**2.14**	49.20	No change
American Robin	North	**1.11**	25.42	Decreasing
Sage Thrasher	No shift	-0.34	No shift	Decreasing
Cedar Waxwing	No shift	-1.57	No shift	Decreasing
Yellow Warbler	South	**-3.06**	-70.30	Decreasing
Common Yellowthroat	No shift	0.20	No shift	Increasing
Nashville Warbler	North	**4.69**	107.90	No change
Black-throated Gray Warbler	South	**-1.83**	-41.99	Decreasing

Yellow-breasted Chat	South	**-1.64**	-37.70	Increasing
Song Sparrow	South	**-1.66**	-38.25	Decreasing
Dark-eyed Junco (Oregon Junco)	South	**-4.13**	-94.97	Decreasing
Dark-eyed Junco (Gray-headed Junco)	South	**-3.17**	-72.81	No change
Purple Finch	No shift	0.12	No shift	Decreasing
American Goldfinch	South	**-2.96**	-68.19	Decreasing
Cassin's Finch	No shift	-0.72	No shift	Decreasing

Table 2.3. Summary of central region breeding distribution centroid shift results, 1994-2017. Bold type indicates significant shift velocities, inferred by 95% of posterior samples positive (north shift) or negative (south shift). Population status was computed at the regional level by regressing the sum of all stratum abundance weights by year. (Increasing: 95% of posterior samples for regression slope > 0; decreasing: 95% of posterior samples < 0)

Common Name	Shift Direction	Shift Velocity (km/yr)	Projected Total Shift (km)	Population Status
Red-tailed Hawk	South	**-1.32**	-30.33	Increasing
Golden Eagle	North	**17.62**	405.35	Increasing
Northern Harrier	No shift	0.98	No shift	Decreasing
Swainson's Hawk	South	**-2.55**	-58.61	Increasing
Sharp-shinned Hawk	No shift	6.93	No shift	No change
Killdeer	No shift	0.05	No shift	Decreasing
Long-billed Curlew	No shift	-1.16	No shift	Decreasing
Chimney Swift	North	**5.49**	126.24	Decreasing
Ruby-throated Hummingbird	No shift	-2.61	No shift	No change
Northern Flicker (Yellow-shafted)	North	**2.08**	47.73	Decreasing
Northern Flicker (Red-shafted)	North	**3.88**	89.21	Decreasing
Northern Flicker (unid. Red/Yellow shafted)	No shift	4.97	No shift	Increasing
American Kestrel	No shift	-1.26	No shift	Decreasing

Prairie Falcon	No shift	-0.23	No shift	Increasing
Least Flycatcher	South	**-1.72**	-39.53	Increasing
Western Wood-Pewee	North	**1.74**	39.93	No change
Say's Phoebe	North	**2.27**	52.17	No change
Eastern Phoebe	South	**-2.28**	-52.50	Increasing
Eastern Kingbird	North	**1.51**	34.81	Decreasing
Loggerhead Shrike	North	**6.37**	146.52	Decreasing
Red-eyed Vireo	North	**3.23**	74.39	Increasing
Yellow-throated Vireo	No shift	-6.54	No shift	Increasing
Warbling Vireo	South	**-2.91**	-67.03	Increasing
Bell's Vireo	No shift	0.27	No shift	Increasing
Purple Martin	North	**1.38**	31.71	Decreasing
Barn Swallow	South	**-2.63**	-60.54	Decreasing
Tree Swallow	South	**-2.62**	-60.26	Increasing
Sedge Wren	No shift	0.68	No shift	No change
Marsh Wren	North	**0.81**	18.74	Increasing
House Wren	North	**1.66**	38.16	Decreasing
Blue-gray Gnatcatcher	No shift	0.14	No shift	Increasing
Mountain Bluebird	No shift	-1.94	No shift	Decreasing
Eastern Bluebird	No shift	-0.88	No shift	Increasing
American Robin	North	**1.35**	31.06	Increasing
Cedar Waxwing	South	**-3.54**	-81.36	Increasing

Chestnut-collared Longspur	No shift	-0.22	No shift	Decreasing
Yellow Warbler	No shift	-0.28	No shift	Increasing
Common Yellowthroat	North	**4.29**	98.61	Decreasing
American Redstart	North	**1.29**	29.75	Increasing
Yellow-breasted Chat	South	**-10.01**	-230.30	Increasing
Song Sparrow	No shift	0.13	No shift	Increasing
Bobolink	South	**-0.34**	-7.87	Increasing
Baltimore Oriole	South	**-4.06**	-93.33	Decreasing
American Goldfinch	South	**-0.84**	-19.28	Decreasing

Table 2.4. Ninety-five percent (95%) credible intervals for breeding distribution centroid shift velocity (km per year) by regional population status for East, West, and Central regions from 1994-2017. Population status did not predict shift velocity, except in the east region, where species with no change or an increase in abundance index were slightly more likely than species with a decreasing population abundance to shift north.

	East	West	Central
No change	(-3.51, 9.49)	(-6.60, 8.61)	(-7.81, 10.86)
Increasing	(-4.34, 7.35)	(-5.22, 8.03)	(-9.28, 8.33)
Decreasing	(-5.65, 5.99)	(-7.42, 6.09)	(-7.80, 9.55)

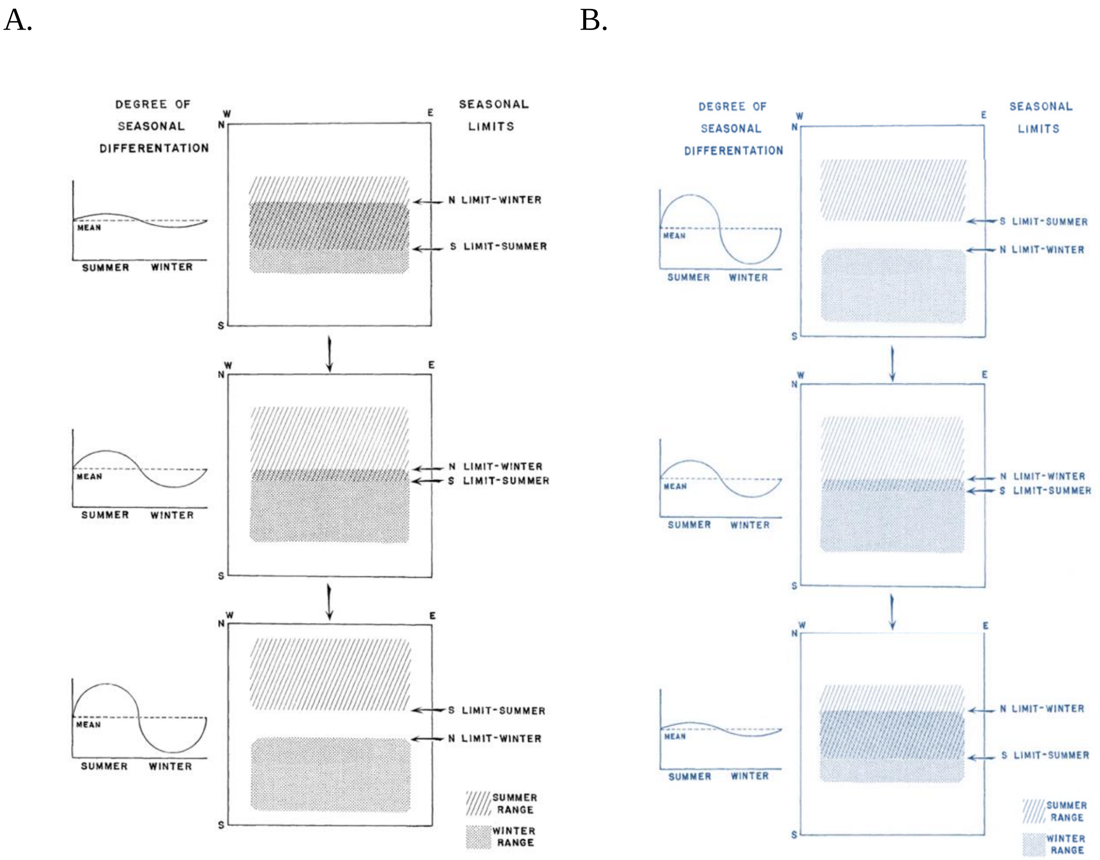

Figure 2.1. (A) Conceptual diagram reprinted from Cox (1968), illustrating the influence of seasonality on the transition of a partial migrant to a migrant with disjunct breeding and wintering ranges. (B) Reversal of panel A, schematic illustrating how under current climate change, as seasonality becomes less pronounced throughout part of the temperate region (warming winter temperatures), Cox's theory can also explain a shift of a migrant to a less migratory strategy via the shortening of the fall and spring legs of migration.

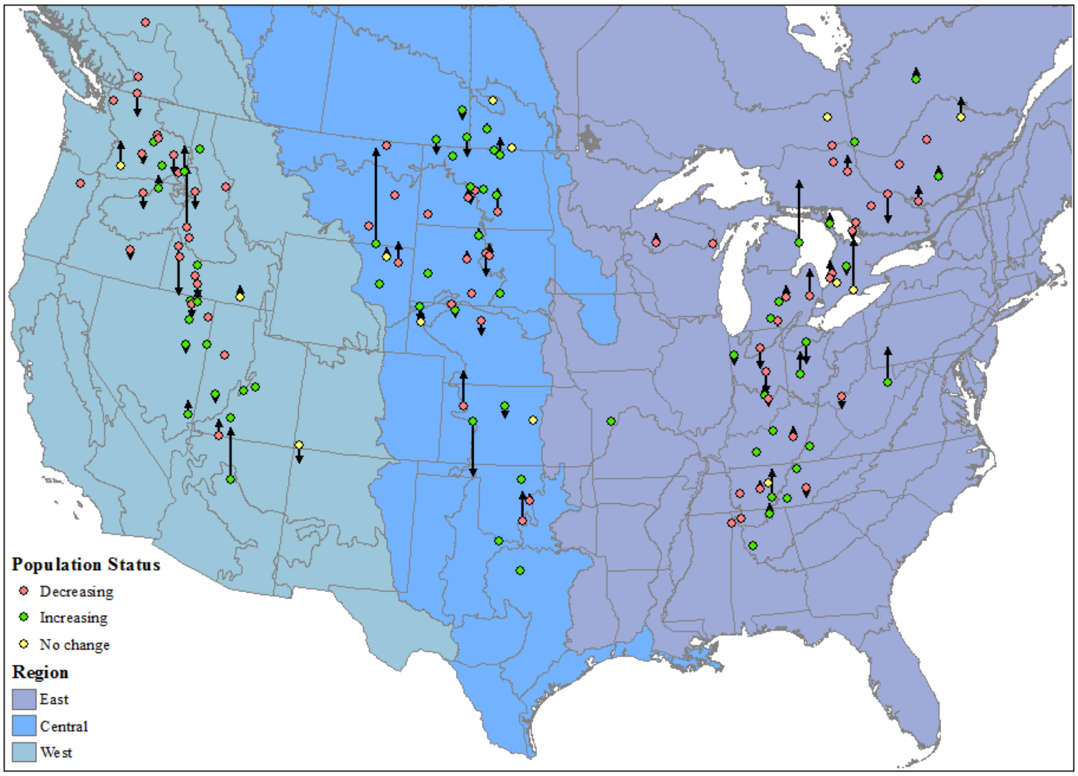

Figure 2.2. Map illustrating regions, strata, and centroids for 73 species and subspecies of North American migratory birds. Strata, outlined in black, are the intersections between Bird Conservation Region boundaries and state or province boundaries. Dots are regional species centroids in 1994 and color represents whether regional species abundance, estimated using a hierarchical model to account for stratum, route, and observer sampling bias, decreased (orange), increased (green), or did not change (yellow) from 1994-2017. Fifty-four regional species centroids shifted over the 23-year period, and black arrows illustrate the projected latitudinal shift of the species centroid, based on the average shift velocity (km per year) for the species over the 23 years. Note that these arrows do not illustrate longitudinal shift in centroid, which is outside the scope of this study.

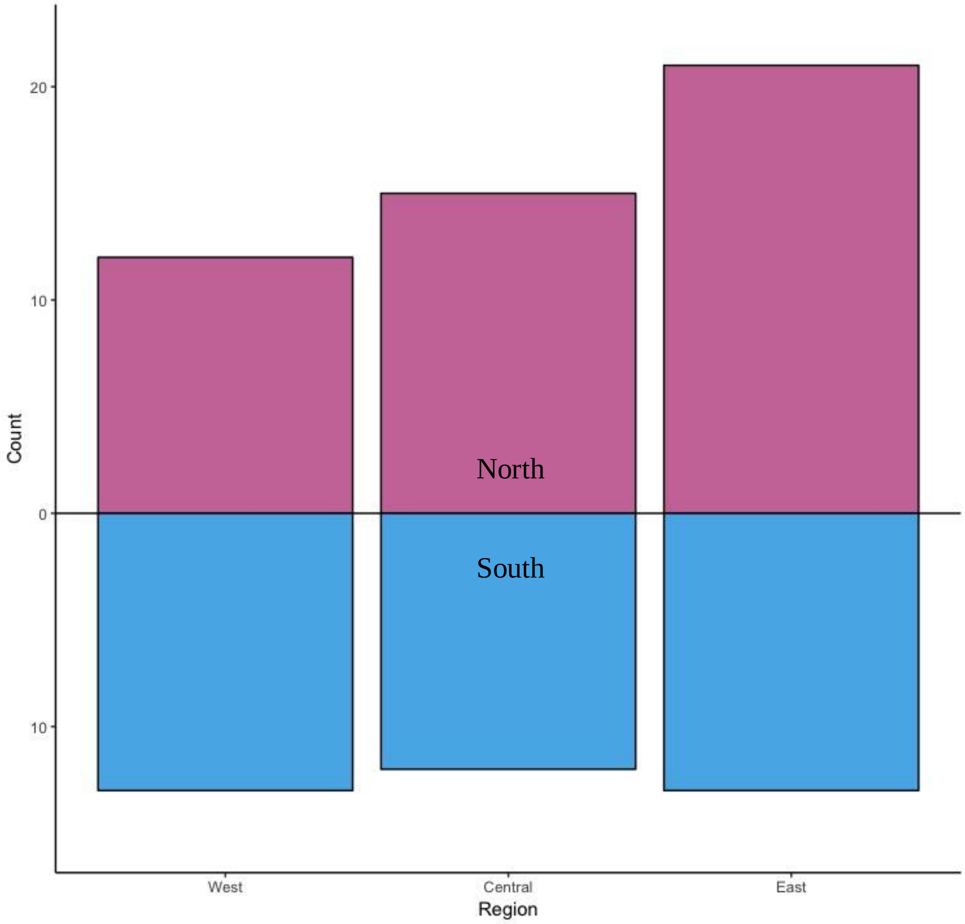

Figure 2.3. Significant shifts in breeding distribution centroids for North American migratory bird species by region from 1994 – 2017.

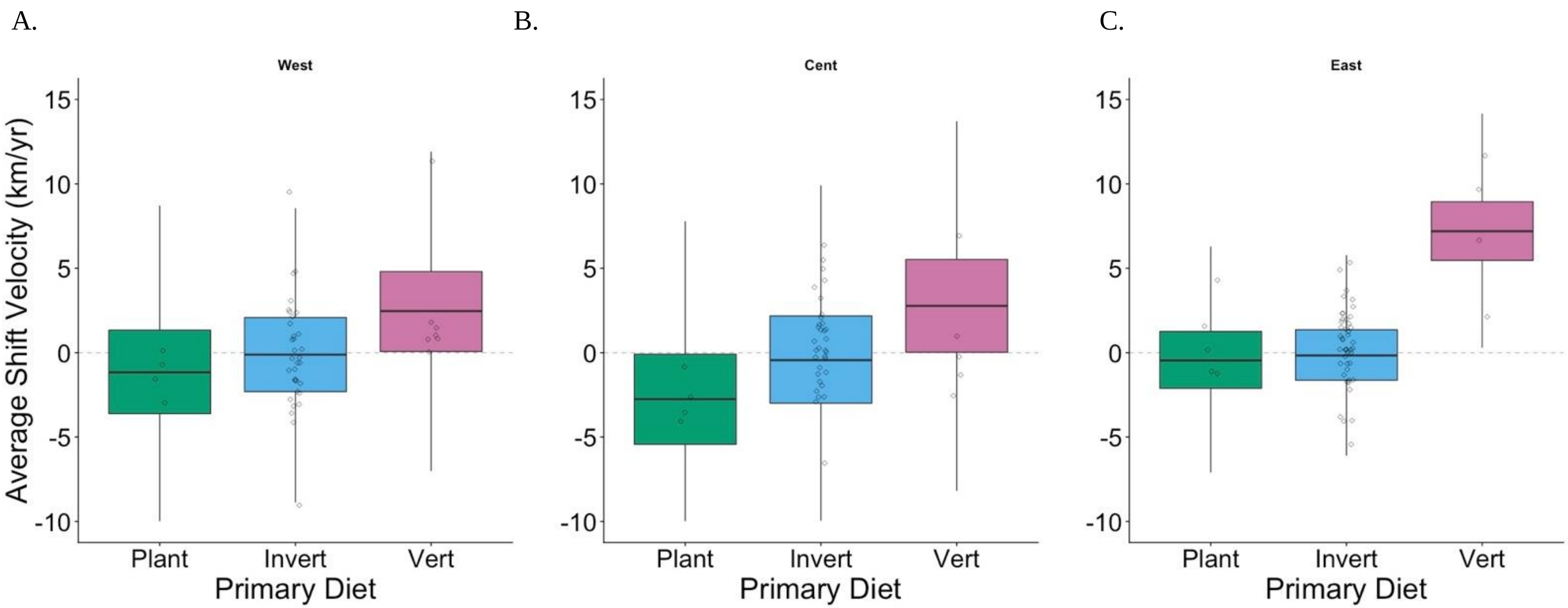

Figure 2.4. **Relationship between primary diet and species' breeding distribution shift velocities in the (A) western, (B) central, and (C) eastern regions from 1994-2017 based on predictions for simulated data from the posterior distributions of the best performing model for each region. Vertebrate-eating species shifted northward with average velocities of 2.5, 3.6 and 7.5 km per year in the west, central, and east regions respectively. Species with primarily invertebrate diets did not shift in either direction, and plant-eating species were slightly more likely to shift southward than northward.**

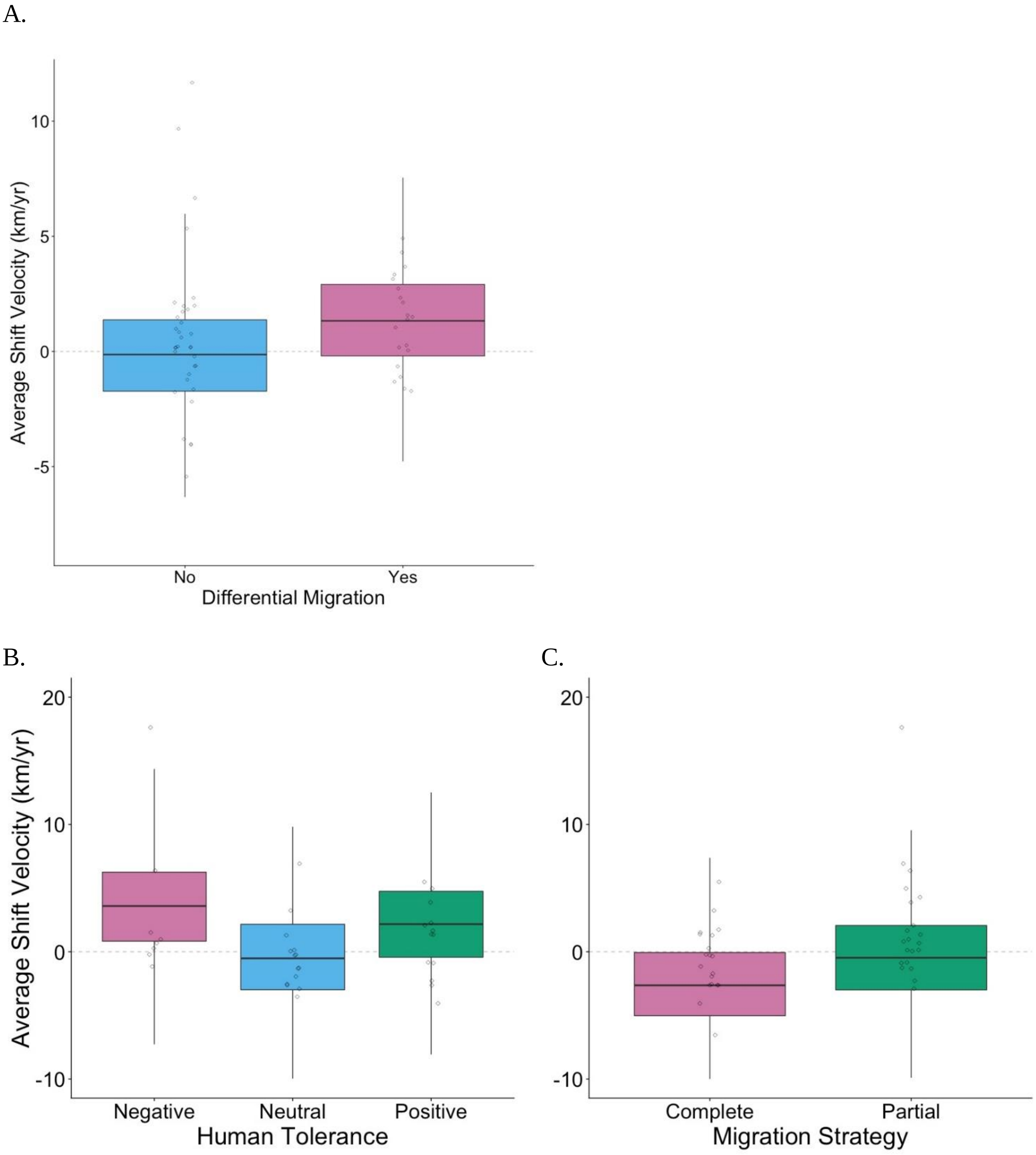

Figure 2.5. **Relationship between (A) presence of differential migration in the eastern region, (B) human tolerance, and (C) migratory strategy in the central region and species' breeding distribution shift velocities from 1994-2017 based on predictions for simulated data from the posterior distributions of the best performing model for each region. (A) In the eastern region, species with differential migration were slightly more likely to shift northward than those that do not display differential**

migration. (B) In the central region, species that are negatively affected by humans and those with positive associations with humans shifted northward over the 23-year period, while species that are not affected by humans showed a slight tendency to shift southward. (C) In the central region, partial migrants were more likely to shift northward and complete migrants were more likely to shift southward, although neither group shifted substantially in either direction.

Supplemental Material

Table S2.1. **List of species for which we calculated breeding season abundance centroids to estimate shifts in distribution centroid from 1994-2017. Each species was analyzed in the region(s) listed (East, Central, West) and diet and habitat traits used to model distribution shifts were compiled from each species' Birds of North America Online account (Rodewald 2015, ed.).**

Common Name	**Scientific Name**	**Region**	**Family**	**Primary Diet**	**Foraging Type**	**Habitat Specialist**	**Human Association**	**Territorial**
Osprey	*Pandion haliaetus*	EW	Pandionidae	Vertebrate	--	No	Positive	No
Red-tailed Hawk	*Buteo jamaicensis*	ECW	Accipitridae	Vertebrate	Aerial, sitwait	No	Neutral	Yes
Golden Eagle	*Aquila chrysaetos*	CW	Accipitridae	Vertebrate	Aerial, sitwait	No	Negative	Yes
Northern Harrier	*Circus hudsonius*	ECW	Accipitridae	Vertebrate	Aerial	No	Negative	No
Swainson's Hawk	*Buteo swainsoni*	CW	Accipitridae	Vertebrate	Aerial, sitwait	No	Neutral	Yes
Sharp-shinned Hawk	*Accipiter striatus*	ECW	Accipitridae	Vertebrate	Sitwait	No	Neutral	Yes
Killdeer	*Charadrius vociferus*	ECW	Charadriidae	Invertebrate	Ground	No	Neutral	Yes
Long-billed Curlew	*Numenius americanus*	CW	Scolopacidae	Invertebrate	Ground	Yes	Negative	Yes
Chimney Swift	*Chaetura pelagica*	EC	Apodidae	Invertebrate	Aerial	No	Positive	No

Vaux's Swift	*Chaetura vauxi*	W	Apodidae	Invertebrate	Aerial	Yes	--	No
Ruby-throated Hummingbird	*Archilochus colubris*	EC	Trochilidae	Plant	--	No	--	Yes
Northern Flicker (Yellow-shafted)	*Colaptes auratus auratus*	EC	Picidae	Invertebrate	Ground	No	Positive	Yes
Northern Flicker (Red-shafted)	*Colaptes auratus cafer*	CW	Picidae	Invertebrate	Ground	No	Positive	Yes
Northern Flicker (unid. subspp)	*Colaptes auratus*	C	Picidae	Invertebrate	Ground	No	Positive	Yes
American Kestrel	*Falco sparverius*	ECW	Falconidae	Invertebrate	Sitwait, aerial	No	Neutral	Yes
Prairie Falcon	*Falco mexicanus*	CW	Falconidae	Vertebrate	Sitwait, aerial	Yes	Neutral	Yes
Acadian Flycatcher	*Empidonax virescens*	E	Tyrannidae	Invertebrate	Sitwait	No	Negative	Yes

Least Flycatcher	*Empidonax minimus*	EC	Tyrannidae	Invertebrate	Aerial, glean	No	--	Yes
Dusky Flycatcher	*Empidonax oberholseri*	W	Tyrannidae	Invertebrate	Aerial, sitwait	No	Neutral	Yes
Gray Flycatcher	*Empidonax wrightii*	W	Tyrannidae	Invertebrate	Sitwait, ground	Yes	Negative	Yes
Western Wood-Pewee	*Contopus sordidulus*	CW	Tyrannidae	Invertebrate	Sitwait	No	--	Yes
Say's Phoebe	*Sayornis saya*	CW	Tyrannidae	Invertebrate	Aerial, glean	No	Positive	--
Eastern Phoebe	*Sayornis phoebe*	EC	Tyrannidae	Invertebrate	Sitwait	No	Positive	Yes
Eastern Kingbird	*Tyrannus tyrannus*	ECW	Tyrannidae	Invertebrate	Sitwait	No	Negative	Yes
Loggerhead Shrike	*Lanius ludovicianus*	ECW	Laniidae	Invertebrate	Sitwait	No	Negative	Yes
Red-eyed Vireo	*Vireo olivaceus*	ECW	Vireonidae	Invertebrate	Glean	No	Neutral	Yes
White-eyed Vireo	*Vireo griseus*	E	Vireonidae	Invertebrate	Glean	No	Negative	Yes

Yellow-throated Vireo	*Vireo flavifrons*	EC	Vireonidae	Invertebrate	Glean	Yes	--	No
Warbling Vireo	*Vireo gilvus*	ECW	Vireonidae	Invertebrate	Glean	No	Neutral	Yes
Bell's Vireo	*Vireo bellii*	EC	Vireonidae	Invertebrate	Glean	No	Negative	Yes
Purple Martin	*Progne subis*	ECW	Hirundinidae	Invertebrate	Aerial	No	Positive	Yes
Barn Swallow	*Hirundo rustica*	ECW	Hirundinidae	Invertebrate	Aerial	No	Positive	Yes
Tree Swallow	*Tachycineta bicolor*	ECW	Hirundinidae	Invertebrate	Aerial	No	Neutral	Yes
Red-breasted Nuthatch	*Sitta canadensis*	EW	Sittidae	Invertebrate	Glean	No	--	Yes
Sedge Wren	*Cistothorus platensis*	EC	Troglodytidae	Invertebrate	Ground	Yes	Negative	Yes
Marsh Wren	*Cistothorus palustris*	ECW	Troglodytidae	Invertebrate	Glean	No	--	Yes
House Wren	*Troglodytes aedon*	ECW	Troglodytidae	Invertebrate	Glean	No	Positive	Yes

Blue-gray Gnatcatcher	*Polioptila caerulea*	ECW	Polioptilidae	Invertebrate	Glean	No	--	Yes
Ruby-crowned Kinglet	*Regulus calendula*	EW	Regulidae	Invertebrate	Glean, aerial	No	Neutral	Yes
Western Bluebird	*Sialia mexicana*	W	Turdidae	Invertebrate	Sitwait, ground	Yes	Negative	Yes
Mountain Bluebird	*Sialia currucoides*	CW	Turdidae	Invertebrate	Sitwait, ground	No	Neutral	Yes
Eastern Bluebird	*Sialia sialis*	EC	Turdidae	Invertebrate	Sitwait	No	Positive	Yes
Wood Thrush	*Hylocichla mustelina*	E	Turdidae	Invertebrate	Glean	No	Negative	Yes
American Robin	*Turdus migratorius*	ECW	Turdidae	Invertebrate	Ground, glean	No	Positive	Yes
Sage Thrasher	*Oreoscoptes montanus*	W	Mimidae	Invertebrate	Ground	Yes	Negative	Yes
Cedar Waxwing	*Bombycilla cedrorum*	ECW	Bombycillidae	Invertebrate	Glean, sitwait	No	Neutral	No

Chestnut-collared Longspur	*Calcarius ornatus*	C	Calcariidae	Invertebrate	Ground	Yes	Negative	Yes
Pine Warbler	*Setophaga pinus*	E	Parulidae	Invertebrate	Glean	Yes	Negative	Yes
Yellow Warbler	*Setophaga petechia*	ECW	Parulidae	Invertebrate	Glean, aerial	No	Neutral	Yes
Common Yellowthroat	*Geothlypis trichas*	ECW	Parulidae	Invertebrate	Glean, aerial	No	--	Yes
Kentucky Warbler	*Geothlypis formosa*	E	Parulidae	Invertebrate	Ground	No	Neutral	--
Yellow-throated Warbler	*Setophaga dominica*	E	Parulidae	Invertebrate	Glean	No	--	Yes
Black-and-white Warbler	*Mniotilta varia*	E	Parulidae	Invertebrate	Glean	No	Negative	Yes
Chestnut-sided Warbler	*Setophaga pensylvanica*	E	Parulidae	Invertebrate	Ground, glean	Yes	Negative	Yes

Worm-eating Warbler	*Helmitheros vermivorum*	E	Parulidae	Invertebrate	Glean	Yes	--	Yes
Hooded Warbler	*Setophaga citrina*	E	Parulidae	Invertebrate	Aerial, glean	No	--	Yes
Prairie Warbler	*Setophaga discolor*	E	Parulidae	Invertebrate	Glean, aerial	No	Neutral	Yes
American Redstart	*Setophaga ruticilla*	EC	Parulidae	Invertebrate	Glean	No	Neutral	Yes
Black-throated Blue Warbler	*Setophaga caerulescens*	E	Parulidae	Invertebrate	Glean	No	Neutral	Yes
Canada Warbler	*Cardellina canadensis*	E	Parulidae	Invertebrate	Glean, aerial	No	Negative	Yes
Nashville Warbler	*Oreothlypis ruficapilla*	EW	Parulidae	Invertebrate	Glean	No	Neutral	Yes
Black-throated Gray Warbler	*Setophaga nigrescens*	West	Parulidae	Invertebrate	Glean	No	--	--

Yellow-breasted Chat	*Icteria virens*	ECW	Icteriidae	Invertebrate	Glean, ground	No	Neutral	Yes
Henslow's Sparrow	*Ammodramus henslowii*	E	Passerellidae	Invertebrate	Ground	Yes	Negative	No
Song Sparrow	*Melospiza melodia*	ECW	Passerellidae	Invertebrate	Ground, glean	No	Neutral	Yes
Dark-eyed Junco (Slate-colored)	*Junco hyemalis hyemalis*	E	Emberizidae	Invertebrate	Ground	No	Positive	Yes
Dark-eyed Junco (Oregon)	*Junco hyemalis oreganus*	W	Emberizidae	Invertebrate	Ground	No	Positive	Yes
Dark-eyed Junco (Gray-headed)	*Junco hyemalis caniceps*	W	Emberizidae	Invertebrate	Ground	No	Positive	Yes
Bobolink	*Dolichonyx oryzivorus*	EC	Icteridae	Invertebrate	Glean	No	--	Yes
Baltimore Oriole	*Icterus galbula*	EC	Icteridae	Plant	Glean, ground	No	Positive	Yes

Purple Finch	*Haemorhous purpureus*	EWC	Fringillidae	Plant	--	No	--	--
American Goldfinch	*Spinus tristis*	ECW	Fringillidae	Plant	--	No	Positive	--
Cassin's Finch	*Haemorhous cassinii*	W	Fringillidae	Plant	Ground	Yes	--	Yes

Table S2.2. Species for which we estimated breeding distribution abundance centroid shifts from 1994-2017 and migratory traits used to model shifts in centroid abundance. Migratory traits were compiled from each species' Birds of North America Online account (Rodewald 2015, ed.).

Common Name	Migration Strategy	Migratory Distance	Migration Time	Migrant Group Size	Diff. Mig. by Sex	Breeding Latitude	Average wintering Latitude	Overlapping Breed. & Wint. Ranges
Osprey	Complete	Long	Day/Night	Individual	No	High	C. America	No
Red-tailed Hawk	Partial	Short	Day	--	No	All	USA	Yes
Golden Eagle	Partial	Short	Day	Individual	No	All	USA	Yes
Northern Harrier	Partial	Long	Day	--	No	High	USA	Yes
Swainson's Hawk	Complete	Very long	Day	Consp. grp.	No	Mid	S. America	No
Sharp-shinned Hawk	Partial	Mid	Day	Individual	No	High	USA	Yes
Killdeer	Partial	Mid	Day/Night	Consp. grp.	No	All	USA	Yes
Long-billed Curlew	Complete	Mid	--	Consp. grp.	No	Mid	C. America	No

Chimney Swift	Complete	Very long	Day	Consp. grp.	No	All	S. America	No
Vaux's Swift	Complete	Very long	Day	Consp. grp.	No	High	S. America	No
Ruby-throated Hummingbird	Complete	Long	--	--	Yes	All	C. America	No
Northern Flicker (Yellow-shafted)	Partial	Mid	Day/Night	Consp. grp.	Yes	All	USA	Yes
Northern Flicker (Red-shafted)	Partial	Mid	Day/Night	--	No	All	USA	Yes
Northern Flicker (unid. subspp)	Partial	Mid	Day/Night	--	No	All	USA	Yes
American Kestrel	Partial	Short	Day	Individual	No	All	USA	Yes
Prairie Falcon	--	--	Day	--	No	Mid-low	USA	Yes
Acadian Flycatcher	Complete	Mid	--	--	Yes	Mid-low	C. America	No
Least Flycatcher	Complete	Mid	--	--	Yes	High	C. America	No

Dusky Flycatcher	Complete	Short	Night	--	Yes	Mid	C. America	No
Gray Flycatcher	Complete	Short	Night	--	Yes	Mid	C. America	No
Western Wood-Pewee	Complete	Very long	--	--	No	All	S. America	No
Say's Phoebe	--	Short	Day	Individual	Yes	Mid	USA	Yes
Eastern Phoebe	Partial	Long	Day	--	No	Mid	USA	Yes
Eastern Kingbird	Complete	Very long	Day	Consp. grp.	Yes	All	S. America	No
Loggerhead Shrike	Partial	Short	Day	--	No	All	USA	Yes
Red-eyed Vireo	Complete	Very long	Night	--	No	All	S. America	No
White-eyed Vireo	Partial	Mid	Night	--	No	Mid	USA	Yes
Yellow-throated Vireo	Complete	Long	Night	--	No	Mid	USA	No
Warbling Vireo	Partial	Mid	Night	Mixed fl.	No	Mid	C. America	Yes
Bell's Vireo	Complete	Short	Night	--	No	Mid-low	C. America	No

Purple Martin	Complete	Very long	Day	Consp. grp.	No	All	S. America	No
Barn Swallow	Complete	Very long	Day	Mixed fl.	No	All	USA	Yes
Tree Swallow	Complete	--	Day	Consp. grp.	No	High-mid	C. America	No
Red-breasted Nuthatch	Partial	--	Day/Night	Mixed fl.	No	High-mid	USA	Yes
Sedge Wren	Partial	Short	Night	Consp. grp.	No	High-mid	USA	No
Marsh Wren	Partial	--	Night	--	No	High-mid	C. America	Yes
House Wren	Partial	Mid	Night	--	No	All	C. America	No
Blue-gray Gnatcatcher	Partial	--	--	--	No	Mid-low	C. America	Yes
Ruby-crowned Kinglet	Partial	Short	--	--	Yes	High	USA	Yes
Western Bluebird	Partial	Mid	Day	Mixed fl.	No	Mid-low	USA	Yes
Mountain Bluebird	Complete	Short	--	Mixed fl.	Yes	High-mid	USA	Yes

Eastern Bluebird	Partial	Short	Day	Consp. grp.	No	All	USA	Yes
Wood Thrush	Complete	Mid	Night	--	No	All	C. America	No
American Robin	Partial	Short	Day	Consp. grp.	No	All	USA	Yes
Sage Thrasher	Complete	Short	--	--	Yes	Mid	USA	No
Cedar Waxwing	--	--	Day/Night	--	No	High-mid	USA	Yes
Chestnut-collared Longspur	Complete	Mid	--	Individual	Yes	High	USA	No
Pine Warbler	Partial	Short	Night	Mixed fl.	No	Mid	USA	Yes
Yellow Warbler	Complete	Long	Night	Consp. grp.	Yes	High-mid	USA	No
Common Yellowthroat	Partial	--	Night	--	Yes	All	USA	Yes
Kentucky Warbler	Complete	Mid	Night	Individual	No	Mid-low	C. America	No
Yellow-throated Warbler	Partial	Mid	Night	--	No	Mid-low	C. America	Yes

Black-and-white Warbler	Complete	Long	Night	Mixed fl.	Yes	All	C. America	No
Chestnut-sided Warbler	Complete	Mid	Night	--	No	High	C. America	No
Worm-eating Warbler	Complete	Mid	Night	--	No	Mid	C. America	No
Hooded Warbler	Complete	Mid	Night	--	No	Mid-low	C.America	No
Prairie Warbler	Partial	Mid	Day/Night	Consp. grp.	Yes	Mid-low	C. America	No
American Redstart	Complete	Mid	Night	Mixed fl.	No	All	C. America	No
Black-throated Blue Warbler	Complete	Mid	--	--	Yes	High	C. America	No
Canada Warbler	Complete	Long	Night	Mixed fl.	Yes	High	S. America	No
Nashville Warbler	Complete	Mid	Night	Mixed fl.	Yes	High	C. America	No

Black-throated Gray Warbler	Complete	Short	Night	Mixed fl.	No	Mid-low	C.America	No
Yellow-breasted Chat	Complete	Mid	Night	Individual	Yes	Mid-low	C. America	No
Henslow's Sparrow	Complete	Short	--	--	No	Mid	USA	No
Song Sparrow	Partial	Mid	Night	--	Yes	High-mid	USA	Yes
Dark-eyed Junco (Slate-colored)	Partial	Short	Night	--	Yes	High	USA	Yes
Dark-eyed Junco (Oregon)	Partial	Short	Night	--	Yes	High-mid	USA	Yes
Dark-eyed Junco (Gray-headed)	Partial	Short	Night	--	Yes	Mid	USA	Yes
Bobolink	Partial	Very long	Night	Consp. grp.	Yes	High	S. America	No
Baltimore Oriole	Complete	Long	Day/Night	Consp. grp.	Yes	All	C. America	No

Purple Finch	--	--	Night	--	Yes	High	USA	Yes
American Goldfinch	Partial	Mid	Day	Consp. grp.	Yes	High-mid	USA	Yes
Cassin's Finch	Partial	Short	--	--	No	Mid	USA	Yes

CONCLUSION

Dispersal and species distributions are fundamental ecological processes for almost all organisms, and while both have strong histories of theoretical and empirical research, new perspectives can yield important insight into the processes underlying these events, particularly in the current era of global change. Dispersal capacity and the ability to colonize new areas are likely important characteristics of species that will persist despite continuing global change (Barbet-Massin et al. 2011). Thus, understanding the mechanisms underlying processes like dispersal that will likely promote or constrain adaptation to rapidly changing environments is of key conservation concern. We aimed to identify drivers of individual dispersal movements and then scale up our perspective to breeding distribution shifts, population-level processes shaped by individual dispersal, because global change affects species across many scales and selective pressures may not be the same across all scales (Levin 1992). We found that long-distance dispersal in American kestrels is more frequent than previously measured, which may either have positive or negative fitness consequences for kestrels (Kokko and López-Sepulchre 2006, Lowe and McPeek 2012). Additionally, we found evidence that long-distance and short-distance dispersal may be distinct processes, suggesting that they may experience and respond to different selective pressures, leading to different implications of the two types of dispersal. We also found that equatorward shifts in breeding distributions are occurring in many migratory species and may be a viable adaptive strategy for coping with climate change, challenging the claim that species will universally track climate niches. Still, drivers of dispersal and distributions are complex and not fully understood, and continued investigation into phenomena previously attributed to stochasticity or error, like long-distance dispersal and equatorward distribution shifts, is critical for further developing our concept of adaptation and responses to global change.

REFERENCES

Barbet-Massin, M., W. Thuiller, and F. Jiguet. 2011. The fate of European breeding birds under climate, land-use and dispersal scenarios. *Global Change Biology* 18:881-890.

Kokko, H. and A. López-Sepulchre. 2006. From individual dispersal to species ranges: perspectives for a changing world. *Science* 313: 789-791.

Levin, S. A. 1992. The problem of pattern and scale in ecology: The Robert H. MacArthur Award Lecture. *Ecology* 73: 1943-1967.

Lowe, W. H. and M. A. McPeek. 2012. Can natural selection maintain long-distance dispersal? Insight from a stream salamander system. *Evolutionary Ecology* 26: 11-24.

APPENDIX A

Model selection for Chapter 2 life history traits analysis

We organized life history traits into three groups corresponding to the three parts of our hypothesis about directions of shifts for different traits: (1) plasticity, including covariates migration type (partial or complete), habitat specialization, and human association (positive, negative, or neutral); (2) supplemental cues encountered/used, including primary diet type (insects/invertebrates, plants, or vertebrates), foraging strategy (aerial, sit and wait, glean, or ground), migration time (day or night), and wintering latitude (USA, Central America, or South America); and (3) gain in survival or reproduction from shift, including covariates migration distance, whether breeding and wintering distributions are conterminous or disjunct, whether species are territorial, presence of differential migration by sex, and migratory group size (individual, conspecific group, mixed flock). For each of these three sets of covariates, we ran linear mixed models with all single covariates and possible combinations of covariates and a random effect of family. We ran all combinations and interactions in each region unless a covariate was limited by insufficient sample size or covariates were correlated within a region. We selected the best model from each hypothesis in each region using a combination of LOO-CV and Bayesian model stacking, and then created a final model set of the best models from each hypothesis and combinations of these models.

We used a combination of efficient leave-one-out cross validation (LOO-CV) and Bayesian model stacking (Yao et al. 2018) via the R package loo (Vehtari et al. 2018) for model selection, because on its own, LOO-CV was not a reliable metric for selecting a single best model from a set of many models because of potential overfitting and small sample sizes (Piironen and Vehtari 2017). Our goal with analysis was inference rather than prediction, so we used LOO-CV and Bayesian stacking to guide variable selection rather than computing averaged models. If the most-supported model by LOO-CV was not also the most-supported model by model stacking weights, we used the weights of the individual covariates to assess if interactions between covariates were causing overfitting of interaction levels with few observations. We did not use model weights of the full set of models on their own to determine the most-supported model because model stacking weights penalize covariates that appear across many models by splitting their weights across all models, so using the single covariate weights was the best way to assess if covariates were overfit.

Model Selection Results

East Region

Table A1.1 – 3 Model selection results for model set including **(1)** migration type (Mig), habitat specialization (Hab), and human association (Human); **(2)** primary diet type (Diet), foraging strategy (For), migration time (Time), and wintering latitude (Wint); and **(3)** migration distance (Dist1 with levels short, mid, long, very long; or Dist2 with levels short, long), whether breeding and wintering distributions (Overlap), whether species are territorial (Terr), presence of differential migration by sex (Sex), and migratory group size (Group) in the east region, from leave-one-out cross validation and Bayesian model stacking (BMS) weights. All models include a random effect of taxonomic family. Models are in ordered most-supported to least-supported based on Expected Log Pointwise Posterior Density (ELPD) from LOO-CV, although model weights were also considered to determine most-supported model because LOO-CV can cause overfitting with small sample sizes. The models used to determine the most-supported model across the three hypotheses is indicated in bold.

Table A1.1

MODEL	ELPD DIFF	ELPD LOO	SE ELPD	Eff Pars LOO	SE Eff Pars	LOO IC	SE LOO IC	BMS Weight
Mig × Hab + Human	**0**	**-131.1**	**6.5**	**22.7**	**4.1**	**262.1**	**13**	**0.238**

Intercept	-0.7	-131.7	6.5	16.2	3.5	263.5	13	0.41
Hab × Mig	-1.6	-132.7	7	20.4	4	265.4	13.9	0
Human	-1.8	-132.9	5.6	17.7	3.1	265.7	11.1	0
Hab	-2.1	-133.1	6.5	16.9	3.4	266.3	13	0
Mig	-2.8	-133.8	6.3	16.9	3.3	267.7	12.6	0
Mig × Hab × Human	-2.9	-134	5.1	20.1	3.4	268	10.1	0.212
Mig × Human	-3.1	-134.1	5	21.7	3	268.3	9.9	0
Hab + Human	-3.5	-134.6	5.6	19.3	3.2	269.2	11.2	0
Mig + Hab	-3.9	-134.9	6.2	17.3	3.2	269.9	12.3	0
Hab × Human	-4.1	-135.1	5.6	19.6	3.2	270.3	11.2	0
Mig + Human	-4.8	-135.8	5.4	19.3	3.1	271.7	10.9	0
Mig + Hab + Human	-5.7	-136.8	5.4	19.6	3.2	273.5	10.9	0.14
Mig + Hab × Human	-6.7	-137.7	5.5	20.3	3.2	275.4	10.9	0

Table A1.2

MODEL	ELPD DIFF	ELPD LOO	SE ELPD	Eff Pars LOO	SE Eff Pars	LOO IC	SE LOO IC	BMS Weight
Diet + Time + Wint	0	-127.8	7.7	16.8	4.2	255.6	15.5	0.293
Diet	**-0.1**	**-127.9**	**6.2**	**10.7**	**2.7**	**255.8**	**12.5**	**0.131**
Diet + Wint	-0.7	-128.5	6.8	14.3	3.4	257	13.7	0
Diet + Time	-0.8	-128.7	6.4	11.9	3	257.3	12.7	0
Diet × For + Wint	-1.4	-12 9.1	5.1	20.3	3.1	258.2	10.1	0.179
Diet + For	-2.5	-130.3	5.8	14	2.7	260.6	11.7	0.023
Diet × For	-2.8	-130.6	5.7	16	3.1	261.2	11.4	0.040
Diet × Time	3.4	-131.2	6.3	13.5	3.3	262.3	12.7	0
Intercept	-3.9	-131.7	6.5	16.2	3.5	263.5	13	0.334
Wint	-4.8	-132.6	6.8	19.4	3.9	265.2	13.7	0
Diet × For + Time	-5.6	-133.4	6.6	19.6	4	266.9	13.2	0
Time + Wint	-5.7	-133.5	7.4	22.9	4.6	266.9	14.7	0

For + Wint	-5.9	-133.7	5.7	22.4	3.5	267.4	11.4	0
For	-6.1	-133.9	6.1	19.2	3.5	267.8	12.1	0
Time	-6.5	-134.3	6.4	18.8	3.6	268.6	12.9	0
Time × Wint	-6.6	-134.4	8	24.3	5.1	268.8	16	0.082
For + Time	-9.3	-137.1	6.3	21.6	3.8	274.2	12.6	0
For × Wint	-14.5	-142.3	6.9	25	4	284.7	13.7	0
For × Time	-19.1	-146.9	6.9	26.3	4.5	293.8	13.9	0

Table A1.3

MODEL	ELPD DIFF	ELPD LOO	SE ELPD	Eff Pars LOO	SE Eff Pars	LOO IC	SE LOO IC	BMS Weight
Sex	**0**	**-131.4**	**7**	**17.2**	**3.7**	**262.7**	**13.9**	**0.309**
Intercept	-0.4	-131.7	6.5	16.2	3.5	263.5	13	0.239
Sex	-1	-132.3	6.6	17.5	3.5	264.6	13.2	0
Sex × Terr	-1.2	-132.5	5.8	17.8	3.2	265.1	11.7	0
Dist2	-1.2	-132.6	6.3	18	3.4	265.1	12.6	0.235
Overlap × Sex	-1.5	-132.8	6.9	18.1	3.7	265.7	13.8	0
Overlap × Sex + Terr	-1.7	-133.1	5.8	18.6	3.2	266.2	11.6	0
Overlap + Terr × Sex	-1.8	-133.2	5.6	17	3.2	266.4	11.2	0.215
Overlap	-1.8	-133.2	6.3	16.9	3.3	266.4	12.6	0
Terr	-2.3	-133.6	5.8	17.1	3.3	267.3	11.5	0
Dist2 + Sex	-2.3	-133.7	6.8	19.8	3.8	267.4	13.5	0
Group	-4.3	-135.7	7	17.4	3.8	271.3	14	0

Dist1	-5.1	-136.5	6.6	19.2	3.8	273	13.2	0
Dist2 × Sex	-5.5	-136.8	7.1	21.7	4.4	273.6	14.1	0
Overlap × Terr × Sex	-6.3	-137.7	6.7	20.7	4.3	275.4	13.4	0
Dist2 × Overlap	-9.2	-140.5	10.1	24.1	6.5	281.1	20.1	0

Table A1.4 Bayesian model stacking weights for single covariates in the east region, for each set of covariates corresponding to the three hypotheses: (A) migration type (Mig), habitat specialization (Hab), and human association (Human); (B) primary diet type (Diet), foraging strategy (For), migration time (Time), and wintering latitude (Wint); and (C) migration distance (Dist2), whether breeding and wintering distributions (Overlap), whether species are territorial (Terr), presence of differential migration by sex (Sex), and migratory group size (Group).

Hypothesis 1		**Hypothesis 2**		**Hypothesis 3**	
Covariate	BMS Weight	Covariate	BMS Weight	Covariate	BMS Weight
Intercept	0.885	Diet	0.792	Sex	0.678
Human	0.115	Wint	0.127	Dist2	0.21
Mig	0	Intercept	0.081	Terr	0.111
Hab	0	For	0	Overlap	0
		Time	0	Dist1	0
				Group	0
				Intercept	0

Table A1.5 Model selection results for model set including covariates from most-supported model from each single-hypothesis model set (Tables A1.1-3) and combinations of these covariates in the east region, from leave-one-out cross validation and Bayesian model stacking (BMS) weights. All models include a random effect of taxonomic family. Models are in ordered most-supported to least-supported based on Expected Log Pointwise Posterior Density (ELPD) from LOO-CV, although model weights were also considered to determine most-supported model because LOO-CV can cause overfitting with small sample sizes. The most-supported model used for inference is indicated in bold.

MODEL	ELPD DIFF	ELPD LOO	SE ELPD	Eff Pars LOO	SE Eff Pars	LOO IC	SE LOO IC	BMS Weight
Diet + Sex	**0**	**-126.7**	**6.6**	**11.2**	**2.9**	**253.5**	**13.1**	**0.756**
Diet	-1.2	-127.9	6.2	10.7	2.7	255.8	12.5	0
Mig × Hab + Human + Diet + Sex	-1.3	-128	6.3	18.2	3.6	256.1	12.7	0.021
Mig × Hab + Human + Diet	-3.2	-130	6.1	18.2	3.4	259.9	12.3	0
Mig × Hab + Human + Sex	-3.8	-130.5	7	24.1	4.5	261.1	14	0.218
Mig × Hab + Human	-4.3	-131.1	6.5	22.7	4.1	262.1	13	0
Sex	-4.6	-131.4	7	17.2	3.7	262.7	13.9	0.001
Intercept	-5	-131.7	6.5	16.2	3.5	263.5	13	0.004

West Region

Table A1.6 – 8 Model selection results for model set including **(6)** migration type (Mig), habitat specialization (Hab), and human association (Human); **(7)** primary diet type (Diet), foraging strategy (For), migration time (Time), and wintering latitude (Wint); and **(8)** migration distance (Dist1 with levels short, mid, long, very long; or Dist2 with levels short, long), whether breeding and wintering distributions (Overlap), whether species are territorial (Terr), presence of differential migration by sex (Sex), and migratory group size (Group) in the west region, from leave-one-out cross validation and Bayesian model stacking (BMS) weights. All models include a random effect of taxonomic family. Models are in ordered most-supported to least-supported based on Expected Log Pointwise Posterior Density (ELPD) from LOO-CV, although model weights were also considered to determine most-supported model because LOO-CV can cause overfitting with small sample sizes. The models used to determine the most-supported model across the three hypotheses is indicated in bold.

Table A1.6

MODEL	ELPD DIFF	ELPD LOO	SE ELPD	Eff Pars LOO	SE Eff Pars	LOO IC	SE LOO IC	BMS Weight
Intercept	0	-119.4	8.9	6.1	2.5	238.8	17.8	0.524
Hab	**-0.6**	**-119.9**	**8.7**	**6.3**	**2.5**	**239.9**	**17.4**	**0.029**
Mig	-0.8	-120.2	8.5	6.7	2.5	240.3	17	0.243
Mig + Hab	-1.7	-121.1	8.4	7.2	2.6	242.3	16.8	0.001
Human	-2	-121.4	8.9	7.8	3.1	242.8	17.8	0
Hab + Human	-2.2	-121.6	8.6	7.6	2.8	243.2	17.1	0
Mig × Hab	-2.9	-122.3	8.3	7.9	2.7	244.6	16.6	0
Mig + Human	-3.4	-122.8	9.1	9.4	3.6	245.6	18.2	0.203
Hab × Human	-3.7	-123.1	8.4	8.5	2.9	246.2	16.8	0
Mig + Hab + Human	-4.3	-123.7	9.2	9.9	3.8	247.5	18.4	0
Mig × Hab + Human	-5.5	-124.9	8.7	10.3	3.6	249.7	17.5	0
Hab × Human + Mig	-5.5	-124.9	8.7	10.2	3.6	249.7	17.5	0

Mig × Human	-7.8	-127.2	9.7	13.7	5.3	254.4	19.4	0
Mig × Human + Hab	-8.8	-128.2	9.3	14.1	5	256.3	18.6	0
Mig × Hab × Human	-9.7	-129	8.3	12.1	4.3	258.1	16.5	0

Table A1.7

MODEL	ELPD DIFF	ELPD LOO	SE ELPD	Eff Pars LOO	SE Eff Pars	LOO IC	SE LOO IC	BMS Weight
Diet	**0**	**-118.9**	**8.2**	**6.5**	**2.5**	**237.8**	**16.4**	**0.075**
Intercept	-0.5	-119.4	8.9	6.1	2.5	238.8	17.8	0.388
Diet × Wint + Time	-0.6	-119.5	6.6	8.7	2.6	239	13.1	0.077
Diet + For	-1.6	-120.5	9.4	10.5	4	240.9	18.9	0.094
Diet × Wint	-1.9	-120.8	7.2	9.5	3	241.6	14.3	0
Diet + Wint	-2	-120.9	8	8.8	3.1	241.8	16	0
Diet + Time	-2	-120.9	8	8	2.7	241.9	16	0
Time	-2.2	-121.1	8.5	7.4	2.6	242.1	16.9	0.063

For	-2.3	-121.2	9	9.5	3.6	242.4	18.1	0
Wint	-2.4	-121.3	8.9	8.3	3.3	242.6	17.7	0
Diet + For + Time	-2.9	-121.8	9.7	12.6	4.6	243.7	19.4	0.152
For + Time	-3.1	-122	8.7	10.8	3.6	244	17.4	0
Diet × For	-3.1	-122	9.6	10.4	4.9	244.1	19.3	0.071
Time + Wint	-3.6	-122.5	8.5	9.2	3.2	245	16.9	0
For × Wint	-3.9	-122.8	6.4	15	3.5	245.5	12.8	0.081
Diet × Time	-3.9	-122.8	7.5	8.9	2.6	245.7	15	0
Diet + Time + Wint	-4.3	-123.2	7.9	10.3	3.3	246.4	15.8	0
For + Wint	-5.2	-124.1	9.3	12.1	4.8	248.2	18.7	0
Time × Wint	-5.4	-124.3	7.8	10.2	3	248.6	15.7	0
Diet + Time × Wint	-7.2	-126.1	7.3	12.1	3.3	252.1	14.6	0
For × Time	-9.2	-128.1	8.3	14.2	3.9	256.2	16.7	0

Table A1.8

MODEL	ELPD DIFF	ELPD LOO	SE ELPD	Eff Pars LOO	SE Eff Pars	LOO IC	SE LOO IC	BMS Weight
Sex	**0**	**-119.1**	**8.6**	**6**	**2.3**	**238.2**	**17.2**	**0.605**
Intercept	-0.3	-119.4	8.9	6.1	2.5	238.8	17.8	0.267
Overlap	-1	-120.1	8.8	6.6	2.6	240.2	17.5	0
Terr	-1.1	-120.2	8.3	6.4	2.3	240.4	16.6	0
Overlap + Sex	-1.3	-120.4	8.6	7.1	2.6	240.8	17.3	0
Terr + Sex	-1.6	-120.7	8.4	7.2	2.5	241.3	16.8	0
Terr × Sex	-1.7	-120.8	8.4	7.4	2.5	241.7	16.7	0
Overlap + Terr	-2.1	-121.2	8.4	7.3	2.6	242.3	16.9	0
Overlap × Sex	-2.1	-121.2	8.6	7.7	2.7	242.4	17.2	0
Overlap + Terr + Sex	-2.3	-121.4	8.2	7.7	2.5	242.7	16.4	0
Terr × Sex + Overlap	-2.6	-121.7	8.2	8.1	2.6	243.3	16.4	0
Dist2	-3.1	-122.1	8.8	9.2	3.5	244.3	17.7	0

Overlap × Terr	-3.2	-122.3	8.2	8	2.6	244.6	16.4	0
Group	-3.3	-122.4	8.9	9.4	3.6	244.8	17.8	0
Dist1	-3.8	-122.9	9.4	10.3	4.3	245.8	18.8	0.128

Table A1.9 Bayesian model stacking weights for single covariates in the west region, for each set of covariates corresponding to the three hypotheses: (A) migration type (Mig), habitat specialization (Hab), and human association (Human); (B) primary diet type (Diet), foraging strategy (For), migration time (Time), and wintering latitude (Wint); and (C) migration distance (Dist2), whether breeding and wintering distributions (Overlap), whether species are territorial (Terr), presence of differential migration by sex (Sex), and migratory group size (Group).

Hypothesis 1		**Hypothesis 2**		**Hypothesis 3**	
Covariate	BMS Weight	Covariate	BMS Weight	Covariate	BMS Weight
Intercept	1	Diet	0.727	Sex	0.725
Human	0	Intercept	0.273	Intercept	0.252
Mig	0	For	0	Dist1	0.023
Hab	0	Time	0	Dist2	0
		Wint	0	Overlap	0
				Terr	0
				Group	0

Table A1.10 Model selection results for model set including covariates from most-supported model from each single-hypothesis model set (Tables A1.6-8) and combinations of these covariates in the west region, from leave-one-out cross validation and Bayesian model stacking (BMS) weights. All models include a random effect of taxonomic family. Models are in ordered most-supported to least-supported based on Expected Log Pointwise Posterior Density (ELPD) from LOO-CV, although model weights were also considered to determine most-supported model because LOO-CV can cause overfitting with small sample sizes. The most-supported model used for inference is indicated in bold.

MODEL	ELPD DIFF	ELPD LOO	SE ELPD	Eff Pars LOO	SE Eff Pars	LOO IC	SE LOO IC	BMS Weight
Diet	**0**	**-118.9**	**8.2**	**6.5**	**2.5**	**237.8**	**16.4**	**0.286**
Sex	-0.2	-119.1	8.6	6	2.3	238.2	17.2	0.404
Hab + Diet	-0.4	-119.3	7.8	6.5	2.3	238.6	15.6	0.209
Intercept	-0.5	-119.4	8.9	6.1	2.5	238.8	17.8	0
Diet + Sex	-0.5	-119.4	8.1	7.1	2.6	238.9	16.3	0
Hab	-1	-119.9	8.7	6.3	2.5	239.9	17.4	0
Hab + Sex	-1.2	-120.1	8.5	6.6	2.4	240.2	17	0
Hab + Diet + Sex	-1.5	-120.4	8	7.6	2.6	240.8	16	0

Central Region

Table A1.11 – 13 Model selection results for model set including **(11)** migration type (Mig) and human association (Human); **(12)** primary diet type (Diet), foraging strategy (For), migration time (Time), and wintering latitude (Wint); and **(13)** migration distance (Dist1 with levels short, mid, long, very long; or Dist2 with levels short, long), whether breeding and wintering distributions (Overlap), whether species are territorial (Terr), presence of differential migration by sex (Sex), and migratory group size (Group) in the central region, from leave-one-out cross validation and Bayesian model stacking (BMS) weights. Some covariates included in other regions were not included in models for the central region because there was not adequate sample size in this region. All models include a random effect of taxonomic family. Models are in ordered most-supported to least-supported based on Expected Log Pointwise Posterior Density (ELPD) from LOO-CV, although model weights were also considered to determine most-supported model because LOO-CV can cause overfitting with small sample sizes.

Table A1.11

MODEL	ELPD DIFF	ELPD LOO	SE ELPD	Eff Pars LOO	SE Eff Pars	LOO IC	SE LOO IC	BMS Weight
Mig + Human	**0**	**-127.5**	**8.8**	**10.6**	**4.1**	**255**	**17.6**	**0.009**
Mig	-0.3	-127.8	10.6	8.2	4.2	255.6	21.1	0.379
Human	-1.1	-128.5	9.8	10.4	4.6	257.1	19.5	0
Mig × Human	-1.4	-128.9	7.7	11.9	3.8	257.8	15.5	0.289
Intercept	-1.5	-129	11.6	8.5	4.7	258	23.1	0.323

Table A1.12

MODEL	ELPD DIFF	ELPD LOO	SE ELPD	Eff Pars LOO	SE Eff Pars	LOO IC	SE LOO IC	BMS Weight
Diet	**0**	**-128.9**	**10.8**	**9.6**	**5.2**	**257.9**	**21.6**	**0.268**
Intercept	-0.1	-129	11.6	8.5	4.7	258	23.1	0.171
Wint	-0.1	-129	11.6	9.3	5	258	23.2	0.428
Diet + Wint	-0.7	-129.6	10.9	10.7	5.4	259.2	21.8	0
Diet + Time	-1	-130	10.3	10.7	5	259.9	20.6	0
Time	-1.2	-130.1	10.5	9.5	4.4	260.2	21	0
Diet × Time	-1.4	-130.3	10	10.5	4.8	260.7	20	0
Time + Wint	-2.2	-131.1	10.8	10.6	4.9	262.2	21.6	0
For	-2.4	-131.3	10.5	10.5	5.1	262.6	21	0
Diet + For	-3	-131.9	10.6	11.8	5.6	263.9	21.3	0
Diet × For	-3.4	-132.4	8.4	10.7	3.7	264.8	16.8	0.133
For + Wint	-3.6	-132.5	11.2	12.2	5.8	265.1	22.4	0

For + Time	-4.9	-133.8	10	12.2	5	267.6	20	0
For × Time	-8.4	-137.3	10.3	12.7	5.7	274.7	20.6	0

Table A1.13

MODEL	ELPD DIFF	ELPD LOO	SE ELPD	Eff Pars LOO	SE Eff Pars	LOO IC	SE LOO IC	BMS Weight
Overlap × Sex	**0**	**-128.3**	**9.8**	**8.2**	**3.6**	**256.6**	**19.6**	**0.360**
Overlap	-0.4	-128.7	10.9	8.5	4.5	257.5	21.9	0.077
Overlap + Sex	-0.5	-128.9	10.8	8.8	4.6	257.8	21.5	0
Sex	-0.6	-128.9	11.1	8.6	4.6	257.8	22.1	0.001
Intercept	-0.6	-129	11.6	8.5	4.7	258	23.1	0.263
Dist1 + Overlap	-1.5	-129.9	10.4	12.2	5.1	259.7	20.9	0.195
Overlap + Terr + Sex	-1.7	-130	10	10.3	4.3	260.1	20.1	0
Dist1 + Overlap + Sex	-1.7	-130.1	10.2	12.3	5	260.1	20.3	0.050
Dist1	-1.7	-130.1	10.8	12.4	5.4	260.1	21.7	0.053
Overlap + Terr	-1.8	-130.2	10.3	10	4.3	260.3	20.5	0
Dist1 + Sex	-1.9	-130.2	10.1	12.3	4.9	260.4	20.2	0
Dist2	-2.2	-130.6	11.3	11.1	5.3	261.2	22.6	0

Dist1 + Overlap × Sex	-3.2	-131.5	10.3	13.3	5.3	263.1	20.6	0
Dist1 × Overlap	-3.4	-131.7	10.6	14.1	5.6	263.4	21.1	0
Dist1 × Sex	-3.5	-131.8	10.1	13.8	5.1	263.6	20.2	0
Dist1 + Overlap + Terr + Sex	-3.8	-132.1	9.6	13.6	4.8	264.3	19.3	0
Dist1 × Sex + Overlap	-4.0	-132.3	10.4	14.4	5.6	264.7	20.8	0

Table A1.14 Bayesian model stacking weights for single covariates in the central region, for each set of covariates corresponding to the three hypotheses: (A) migration type (Mig) and human association (Human); (B) primary diet type (Diet), foraging strategy (For), migration time (Time), and wintering latitude (Wint); and (C) migration distance (Dist2), whether breeding and wintering distributions (Overlap), whether species are territorial (Terr), presence of differential migration by sex (Sex), and migratory group size (Group).

Hypothesis 1		**Hypothesis 2**		**Hypothesis 3**	
Covariate	BMS Weight	Covariate	BMS Weight	Covariate	BMS Weight
Mig	0.619	Diet	0.475	Overlap	0.518
Human	0.381	Wint	0.416	Sex	0.358
Intercept	0	Intercept	0.109	Dist1	0.068
		For	0	Intercept	0.056
		Time	0	Dist2	0
				Terr	0
				Group	0

*****Habitat specialist was not included in this region because of insufficient sample size

Table A1.15 Model selection results for model set including covariates from most-supported model from each single-hypothesis model set (Tables A1.11-13) and combinations of these covariates in the central region, from leave-one-out cross validation and Bayesian model stacking (BMS) weights. All models include a random effect of taxonomic family. Models are in ordered most-supported to least-supported based on Expected Log Pointwise Posterior Density (ELPD) from LOO-CV, although model weights were also considered to determine most-supported model because LOO-CV can cause overfitting with small sample sizes. The most-supported model used for inference is indicated in bold.

MODEL	ELPD DIFF	ELPD LOO	SE ELPD	Eff Pars LOO	SE Eff Pars	LOO IC	SE LOO IC	BMS Weight
Mig + Human + Diet	**0**	**-127**	**8.1**	**11.5**	**4.3**	**254**	**16.3**	**0.471**
Mig + Human	-0.5	-127.5	8.8	10.6	4.1	255	17.6	0
Mig	-0.8	-127.8	10.6	8.2	4.2	255.6	21.1	0.137
Overlap × Sex	-1.3	-128.3	9.8	8.2	3.6	256.6	19.6	0
Mig + Human + Diet + Overlap × Sex	-1.9	-128.9	7.5	12.8	4	257.8	15.1	0.068
Diet	-1.9	-128.9	10.8	9.6	5.2	257.9	21.6	0
Intercept	-2.0	-129	11.6	8.5	4.7	258	23.1	0.324
Mig + Human + Overlap × Sex	-2.1	-129.1	8.5	12	4.2	258.3	17	0

Diet + Overlap × Sex	-3.0	-130	10.2	10.7	5.1	260	20.4	0

*****Wintering latitude received support in this model set but could not be included with migration type because these variables were strongly correlated.