

2013

Population-level scaling of avian migration speed with body size and migration distance for powered fliers

Frank A. La Sorte

Cornell Lab of Ornithology, Ithaca, New York, fal42@cornell.edu

Daniel Fink

Cornell Lab of Ornithology, Ithaca, New York

Wesley M. Hochachka

Cornell Lab of Ornithology, Ithaca, New York

John DeLong

University of Nebraska-Lincoln, jpdelong@unl.edu

Steve Kelling

Cornell Lab of Ornithology, Ithaca, New York

Follow this and additional works at: <http://digitalcommons.unl.edu/bioscifacpub>

La Sorte, Frank A.; Fink, Daniel; Hochachka, Wesley M.; DeLong, John; and Kelling, Steve, "Population-level scaling of avian migration speed with body size and migration distance for powered fliers" (2013). *Faculty Publications in the Biological Sciences*. 408.
<http://digitalcommons.unl.edu/bioscifacpub/408>

This Article is brought to you for free and open access by the Papers in the Biological Sciences at DigitalCommons@University of Nebraska - Lincoln. It has been accepted for inclusion in Faculty Publications in the Biological Sciences by an authorized administrator of DigitalCommons@University of Nebraska - Lincoln.

Population-level scaling of avian migration speed with body size and migration distance for powered fliers

FRANK A. LA SORTE,^{1,3} DANIEL FINK,¹ WESLEY M. HOCHACHKA,¹ JOHN P. DELONG,² AND STEVE KELLING¹

¹*Cornell Lab of Ornithology, Ithaca, New York 14850 USA*

²*School of Biological Sciences, University of Nebraska, Lincoln, Nebraska 68588 USA*

Abstract. Optimal migration theory suggests specific scaling relationships between body size and migration speed for individual birds based on the minimization of time, energy, and risk. Here we test if the quantitative predictions originating from this theory can be detected when migration decisions are integrated across individuals. We estimated population-level migration trajectories and daily migration speeds for the combined period 2007–2011 using the eBird data set. We considered 102 North American bird species that use flapping or powered flight during migration. Many species, especially in eastern North America, had looped migration trajectories that traced a clockwise path with an eastward shift during autumn migration. Population-level migration speeds decelerated rapidly going into the breeding season, and accelerated more slowly during the transition to autumn migration. In accordance with time minimization predictions, spring migration speeds were faster than autumn migration speeds. In agreement with optimality predictions, migration speeds of powered flyers scaled negatively with body mass similarly during spring and autumn migration. Powered fliers with longer migration journeys also had faster migration speeds, a relationship that was more pronounced during spring migration. Our findings indicate that powered fliers employed a migration strategy that, when examined at the population level, was in compliance with optimality predictions. These results suggest that the integration of migration decisions across individuals does result in population-level patterns that agree with theoretical expectations developed at the individual level, indicating a role for optimal migration theory in describing the mechanisms underlying broadscale patterns of avian migration for species that use powered flight.

Key words: avian migration; body size; eBird; macroecology; migration distance; migration speed; North America; optimal migration theory; powered flight; scale.

INTRODUCTION

Birds have evolved highly diverse migration strategies to take advantage of favorable environmental conditions during the breeding season and avoid unfavorable conditions during the nonbreeding season (Lack 1968, Alerstam et al. 2003, Zink 2011). These strategies encompass a complete spectrum from partial to full migration conducted over short to long distances. Birds that migrate long distances often travel thousands of kilometers annually, frequently flying over large regions of inhospitable terrain. In addition to the broader benefits associated with migration, which can be substantial for migrants that inhabit productive environments year round (Møller 2007), there are direct fitness costs related to migration itself. Annual mortality rates for birds are often highest during migration due to the increased physiological stress, environmental hazards, and predation risk associated with the journey (Silllett and Holmes 2002). In addition to the risk of

mortality during migration, another constraint is time. Each species' annual cycle includes time devoted to a variety of activities including migration, breeding, and molting, each having its own unique temporal restrictions and energy requirements.

Optimal migration theory posits that these costs have shaped individuals' migratory behaviors to maximize fitness (Alerstam and Linderström 1990, Alerstam and Hedenström 1998, Houston 1998, Alerstam 2011). Maximizing fitness requires, at a minimum, surviving the migratory journey. Given the high mortality rate associated with migration, survival can be maximized by minimizing the overall time in migration or, equivalently, maximizing migration speed (Alerstam and Linderström 1990), with migration speed being defined as an individual's total migration distance divided by the total time necessary to complete the migration journey. This measure of migration speed combines time at stopover sites, where refueling occurs, and time in flight, where energy is consumed. In addition to time minimization, natural selection might be acting on alternative currencies that could affect migration speed: energy costs and predation risk. In general, however, even though tests of optimality criteria often focus on time minimization

Manuscript received 12 October 2012; revised 13 February 2013; accepted 25 February 2013. Corresponding Editor: N. J. Gotelli.

³ E-mail: fal42@cornell.edu

(Lindstrom and Alerstam 1992, Schmaljohann and Dierschke 2005, Karlsson et al. 2012), all three currencies are relevant but probably vary in importance across species (Scheiffarth et al. 2002) and potentially within species, based on how conditions change during migration (Spaar et al. 1998, Vrugt et al. 2007).

Several factors are thought to be critical in determining the speed with which individuals of a species should migrate; primary among them is body size (Hedenström 2008). Models have been developed to predict how migration speeds among species should scale with their body mass, given an optimality strategy based on the minimization of time, energy, and risk (Hedenström and Alerstam 1998, Hedenström 2003, 2008). These models make use of prior work on avian flight biomechanics and energetics (Pennycuik 1975, 1989) and are parameterized based on simplifying assumptions related to differences in avian behavior, physiology, and morphology. The quantitative predictions originating from these models can be tested against data (Hedenström and Alerstam 1998, Hedenström 2003, 2008). For example, for species that actively flap their wings during flight (powered flight), theory predicts that, among species, migration speeds (V) should scale negatively with body mass ($V \propto m^{-0.19}$). Currently, empirical tests of these predictions are few in number and typically rely on data compiled on a few individuals from a limited number of larger-bodied species whose locations during migration can be more readily documented (e.g., Hedenström 2008). In contrast, the majority of the world's birds are small-bodied powered fliers from which estimates of migration speed are much more difficult to acquire.

In addition to body mass, an additional factor that we expect to be an important determinant of optimal migration speed among species is total migration distance. Conceivably, the increased time, energy, and risk associated with longer migration journeys can be minimized through faster migration speeds. There is evidence at the individual level that migration speeds do scale positively with total migration distance (Klaassen et al. 2012) and total migration duration (Strandberg et al. 2009a). However, these findings are based a limited number of primarily soaring fliers and lack quantitative predictions that could be compared with data.

An unexplored aspect of optimal migration theory is the extent to which its predictions, based on the decisions of individual birds, directly translate to migration patterns observed at the population level, either qualitatively or quantitatively. Here, population level refers to spatiotemporal observations compiled across many individuals within a geographic region, where individual identity is not retained over time. Population-level migration patterns and dynamics cannot be replicated easily using individual-based methods and, up to now, migration patterns at the population level have not been thoroughly documented or studied.

Considering how patterns might translate across these levels of biological organization, two outcomes are

possible. First, the individual-level predictions may fail to describe population-level patterns, suggesting no explanatory link between the two perspectives. Alternatively, evidence for a successful translation would suggest that the theoretical explanations developed at the individual level are relevant for explaining patterns observed at the population level. The first outcome could be caused by the process of integration, where individual-level relationships that exist among species are dampened or removed through the addition of new sources of variation operating at the population level. The second outcome would suggest that these new sources of variation are not sufficient to hinder successful translation. Common sources of variation occurring within or between migratory seasons that are likely to be relevant at the population level are related to differences in migratory behavior associated with age or sex (Newton 2008). An additional and potentially broader source of variation is divergent spatiotemporal structuring of migration strategies by subpopulations with different migration timing and routes (Newton 2008). These sources of variation in migratory behavior, when integrated across individuals within a species, might be substantial enough that differences among species that exist at the individual level may become increasingly difficult to detect at the population level.

Here we test the individual-level quantitative predictions originating from optimal migration theory at the population level for a broad array of species and body sizes. Specifically, we use the eBird citizen science database (Sullivan et al. 2009) to estimate spring and autumn population-level migration speeds for the combined period 2007–2011 for 102 North American migratory bird species that use powered flight. Our goal is to determine if the individual-based optimality predictions can be detected at the population level. Specifically, among species of powered fliers, our objectives are to test the predicted scaling relationship between body size and migration speed and to conduct a preliminary exploration of the scaling relationship between migration speed and migration distance.

METHODS

Data compilation

Lists of bird observations (checklists) from 2007 to 2011 were extracted from the eBird database (*available online*).⁴ Our data included all surveys that used stationary, traveling, or area sampling protocols. The geographic location of each checklist was used to place observations within equal-area cells of an icosahedron map of North America (Appendix A: Fig. A1) containing hexagons with cell areas of 12 452 km² (Sahr et al. 2003). The number of checklists submitted and the number of checklists where each species was observed were recorded for each cell for the combined period

⁴ www.ebird.org

2007–2011. Because checklists were not submitted uniformly across cells (Appendix A: Fig. A2), we limited the study area to 1779 cells located between 24° and 54° N. Virtually all of the cells in the study area contained data (Appendix A: Fig. A3). Approximately 2.29 million checklists were submitted within the study area, representing ~96% of all the checklists submitted in the Western Hemisphere during this period.

Centroids for species' breeding and winter ranges were estimated using NatureServe Western Hemisphere range maps (Ridgely et al. 2007). Breeding and winter range map polygons were converted to 12 452-km² hexagons using the equal-area icosahedron, and the centroids were calculated by averaging the latitude and longitude of the hexagon centers located in each range. We estimated the total migration distance for each species in the NatureServe database using the great-circle or orthodromic distances between the centroids of the breeding and winter ranges. Only species' breeding and winter distributions that were linked by migration were considered in these measurements.

Occurrence centroids

Species' daily occurrences were compiled from eBird checklists for each equal-area hexagon cell from 2007 to 2011. We initially selected 325 diurnal non-marine species that occurred within the study area (Appendix A: Fig. A3), had migratory distances >0, and occurred in 20 or more cells during at least one day for all years combined (for examples, see Appendix A: Fig. A4). We calculated for each of the 325 species daily occurrence centroids from the beginning of spring migration to the end of fall migration for each year. Specifically, we used the latitude and longitude of the centers of the equal-area cells to calculate the weighted mean of each species' daily latitude and longitude for each year. Weights accounted for spatiotemporal variation in observer effort and were defined for each cell and day as the proportion of checklists in which the species was reported. Our choice of hexagon size in the icosahedron was at a fine enough resolution to minimize biases in our estimates of species daily occurrence centroids (see Appendix B for sensitivity analysis) and at a coarse enough resolution to allow us to estimate spatial variation in observer effort among cells.

We summarized the locations of daily occurrence centroids over time for each species using a generalized additive mixed model (GAMM). A GAMM was separately fit to the latitudinal and longitudinal components of the daily centroids as a function of time (day), with year as a random effect. Generalized additive models represent an adaptive method that adjusts automatically to the nonlinear associations observed between our predictor and response variables (see Appendix A: Fig. A4). The latitudinal and longitudinal predictions were then combined for each day to estimate the daily occurrence centroid of the population.

We narrowed the initial list of 325 species to 102 species of powered fliers that had well-defined patterns of occurrence during spring and autumn migration and were composed of a single primary migratory population (Appendix C). Species were identified as powered fliers if they were classified in Viscor and Fuster (1987) as using high-frequency flapping flight or flapping flight. Patterns of occurrence were based on the daily frequency of cells where each species was documented for all years combined (Appendix A: Fig. A4). Only species with clearly delineated spring and autumn migration peaks in occurrence were retained for analysis. The spatial trajectories of species' estimated population centroids were then examined, in combination with breeding and winter range maps, to verify that the selected species did not contain multiple migratory populations. Spatial trajectories that contained substantial longitudinal or latitudinal variation suggested the presence of multiple, independent migratory populations, which could then be verified in some cases based on the structure of breeding and winter ranges. Of the many potential migration patterns (Newton 2008), our approach was able to identify those characterized by strong spatiotemporal separation. Multiple migratory populations that overlap substantially in space and time could not be detected using this approach. However, in contrast to cases of strong separation, the overlapping nature of these migration strategies would likely add little additional variation to our estimates.

Because migration timing varies among species, we derived species-specific time intervals to define the start of spring and end of autumn migration. For each species, we estimated how occurrence changed over time using a generalized additive model (GAM) applied to the daily frequency of cells where each species was documented for all years combined (Appendix A: Fig. A4). We used the minimum of the upper limit from the 99% confidence band of the predicted daily occurrence as a threshold to define winter season occurrence before spring migration and winter season occurrences after autumn migration. The date at which the predicted frequency of occurrence first reached the threshold during the period 11 January to 9 July was used to define the beginning of spring migration and the date at which the predicted frequency of occurrence first reached the threshold during the period 8 August to 21 December was used to define the end of autumn migration. These periods were selected to capture the full range of dates associated with the start of spring and the end of autumn migration for the 102 species (Appendix A: Fig. A4).

Body mass estimates for the 102 species were based on values from Dunning (1984), which we averaged across sex and subspecies. The 102 species had a median body mass of 14.9 g (range 2.5–636.0 g) and a median migration distance between breeding and wintering grounds of 3158 km (range 1105–9332 km; Appendix A: Fig. A5; Appendix C).

Migration speed

We estimated daily population-level migration speed for each species based on the great-circle distance measured sequentially between pairs of estimated population centroids (Appendix A: Fig. A4). We examined annual variation in daily migration speeds using GAMM with species as a random effect. We calculated spring and autumn migration speeds using the median of the top five fastest speeds documented during each migration interval. This approach minimized the influence of migration speed outliers (extreme speeds that occurred well outside the annual trend), the effect of species' populations transitioning from active migration to breeding over the course of each migration season, and the effects associated with the population entering or exiting the study area (Appendix A: Fig. A4). Our estimates of seasonal migration speeds were then combined with data on body mass and migration distance to test our scaling predictions.

Scaling relationships

We estimated scaling relationships using linear mixed models. The models included migration season as a nominal fixed effect, with an interaction term with body mass or migration distance to account for potential differences in slope between seasons. Likelihood ratio tests were used to examine evidence for differences in intercepts and slopes between migration seasons. Our models accounted for nonindependence between seasons by including species as a random effect, and phylogenetic nonindependence by including Family as a random effect. Our models also accounted for different sampling schemes by including as a random effect a categorical variable that identified how breeding and winter range centroids were situated relative to the study area (Appendix A: Fig. A5). We identified four sampling schemes where the study area contained (1) both the breeding and winter range centroids ($n = 20$), (2) only the breeding range centroid ($n = 64$), (3) only the winter range centroid ($n = 7$), and (4) neither centroid ($n = 11$). We \log_{10} -transformed migration speed, body mass, and migration distance before analysis. All analyses were conducted in R, version 2.15.2 (R Development Core Team 2013). GAM and GAMM were implemented using the *mgcv* library (Wood 2006). Linear mixed models were implemented using the *lme4* library, and conservative ANOVA lower-bound P values for fixed effects were estimated using the *LMERConvenienceFunctions* library (version 1.7; *available online*).⁵

RESULTS

We quantified migration trajectories and speeds based on daily occurrence centroids for 102 species of North American migratory birds (Appendix C). The greatest

concentration of population centroid tracks or migration trajectories occurred north of the Gulf of Mexico and west of the Appalachian Mountains; a second concentration occurred west of the Rocky Mountains (Fig. 1a). Many species, especially in eastern North America, had looped migration trajectories that traced a clockwise path with an eastward shift during autumn migration (Fig. 1a; Appendix A, Fig. A4). Annual population-level migration speeds peaked, on average, during spring and autumn migration, decelerated rapidly going into the breeding season, and accelerated more slowly during the transition to autumn migration (Fig. 1b).

For the 102 species, median spring migration speed was 28.1 km/d and median autumn migration speed was 23.9 km/d (Appendix C). Migration speeds were significantly faster, on average (7.2 km/d; 95% CI: 4.8–9.6 km/d), during spring migration (paired $t_{101} = 5.95$, $P < 0.001$).

For the relationship between body mass and migration speed, there were significant negative scaling coefficients for both spring and autumn migration (Table 1, Fig. 2a). The intercepts differed between seasons ($\chi^2 = 32.32$, $df = 1$, $P < 0.001$) and the slopes did not differ between seasons ($\chi^2 = 0.33$, $df = 1$, $P = 0.567$), suggesting faster migration speeds in the spring across all body sizes (Fig. 2a). The slope coefficients for spring (−0.13) and autumn (−0.14) migration and associated 95% confidence intervals for spring (−0.23 to −0.08) and autumn (−0.21 to −0.06) migration excluded zero and contained the predicted value of −0.19 (Table 1, Fig. 2a). The deviance in migration speed explained by body mass was low overall (Table 1).

For the relationship between migration distance and migration speed, there were significant positive scaling relationships during spring and autumn migration (Table 1, Fig. 2b). The intercept differed between seasons ($\chi^2 = 32.32$, $df = 1$, $P < 0.001$) and the slope was stronger for spring ($\chi^2 = 6.10$, $df = 1$, $P = 0.014$), suggesting faster migration speeds overall in the spring, increasing in strength with increasing migration distances (Fig. 2b). The deviance in migration speed explained by migration distance was greater than that for body mass, but was low overall (Table 1).

DISCUSSION

This study provides a population-level assessment of individual-level optimal migration predictions for the scaling relationships between migration speed and body size among species of powered fliers. Testing optimality predictions has been challenging, even at the individual level, because of the difficulty in measuring migration speeds consistently across species of varying body sizes. Our population-level approach overcomes this problem and estimates migration speeds for a large number of powered fliers of varying body sizes at a continental extent. Our results provide quantitative support for some optimality predictions. Migration speeds for

⁵ <http://www.cran.r-project.org/web/packages/LMERConvenienceFunctions/>

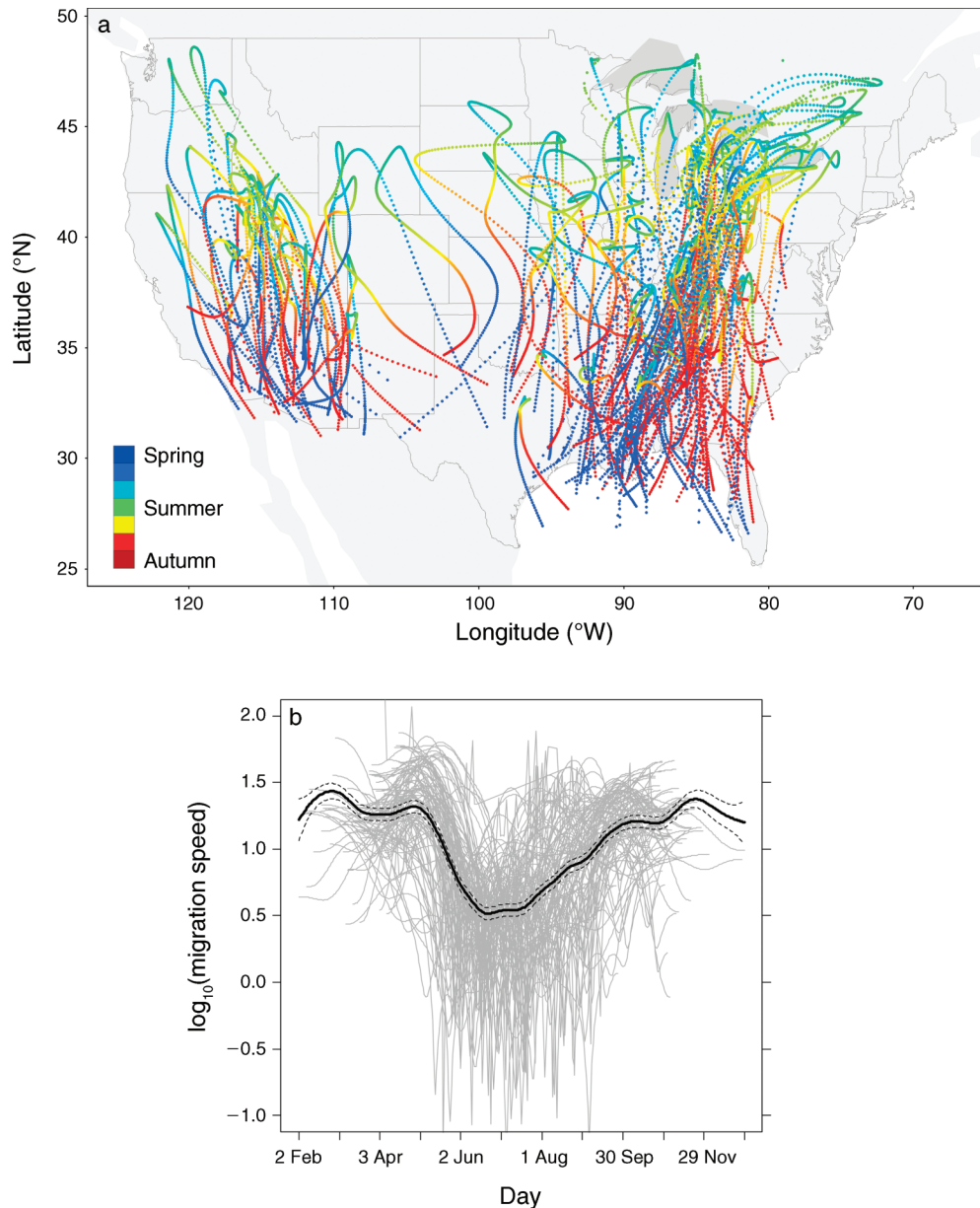


FIG. 1. (a) Migration trajectories and (b) associated migration speeds from the beginning of spring migration up to the end of autumn migration during the combined period 2007–2011 for 102 species of North American migratory birds that use powered flight. The mapped migration trajectories summarize the location of observed daily occurrence centroids of the population using generalized additive mixed models (GAMM) with year as a random effect. Log-transformed migration speeds (original measured as km/d) were summarized across species (gray lines) using GAMM with species as a random effect. Dashed lines are the 95% confidence bands.

powered fliers for both spring and autumn migration scaled negatively with body mass, with an exponent that was very close to the predicted optimality exponent. Migration speeds increased with migration distance as well. Hence, in the most general terms, our results are consistent with the basic predictions of optimal migration theory that species using powered flight should adopt a strategy during migration that minimizes time, energy, and risk. Moreover, our results suggest that

certain individual-level predictions are evident when migration patterns are integrated across individuals.

In our evaluation of the relationship between migration speed and migration distance at the population level, we found that species whose breeding and wintering grounds are separated by longer distances migrate at faster speeds; this was more pronounced during spring migration. Interestingly, we also found that migration speeds can be predicted more precisely in

TABLE 1. Linear mixed models examining relationships between migration speed and body mass and between migration speed and migration distance.

Model	Parameter	Estimate	SE	<i>t</i>	<i>P</i>	<i>R</i> ²
Body mass						
Fixed effects						
Intercept	β_0	1.563	0.072	21.56	<0.001	
Body mass	β_1	-0.135	0.038	-3.51	0.001	0.029
Season (spring)	β_2	0.121	0.049	2.46	0.015	0.060
Body mass \times Season (spring)	β_3	-0.020	0.035	-0.57	0.572	0.000
Random effects						
Species	σ_1	0.119				
Family	σ_2	0.000				
Trajectory class	σ_3	0.090				
Residual		0.110				
Migration distance						
Fixed effects						
Intercept	β_0	0.092	0.283	0.32	0.746	
Distance	β_1	0.361	0.081	4.48	<0.001	0.061
Season (spring)	β_2	-0.553	0.261	-2.12	0.036	0.060
Body mass \times Season (spring)	β_3	0.185	0.074	2.48	0.014	0.009
Random effects						
Species	σ_1	0.100				
Family	σ_2	0.091				
Trajectory class	σ_3	0.007				
Residual		0.110				

Notes: Each linear mixed model has a sample size of 102 species of North American migratory birds that used powered flight. Model coefficients for fixed effects (β), the deviance explained by each fixed effect (R^2), and the standard deviation for random effects (σ) with the residual variability are given for each model. Migration speed, body mass, and migration distance were \log_{10} -transformed before analysis. *P* values are conservative ANOVA lower-bound values.

some cases by migration distance rather than by body size. In general, our findings suggest that the relationship between migration speed and migration distance could represent a property that integrates across scales, but additional work is needed to clarify its role in optimal migration theory at both scales.

Data limitations have confined the study of migration speed primarily to the individual level, where observations are compiled across the same set of individuals over time. The approach used in this study is unique in that we did not measure and summarize observations made across a collection of individuals, but we integrated individual observations made across an entire population. Sources of variation in our approach are likely to be composed of modified aspects of individual-level variation in combination with other sources unique to this macroecological perspective. The population-level approach therefore allows us to observe migration as a population-level phenomenon while providing a novel conceptual basis for framing biological inferences with sources of variation that are uniquely defined at the population level.

One consideration is how well our estimates of migration speed match individual-level estimates. Although we tried to minimize any negative biases by quantifying migration speed as the median of the five fastest days, we cannot be certain that these five days represent the entire population in full migration. In addition, we did not estimate migration speeds along

species' entire migratory routes; this includes migratory routes that cross both terrestrial and marine environments (e.g., Gulf of Mexico and Atlantic Ocean). Our models took into consideration which component of species' migration routes were represented within the study area, a factor that appeared to be more relevant when assessing the relationship between body mass and migration speed (see Table 1). Nevertheless, our estimates of migration speed are broadly similar to migration speeds of medium-bodied powered fliers estimated from band recovery data (Appendix D, Appendix A: Fig. A6). In contrast, when individual migration speeds are estimated for larger-bodied species using tracking devices (radio or satellite telemetry or geolocator), our population-level estimates tend to be lower (Appendix D, Appendix A: Fig. A6). The differences between band recovery and satellite-based estimates have been previously documented, suggesting that band recovery methods consistently underestimate migration speeds (Strandberg et al. 2009b). Similarly, our population-level approach therefore appears to underestimate individual-based migration speeds, which should lower the intercept, but there is currently no reason to believe this should have an effect on our estimates of slope.

Our finding of faster migration speeds in the spring is broadly consistent with migration theory (time minimization hypothesis) and observation (Fransson 1995, Henningson et al. 2009, Yohannes et al. 2009, Karlsson

et al. 2012). We can now add an additional dimension, based on our findings for migration distance that birds with longer migration journeys should have proportionally higher migration speeds in the spring than in the autumn. In general, birds that arrive at the breeding grounds in a timely manner are in a better position to breed successfully (Kokko 1999), a factor particularly emphasized for males of some species (Morbey and Ydenberg 2001). With some possible exceptions (Mills 2005), this same impetus does not exist for adult birds departing from the breeding grounds, or for juveniles on their first migratory journey, which tend to have slower migration speeds and more erratic migratory routes (Ellegren 1993, Hake et al. 2003, Thorup et al. 2003). An alternative explanation for these differences may be seasonal variation in atmospheric conditions. More favorable wind conditions for migration occur in North America during the spring (Gauthreaux et al. 2005), and similar seasonal differences are associated with faster spring migration speeds in Europe (Kemp et al. 2010). Whatever the explanation, our findings suggest that seasonal differences in migration speeds represent an additional individual-level prediction that can translate to the population level. Conversely, our population-level findings make the prediction that individual-level migration data, when accumulated across individuals of many species, should eventually indicate that migration speeds are faster for species with longer migration distances.

In summary, our findings provide evidence that some individual-based optimality predictions for powered migratory fliers can be detected at the population level. In other words, the integration of individual-level migration decisions results in patterns that follow expectations from models designed and parameterized at the individual level. This outcome suggests that a macroecological perspective can be applied to optimal migration theory to address questions or test predictions in a fashion not feasible at the individual level. Our findings therefore have the potential to broaden our current ecological and evolutionary understanding of avian migration and provide a novel perspective to evaluate current hypotheses and theoretical assumptions and predictions. Contrasting individual- and population-level perspectives also has the potential to support broadscale conservation and policy initiatives directed toward sustaining migratory bird populations (La Sorte and Jetz 2010), which is important because many migrating populations are currently declining or becoming sedentary (Wilcove and Wikelski 2008).

Several avenues of research and application are possible using a population-level perspective when investigating avian migration. For example, we can now observe broadscale divergence in migration patterns, which can add to our current understanding of how phenotypes are structured at macro scales (Jetz et al. 2009) and the role of migration in structuring avian evolution. In addition, hypotheses that address observed

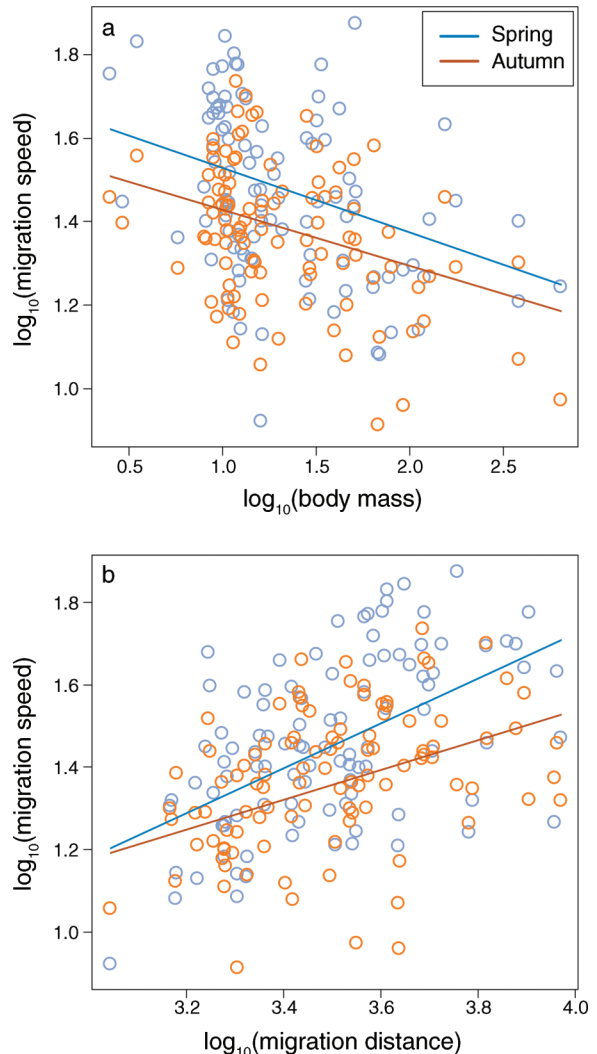


FIG. 2. Scaling relationships for 102 species of North American migratory birds that use powered flight (a) between migration speed and body mass and (b) between migration speed and migration distance during spring and autumn migration. All data were log-transformed for migration speed (km/d), body mass (g), and migration distance (km). Relationships were modeled using linear mixed models (see *Methods* for details).

variation in migratory patterns can be tested from a broader perspective; e.g., the role of atmospheric conditions and stopover habitat as factors responsible for defining seasonal variation in migration routes that results in looped trajectories (Klaassen et al. 2010). Building on these examples, an improved understanding of the spatiotemporal structure and drivers of migration at macro scales can better inform conservation strategies directed toward the broadscale maintenance of genetic diversity and the quality of stopover habitats. Moreover, this knowledge can be used to improve current projections of the impacts of climate change on birds, projections that typically are confined to the breeding

season with little consideration of the consequences of climate change for migration strategies (La Sorte and Jetz 2010). With limited research and conservation resources, the most direct and immediate benefits are likely to come from investigations that combine theory with existing data to build novel insights within and across scales of biological organization on the patterns and dynamics of avian migration.

ACKNOWLEDGMENTS

We thank T. Fredericks, M. Iliff, J. Ward, and K. Webb for assistance with data acquisition and preparation. We thank A. Farnsworth, J. Fitzpatrick, M. Iliff, W. Jetz, B. Sullivan, D. Winkler, and C. Wood for valuable discussions, and two anonymous reviewers for constructive comments. We are grateful to the many eBird participants for their contributions. This work was funded by the Leon Levy Foundation, Wolf Creek Foundation, and the National Science Foundation (DBI-1125098 and IIS-1017793).

LITERATURE CITED

- Alerstam, T. 2011. Optimal bird migration revisited. *Journal of Ornithology* 152:S5–S23.
- Alerstam, T., and A. Hedenström. 1998. The development of bird migration theory. *Journal of Avian Biology* 29:343–369.
- Alerstam, T., A. Hedenström, and S. Åkesson. 2003. Long-distance migration: evolution and determinants. *Oikos* 103: 247–260.
- Alerstam, T., and Å. Linderström. 1990. Optimal bird migration: the relative importance of time, energy and safety. Pages 331–351 in E. Gwinner, editor. *Bird migration: physiology and ecophysiology*. Springer, Berlin, Germany.
- Dunning, J. B., Jr. 1984. Body weights of 686 species of North American birds. Western Bird Banding Association. Monograph 1. Eldon Publishing, Cave Creek, Arizona, USA.
- Ellegren, H. 1993. Speed of migration and migratory flight lengths of passerine birds ringed during autumn migration in Sweden. *Ornis Scandinavica* 24:220–228.
- Fransson, T. 1995. Timing and speed of migration in North and West European populations of *Sylvia* warblers. *Journal of Avian Biology* 26:39–48.
- Gauthreaux, S. A., Jr., J. E. Michi, and C. G. Belser. 2005. The temporal and spatial structure of the atmosphere and its influence on bird migration strategies. Pages 182–193 in R. Greenberg and P. P. Marra, editors. *Birds of two worlds. The ecology and evolution of migration*. Johns Hopkins University Press, Baltimore, Maryland, USA.
- Hake, M., N. Kjellen, and T. Alerstam. 2003. Age-dependent migration strategy in honey buzzards *Pernis apivorus* tracked by satellite. *Oikos* 103:385–396.
- Hedenström, A. 2003. Scaling migration speed in animals that run, swim and fly. *Journal of Zoology* 259:155–160.
- Hedenström, A. 2008. Adaptations to migration in birds: behavioural strategies, morphology and scaling effects. *Philosophical Transactions of the Royal Society B* 363:287–299.
- Hedenström, A., and T. Alerstam. 1998. How fast can birds migrate? *Journal of Avian Biology* 29:424–432.
- Henningsson, P., H. Karlsson, J. Bäckman, T. Alerstam, and A. Hedenström. 2009. Flight speeds of swifts (*Apus apus*): seasonal differences smaller than expected. *Proceedings of the Royal Society B* 276:2395–2401.
- Houston, A. I. 1998. Models of optimal avian migration: state, time and predation. *Journal of Avian Biology* 29:395–404.
- Jetz, W., K. G. Ashton, and F. A. La Sorte. 2009. Phenotypic population divergence in terrestrial vertebrates at macro scales. *Ecology Letters* 12:1137–1146.
- Karlsson, H., C. Nilsson, J. Backman, and T. Alerstam. 2012. Nocturnal passerine migrants fly faster in spring than in autumn: a test of the time minimization hypothesis. *Animal Behaviour* 83:87–93.
- Kemp, M. U., J. Shamoun-Baranes, H. Van Gasteren, W. Bouten, and E. E. Van Loon. 2010. Can wind help explain seasonal differences in avian migration speed? *Journal of Avian Biology* 41:672–677.
- Klaassen, R. H. G., B. J. Ens, J. Shamoun-Baranes, K. M. Exo, and F. Bairlein. 2012. Migration strategy of a flight generalist, the Lesser Black-backed Gull *Larus fuscus*. *Behavioral Ecology* 23:58–68.
- Klaassen, R. H. G., R. Strandberg, M. Hake, P. Olofsson, A. P. Tottrup, and T. Alerstam. 2010. Loop migration in adult marsh harriers *Circus aeruginosus*, as revealed by satellite telemetry. *Journal of Avian Biology* 41:200–207.
- Kokko, H. 1999. Competition for early arrival in migratory birds. *Journal of Animal Ecology* 68:940–950.
- Lack, D. 1968. Bird migration and natural selection. *Oikos* 19: 1–9.
- La Sorte, F. A., and W. Jetz. 2010. Avian distributions under climate change: towards improved projections. *Journal of Experimental Biology* 213:862–869.
- Lindstrom, A., and T. Alerstam. 1992. Optimal fat loads in migrating birds: a test of the time-minimization hypothesis. *American Naturalist* 140:477–491.
- Mills, A. M. 2005. Protogyny in autumn migration: Do male birds “play chicken”? *Auk* 122:71–81.
- Møller, A. P. 2007. Senescence in relation to latitude and migration in birds. *Journal of Evolutionary Biology* 20:750–757.
- Morby, Y. E., and R. C. Ydenberg. 2001. Protandrous arrival timing to breeding areas: a review. *Ecology Letters* 4:663–673.
- Newton, I. 2008. The migration ecology of birds. Academic Press, London, UK.
- Pennycuik, C. J. 1975. Mechanics of flight. Pages 1–75 in D. S. Farner and J. R. King, editors. *Avian Biology*. Volume 5. Academic Press, New York, New York, USA.
- Pennycuik, C. J. 1989. Bird flight performance: A practical calculation manual. Oxford University Press, Oxford, UK.
- R Development Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>
- Ridgely, R. S., T. F. Allnutt, T. Brooks, D. K. McNicol, D. W. Mehlman, B. E. Young, and J. R. Zook. 2007. Digital distribution maps of the birds of the Western Hemisphere. Version 3.0. NatureServe, Arlington, Virginia, USA. <http://www.natureserve.org/getData/birdMaps.jsp>
- Sahr, K., D. White, and A. J. Kimerling. 2003. Geodesic discrete global grid systems. *Cartography and Geographic Information Science* 30:121–134.
- Scheiffarth, G., S. Wahls, C. Ketzenberg, and K. M. Exo. 2002. Spring migration strategies of two populations of bar-tailed godwits, *Limosa lapponica*, in the Wadden Sea: time minimizers or energy minimizers? *Oikos* 96:346–354.
- Schmaljohann, H., and V. Dierschke. 2005. Optimal bird migration and predation risk: a field experiment with northern wheatears *Oenanthe oenanthe*. *Journal of Animal Ecology* 74:131–138.
- Sillett, T. S., and R. T. Holmes. 2002. Variation in survivorship of a migratory songbird throughout its annual cycle. *Journal of Animal Ecology* 71:296–308.
- Spaar, R., H. Stark, and F. Liechti. 1998. Migratory flight strategies of Levant sparrowhawks: time or energy minimization? *Animal Behaviour* 56:1185–1197.
- Strandberg, R., T. Alerstam, M. Hake, and N. Kjellen. 2009a. Short-distance migration of the Common Buzzard *Buteo buteo* recorded by satellite tracking. *Ibis* 151:200–206.
- Strandberg, R., R. H. G. Klaassen, and K. Thorup. 2009b. Spatio-temporal distribution of migrating raptors: a com-

- parison of ringing and satellite tracking. *Journal of Avian Biology* 40:500–510.
- Sullivan, B. L., C. L. Wood, M. J. Iliff, R. E. Bonney, D. Fink, and S. Kelling. 2009. eBird: A citizen-based bird observation network in the biological sciences. *Biological Conservation* 142:2282–2292.
- Thorup, K., T. Alerstam, M. Hake, and N. Kjellen. 2003. Bird orientation: compensation for wind drift in migrating raptors is age dependent. *Proceedings of the Royal Society B* 270:S8–S11.
- Viscor, G., and J. F. Fuster. 1987. Relationships between morphological parameters in birds with different flying habits. *Comparative Biochemistry and Physiology A* 87: 231–249.
- Vrugt, J. A., J. van Belle, and W. Bouten. 2007. Pareto front analysis of flight time and energy use in long-distance bird migration. *Journal of Avian Biology* 38:432–442.
- Wilcove, D. S., and M. Wikelski. 2008. Going, going, gone: Is animal migration disappearing? *PLoS Biology* 6:e188.
- Wood, S. N. 2006. *Generalized additive models: An introduction with R*. Chapman and Hall/CRC, Boca Raton, Florida, USA.
- Yohannes, E., H. Biebach, G. Nikolaus, and D. J. Pearson. 2009. Migration speeds among eleven species of long-distance migrating passerines across Europe, the desert and eastern Africa. *Journal of Avian Biology* 40:126–134.
- Zink, R. M. 2011. The evolution of avian migration. *Biological Journal of the Linnean Society* 104:237–250.

SUPPLEMENTAL MATERIAL

Appendix A

Supporting figures of icosahedron, eBird checklist distribution, study area, examples from the analysis, breeding and winter range centroids, and individual-level scaling relationships between body mass and migration speed compiled from the literature ([Ecological Archives E094-167-A1](#)).

Appendix B

Sensitivity analysis of the effect of cell resolution on centroid estimates ([Ecological Archives E094-167-A2](#)).

Appendix C

Data and parameter estimates for 102 species of North American migratory birds that use powered flight ([Ecological Archives E094-167-A3](#)).

Appendix D

Individual-level migration speeds reported in the literature ([Ecological Archives E094-167-A4](#)).

Supplement

R script used in the sensitivity analysis of the effect of cell resolution on centroid estimates ([Ecological Archives E094-167-S1](#)).