Habitat specialist birds disperse farther and are more migratory than habitat generalist birds

Amanda E. Martin [iD][1,2] and Lenore Fahrig

Geomatics and Landscape Ecology Laboratory (GLEL), Carleton University, 1125 Colonel By Drive, Ottawa, Ontario K1S 5B6 Canada

Abstract. Some theories predict habitat specialists should be less dispersive and migratory than generalists, while other theories predict the opposite. We evaluated the cross-species relationship between the degree of habitat specialization and dispersal and migration status in 101 bird species breeding in North America and the United Kingdom, using empirical estimates of the degree of habitat specialization from breeding bird surveys and mean dispersal distance estimates from large-scale mark–recapture studies. We found that habitat specialists dispersed farther than habitat generalists, and full migrants had more specialized habitat than partial migrants or resident species. To our knowledge this is the first large-scale, multi-species study to demonstrate a positive relationship between the degree of habitat specialization and dispersal, and it is opposite to the pattern found for invertebrates. This finding is particularly interesting because it suggests that trade-offs between the degree of habitat specialization and dispersal ability are not conserved across taxonomic groups. This cautions against extrapolation of trait co-occurrence from one species group to another. In particular, it suggests that efforts aimed at conserving the most habitat-specialist temperate-breeding birds will not lead to conservation of the most dispersal-limited species.

Key words: dispersal ability; dispersal distance; dispersal syndrome; ecological specialization; habitat breadth; habitat specialization; migration; mobility; niche specialization; niche width.

Introduction

Cost–benefit trade-offs between species traits suggest that a species' degree of habitat specialization should be related to its dispersal ability and migratory behavior. However, it is not clear whether we should expect a habitat specialist (that uses only one or a few land cover types as habitat) to be more or less mobile than a habitat generalist (that uses many land cover types as habitat). Several theories suggest a trade-off between the degree of habitat specialization and dispersal, predicting that habitat specialists are less dispersive than habitat generalists. One hypothesis is that higher costs of movement among sparsely distributed resource patches lead to selection for less dispersal (Fig. 1a; Jocque et al. 2010, Stevens et al. 2014). This is mainly because the probability of finding habitat during dispersal is lower when the species can use less of the landscape as habitat, which would lead to increased dispersal mortality for habitat specialists relative to generalists. A second suggests that, if habitat specialists can outcompete habitat generalists for a given resource, higher dispersal allows generalists to access resources unavailable to the specialist, and thus avoid competition (Kisdi 2002, Nagelkerke and Menken 2013). Third, a negative association between dispersal and the degree of habitat specialization could occur if high dispersal leads to high rates of gene flow across the landscape, decreasing local adaptation (Venail et al. 2008).

Conversely, some theory suggests the opposite: that habitat specialists have stronger dispersal abilities than habitat generalists. The idea here is that dispersal compensates for local resource scarcity. In a heterogeneous landscape, as a species' degree of habitat specialization increases, its habitat becomes more rare and more isolated. Thus a habitat specialist needs to move more frequently and farther than a habitat generalist, to locate resources and avoid genetic and demographic isolation (Fig. 1b; Samways and Lu 2007, Centeno-Cuadros et al. 2011).

Empirical studies comparing the degree of habitat specialization to dispersal are limited. Most studies include few species, use expert opinion classifications that could confound the degree of habitat specialization and dispersal, or lack statistical support (e.g., Brouat et al. 2003, Samways and Lu 2007, Öckinger et al. 2009, Stevens et al. 2012). Rigorous studies so far suggest that habitat specialists are less dispersive than generalists (Bonte et al. 2003, Entling et al. 2011, Sekar 2012, Carnicer et al. 2013, Dapporto and Dennis 2013, Stevens et al. 2014, Dahirel et al. 2015). However, these negative relationships between the degree of habitat specialization and dispersal were all observed in invertebrates.

It has also been suggested that resident (i.e., non-migratory) species are more likely to be habitat specialists than migratory species. Resident species can select breeding habitat before migrants return, so migrants who can take advantage of multiple land cover classes can minimize direct competition for resources with resident species. For example, non-migratory *Sylvia atricapilla* dominate in forest and migratory *Sylvia atricapilla* use both forest and shrubland (Pérez-Tris and Tellería 2002). However, the opposite is also possible. Resident species may adapt to fluctuations in resource availability by becoming habitat generalists,

[1] Present address: Environment and Climate Change Canada, National Wildlife Research Centre, 1125 Colonel by Drive, Ottawa, Ontario K1S 5B6 Canada.
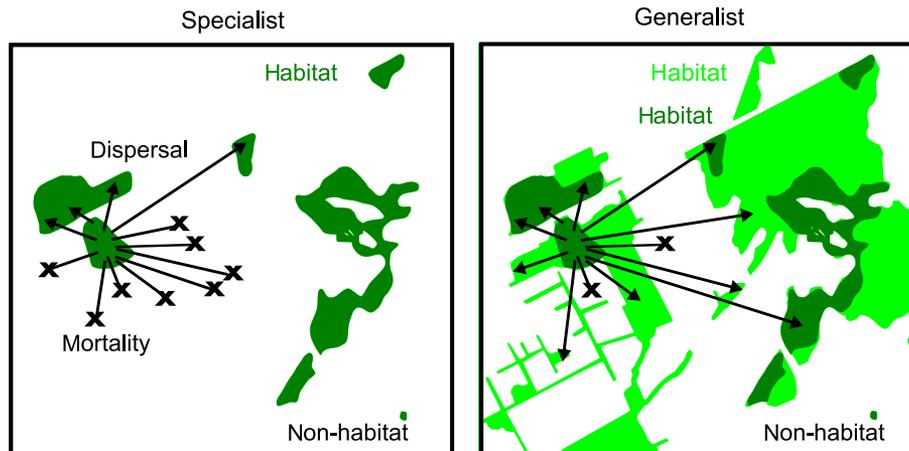[2] E-mail: amanda.martin@canada.ca

a) Habitat generalists disperse farther than specialists, because of higher dispersal costs for specialists

b) Habitat specialists disperse farther than generalists, because habitat patches are farther apart for specialists
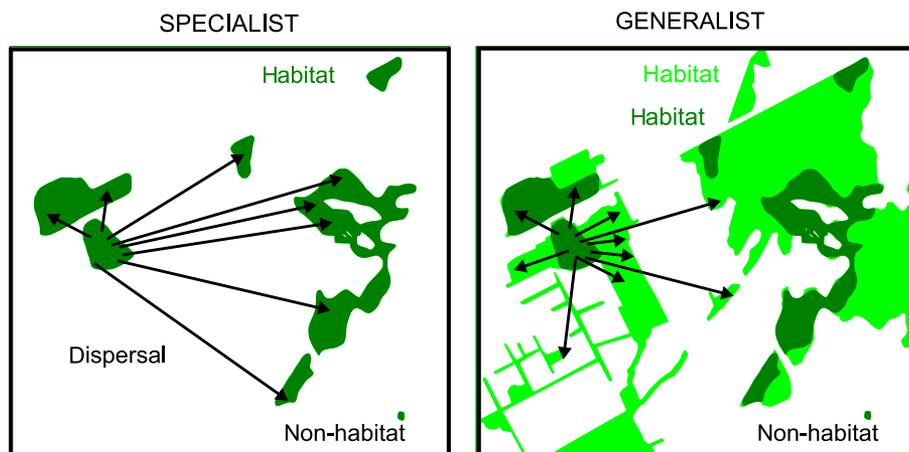

FIG. 1. Illustrations of why (a) habitat generalists may be more dispersive than specialists, because dispersal costs increase with the degree of habitat specialization, and (b) habitat specialists may be more dispersive than generalists, because specialists need to be able to move farther to locate habitat.

whereas migrants do not have to become generalists because they avoid declines in local resource availability through migration (Cox 1985, Holt and Fryxell 2011).

The purpose of this study was to evaluate the cross-species relationship between the degree of habitat specialization and dispersal, and between the degree of habitat specialization and migration status, in temperate breeding birds in North America (N.A.) and the United Kingdom (U.K.).

METHODS

Overview

Analyses were conducted on bird species breeding in N.A. or the U.K., i.e., temperate-breeding birds. We estimated the degree of habitat specialization using the species specialization index (SSI; Julliard et al. 2006), which models the degree of habitat specialization as the coefficient of variation in the estimated species densities among different land cover classes. Geometric mean dispersal distances were estimated from mark–recapture sampling. The migration status of each species was categorized as resident, partial migrant, or full migrant.

We related the SSI to the estimated dispersal distance and migration status. We used model selection based on the Akaike information criterion corrected for sample size (AIC$_c$) to compare among all subsets of our global model, which related the SSI to dispersal distance + migration status + region + dispersal distance × region + migration status × region, plus the null (intercept-only) model. We included interactions with the study region (N.A. or U.K.) to account for possible differences in the relationships between SSI and dispersal distance/migratory status for birds breeding in these regions. To account for phylogenetic non-independence we modeled these relationships using a phylogenetic generalized least squares model (Martins and Hansen 1997).

Estimation of the species specialization index

North America.—We used the N.A. Breeding Bird Survey (BBS) to calculate the SSI for N.A. birds. The N.A. BBS provides a continent-wide, multi-year data set of species counts for breeding birds, begun in 1966 (Appendix S1: Fig. S1; Pardieck et al. 2014). Point counts are conducted once each year during the breeding season, at each of 50 stops spaced along each of approximately 4,100, 39.4 km long, roadside survey routes. At each point count, all birds seen or heard within a 0.4 km radius are recorded over a 3-min interval. Surveys begin approximately one-half hour before sunrise.

To calculate the SSI for each species, we first estimated the density of each species in each land cover class. We used 11 land cover classes derived from an existing, raster, GIS data set that classified land cover at a pixel size of 250 m (Appendix S1: Fig. S2; NRCan et al. 2005). Classification was based on Moderate Resolution Imaging Spectroradiometer imagery for 2005, combining classifications of national land cover performed by the United States, Canada, and Mexico, as part of the North American Agreement on Environmental Cooperation (NRCan et al. 2005). Species counts were taken from the first stop of each N.A. BBS route sampled in 2003–2007. The first stop is the only stop for each route with reliable latitudes and longitudes for all routes. We selected 2003–2007 to bracket the year of land cover data (2005). We estimated the density of a species in a land cover class as the number of individuals observed in that land cover between 2003 and 2007, divided by the number of first stops in that land cover class.

The SSI was then calculated as the coefficient of variation (standard deviation/mean) in the estimated densities among the land cover classes. This produced a continuous index of the degree of habitat specialization, where habitat specialist species had higher coefficients of variation in the estimated densities than habitat generalist species (Fig. 2). To ensure that sample sizes were large enough to allow for reasonable estimation of the species densities in different land cover classes, in our analyses we only included species that were observed at the first stop of at least 10 routes between 2003 and 2007.

United Kingdom.—For U.K. birds, SSI values were taken from Davey et al. (2012), who used species counts and land cover classifications from the U.K. BBS coordinated by the British Trust for Ornithology/Joint Nature Conservation Committee/Royal Society for the Protection of Birds. The U.K. BBS conducts point counts at more than 3,000 1-km squares twice each breeding season, counting all birds seen or heard along two 1-km transects within each square. Observers also classify land cover for each 200-m transect section during surveys, as defined in Crick (1992). The main differences between the U.K. and N.A. SSI calculations were that, in Davey et al. (2012), (1) bird counts included birds within a shorter distance of the count location (within 0.1 km of the transect), (2) land cover was estimated by observers during the U.K. BBS (12 classes) rather than from satellite imagery, and (3) density estimates in each land cover class were based on a longer time series (1994–2006).
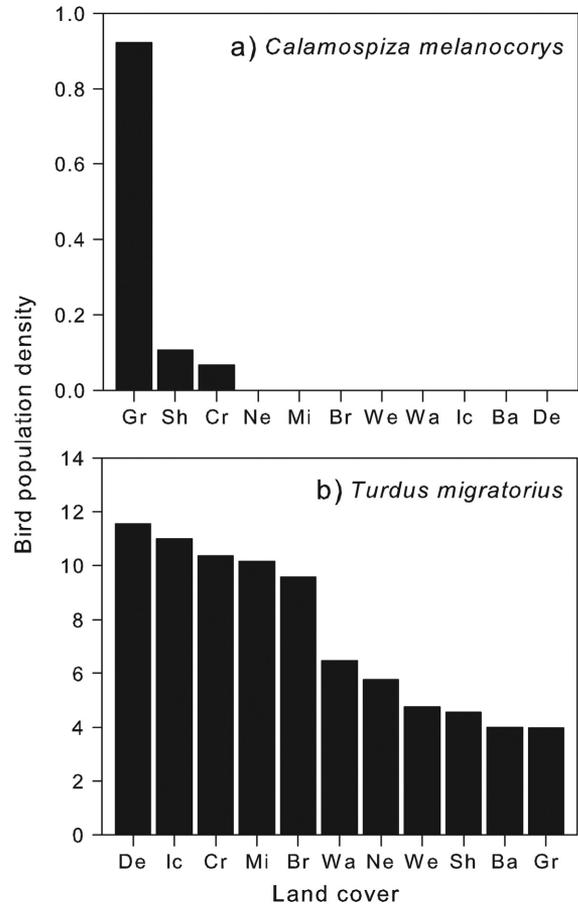

FIG. 2. Example estimation of the species specialization index (SSI) for (a) *Calamospiza melanocorys* (Lark Bunting), a grassland habitat specialist (SSI = 2.77), and (b) *Turdus migratorius* (American Robin), a habitat generalist (SSI = 0.41). The SSI was calculated as the coefficient of variation in densities among land cover classes. Ag, agriculture; Ba, barren; Br, broadleaf forest; De, developed; Gr, grassland; Ic, ice and snow; Mi, mixed forest; Ne, needleaf forest; Sh, shrubland; Wa, water; We, wetland.

Estimation of dispersal distances

North America.—Mean dispersal distances were estimated by mark–recapture sampling, based on the distances between marking and recapture locations for birds taken from the North American Bird Banding Program, Bird Banding Laboratory (USGS 2017), using data collected from 1910–2016. We were able to obtain records of recapture for 192 of the 241 N.A. species with an SSI (see Appendix S2: Table S1).

To estimate dispersal distances from the recapture records, we used methods similar to those of Paradis et al. (1998), who estimated mean dispersal distances for U.K. birds from a mark–recapture data set collected by the British Trust for Ornithology. For each species, we selected the subset of records that met the following criteria. First, we eliminated records with low location precision. The Bird Banding Laboratory primarily classifies the precision of the capture locations as exact, 1-min block, or 10-min block (USGS 2016). We included only the subset of capture events with at least 1-min block precision at both marking and recapture.

Second, we eliminated records that did not include an estimate of the bird's age when marked. Third, we included only individuals that were marked and released in the same 10-min block as they were captured, and that were held in captivity for ≤24 h before release. Fourth, we included only recaptures that occurred during different years than the initial capture and marking, to exclude any transient movements made by individuals after release. Fifth, if a marked individual was recaptured more than once, we retained only the record for the first recapture, to avoid non-independence of observations. Sixth, we included only individuals that were marked and recaptured during the breeding season, to avoid estimating distances moved during seasonal migration (for migratory species) or during irruptive movements during winter (for resident species). We estimated the breeding season for each species using phenological data in Rodewald (2015). Finally, we examined the bearings and distances for the set of retained recapture events for each species and, if the bearings for the largest distances for a given species were along the North-South axis (which we defined as movements along bearings of 345–15° and 165–195°), these distances were excluded.

We estimated the geometric mean natal dispersal distance and breeding dispersal distance for each species using the subset of recapture events that met the criteria above. For natal dispersal distance estimates, we included only dispersal events for individuals marked in the year of birth and recaptured at breeding age. For breeding dispersal distances, we included only dispersal events for individuals marked at breeding age. Mean distances were only estimated for species with at least 10 retained recapture events.

United Kingdom.—Natal and breeding dispersal distances of U.K. birds were taken from Paradis et al. (1998). They collected distances between marking and recapture locations for birds banded by the British Trust for Ornithology from 1909–1994. They divided dispersal records into either natal dispersal, if the individual was marked in its year of birth and recaptured at breeding age, or breeding dispersal, if the recaptured individual was marked at breeding age. They estimated geometric mean natal dispersal distances for all species with at least 10 sampled natal dispersal events, and breeding dispersal distances for all species with at least 10 sampled breeding dispersal events (details in Paradis et al. [1998]).

There were three main differences between the U.K. estimates of dispersal distances and our N.A. estimates. First, to our knowledge, Paradis et al. (1998) did not screen data and remove records due to imprecise location data. Second, Paradis et al. (1998) excluded dispersal events for birds banded as juveniles if juvenile dispersal distances were significantly longer than nestling dispersal distances for that species. We did not do this for N.A. species because only eight species had enough data (i.e., at least 10 juvenile and 10 nestling dispersal events) to test for mean differences between juveniles and nestlings. However, we note that only one of these eight species had significantly longer juvenile dispersal distances than nestling distances. Third, Paradis et al. (1998) excluded all recaptures of live birds from their estimates of dispersal distance. We did not do this for N.A. species because there were only eight and six species with

≥10 natal and breeding dispersal events, respectively, when we excluded recaptures of live birds.

Classification of migration status

We classified each species as a resident, partial migrant, or full migrant, based on its IUCN Red List range map (IUCN 2017). These maps discriminate between resident (year-round) distributions, breeding distributions, and non-breeding distributions. We considered only the migratory behavior of populations found within the study area covered by the BBS data used to calculate the SSI, i.e., Canada and the continental United States for N.A. breeding birds, and Britain for U.K. birds. A species was classified as resident if all populations in the study area were resident year-round or full migrant if all populations within the study area were migratory. If the study area included both resident and migratory populations we classified the species as a partial migrant.

Data analysis

We tested for a cross-species relationship between the SSI and dispersal distance and migration status twice, once using the natal dispersal distance estimates and once using the breeding dispersal distance estimates. We used AIC_c to compare among all subsets of our global model, which related the SSI to dispersal distance + migration status + region + dispersal distance × region + migration status × region, and the null model. Relationships were modeled using a generalized least squares model. To satisfy model assumptions (Mundry 2014; see Appendix S3: Fig. S1), we ln-transformed the SSI and dispersal distances. To account for phylogenetic non-independence, we included a covariance matrix, where covariance between a given pair of species was based on a phylogenetic tree and a Brownian model of evolution (Martins and Hansen 1997). The phylogenetic tree was from Burleigh et al. (2014, 2015), who estimated the phylogenetic relationships among species from a maximum likelihood analysis of a sparse supermatrix, using nuclear and mitochondrial gene sequences from 6,714 bird species.

We note that we did not include models with a dispersal distance × migration status interaction in the above candidate model set because we had no a priori reason to expect that the relationship between the species' SSI and dispersal distance depends on its migration status. However, to confirm this expectation, we conducted supplementary analyses including models with a dispersal distance × migration status interaction. Candidate models without this interaction were more supported than those including it (Appendix S4).

Data analyses were conducted in R (R Core Team 2017), using the ape (Paradis et al. 2004), nlme (Pinheiro et al. 2017), and MuMIn (Barton 2016) packages.

Results

We calculated SSI for 241 N.A. bird species and geometric mean natal and breeding dispersal distances for 20 species and 23 species, respectively (Appendix S2: Table S1). For U.K. birds, we included 75 species in our analyses when

using the natal dispersal distance estimates, and 67 species when using breeding dispersal distance estimates (Appendix S2: Table S2). We note that two species (*Anas platyrhynchos* and *Branta canadensis*) were found in both study regions. To avoid issues of non-independence due to repeat measurements of these species, we used only the estimates for these species in N.A. Our conclusions were identical when we included the estimates from the U.K. In total, we included 93 species in our analyses using natal dispersal distances (37 resident, 36 partial migrant, and 20 full migrant species) and 88 species when using breeding dispersal distances (34 resident, 35 partial migrant, and 19 full migrant species).

For both N.A. and U.K. birds, species with narrower habitat requirements (i.e., larger SSI) had longer dispersal distances than species with more flexible habitat requirements (i.e., smaller SSI). The most supported model of our candidate model set included a dispersal distance × region interaction, regardless of whether we used natal or breeding dispersal distance estimates (Table 1). However, in both regions the relationship between SSI and dispersal distance was positive (Fig. 3). The weight of evidence (i.e., summed Akaike weight) for candidate models including dispersal distance was 1.00 and 0.99 when using natal and breeding dispersal distances, respectively. Additionally, the null model was not included in the most supported model set: the ΔAIC_c for the null model was 70.95 and 47.91 when using natal and breeding dispersal distances, respectively.

TABLE 1. Level of support for relationships between the species specialization index and the geometric mean dispersal distance, migration status (resident, partial migrant, full migrant), and study region (North America, United Kingdom) when using (a) natal dispersal distances (93 species) and (b) breeding dispersal distances (88 species).

Model	df	AIC_c	ΔAIC_c	Weight
a) Natal dispersal				
Dispersal + region + dispersal × region	5	132.78	0.00	0.49
Dispersal	3	134.98	2.20	0.16
Dispersal + migration + region + dispersal × region	7	135.02	2.25	0.16
Dispersal + region	4	136.90	4.13	0.06
Dispersal + migration + region + dispersal × region + migration × region	9	137.38	4.61	0.05
Dispersal + migration	5	137.92	5.15	0.04
Dispersal + migration + region + migration × region	8	139.15	6.37	0.02
b) Breeding dispersal				
Dispersal + migration + region + dispersal × region	7	145.00	0.00	0.76
Dispersal + region + dispersal × region	5	148.63	3.63	0.12
Dispersal + migration + region + dispersal × region + migration × region	9	149.10	4.10	0.10

Notes: Relationships were modeled using generalized least squares, with a covariance matrix to account for phylogenetic relationships among species, comparing among all subsets of the global model (dispersal distance + migration status + region + dispersal distance × region + migration status × region) using the Akaike information criterion corrected for sample size (AIC_c). We present all models with $\Delta AIC_c \leq 7$.

Full migrants tended to have narrower habitat requirements (i.e., larger SSI) than partial migrant or resident species (Fig. 3, Table 1). However, the level of support for a cross-species relationship between the degree of habitat specialization and migration status was much weaker in the models containing natal dispersal distances than in the models containing breeding dispersal distances. The weight of evidence for candidate models containing migration status was only 0.28 when we included natal dispersal distances, but 0.87 when we included breeding dispersal distances.

DISCUSSION

Relationships between the degree of habitat specialization and dispersal distance

Our results suggest that temperate breeding bird species with narrower habitat requirements typically disperse farther than species with more flexible habitat requirements. We speculate that this relationship occurs because dispersal compensates for resource scarcity. When a habitat specialist is restricted to sparsely distributed patches of habitat in an unsuitable matrix it needs to move farther to locate resources and avoid genetic and demographic isolation (Fig. 1b; Samways and Lu 2007, Centeno-Cuadros et al. 2011). To our knowledge, this is the first large-scale, multi-species study to find a positive relationship between the degree of habitat specialization and dispersal.

Our statistical models also predicted that the relationship between the degree of habitat specialization and dispersal distance was stronger in N.A. than in the U.K. However, it is not clear whether this difference reflects actual differences in the strength of the relationship, or differences in the methods used to collect the underlying data or measure dispersal in the two study regions (as summarized in *Methods*). Nevertheless, the direction of the relationship was consistent for the two regions.

It is unlikely that the positive relationship between the degree of habitat specialization and dispersal distance is an artifact of the data sets or the methods for measuring the degree of habitat specialization or dispersal distance. The SSI has advantages over other measures of habitat specialization because it (1) is based on empirical data, rather than expert opinion, (2) takes into account both the number of land cover classes a species occupies and the relative densities of the species in them, and (3) is independent of differences in abundance among species (Julliard et al. 2006). We recognize that, although use of breeding bird survey data for SSI estimation has the obvious advantage of providing a large scale, multi-year data set with sampling points distributed across many land cover types, its sampling protocol does not result in consistently high detectability across all sampled species. For example, if a species rarely occurs near roads, it is less likely to be sampled in the N.A. BBS than other species, because all N.A. BBS point count locations are along roads. However, differences in detectability are unlikely to explain our findings. Overall differences in detectability among birds that lead to differences in their observed abundances should not generally affect the SSI because, as discussed above, this measure is independent of differences in abundance among species. The only way that
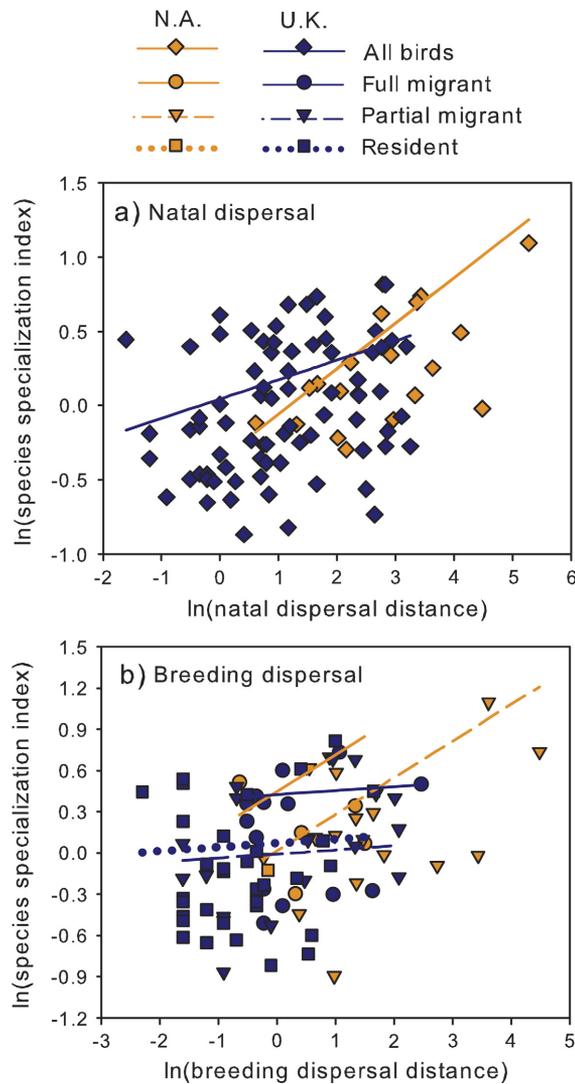
FIG. 3. Relationships between the species specialization index (SSI) and geometric mean dispersal distance and migration status for North American (N.A.) and United Kingdom (U.K.) breeding birds, using the most supported models from our candidate model set. In panel (a), the most supported model predicted SSI as a function of the natal dispersal distance + region + natal dispersal distance × region; in panel (b), the most supported model predicted SSI as a function of the breeding dispersal distance + region + migration status + breeding dispersal distance × region (see Table 1). Relationships were modeled by generalized least squares, with a covariance matrix to account for non-independence due to phylogenetic relatedness. Each point represents a bird species.

among-species variation in detectability could cause a spurious relationship between the SSI and dispersal distances is if all of the following conditions hold: (1) a given species was more detectable in some land cover types than others, (2) variation in species observations among land cover types was more strongly related to detectability than actual habitat selection, and (3) there was greater variation in detectability among land cover types, resulting in overestimated SSI, for species that disperse longer distances. Although it is likely that detectability can vary for a given species among land cover types (e.g., Ruiz-Gutiérrez et al. 2010), we can find no evidence to support the co-occurrence

of all three of these conditions. We also acknowledge that mark–recapture data can produce inaccurate or biased estimates of dispersal distances. For example, there is a tendency for mark–recapture studies to underestimate dispersal distances (Koenig et al. 1996, Yamamura et al. 2003). Mark–recapture dispersal distances also depend on the study area size, with longer mean dispersal distances estimated when the study area is larger (Schneider 2003). However, we can think of no reason to expect this to drive a spurious cross-species relationship between the SSI and our dispersal distance estimates.

The relationship we found between the degree of habitat specialization and dispersal distance for temperate breeding birds was opposite to previously reported relationships for invertebrates (Bonte et al. 2003, Entling et al. 2011, Sekar 2012, Carnicer et al. 2013, Dapporto and Dennis 2013, Stevens et al. 2014, Dahirel et al. 2015). We speculate that this may be because these two taxa differ in other traits that affect the habitat-specialization–dispersal relationship. For example, this relationship may depend on whether the species are endothermic or ectothermic. Since the energetic costs of endothermy are much higher than for ectothermy (Nagy 1987), ectotherms are likely better adapted to survive periods of food scarcity than endotherms (Pough 1980). This suggests that endotherms are more sensitive to local resource scarcity than ectotherms, which is consistent with evidence that the abundance and richness of endotherms is more strongly related to local resource availability than the abundance and richness of ectotherms (Buckley et al. 2012). Thus for ectotherms, which can wait out periods of low food availability, the higher costs of movement for habitat specialists should lead to selection for lower dispersal in habitat specialists than generalists. However, for endotherms, which need to disperse to avoid starvation, habitat specialists will need to move farther than generalists to locate resource patches. A first step in testing this hypothesis would be to test for positive relationships between dispersal distance and the degree of habitat specialization in endotherm taxa other than temperate birds.

The direction of the relationship between the degree of habitat specialization and dispersal distance may also depend on the range of dispersal distances within a species group relative to the distances among habitat patches. Habitat generalist species should move farther than habitat specialists within a species group that has short dispersal distances relative to the distances among habitat patches. For such a group, the costs of dispersing should be an important driver of natural selection, and thus the greater costs of dispersal for habitat specialists relative to habitat generalists should drive selection for shorter dispersal distances in specialists than generalists. Conversely, for a group with typically long dispersal distances (e.g., birds), even the most dispersal-limited species in the group may be able to move farther than the distances among patches. In this case, the costs of dispersal should be a weak driver of natural selection, and selection for dispersal ability would instead be driven by the greater local resource scarcity experienced by specialists than by generalists in the group. This would lead to longer dispersal distances for specialists than generalists. This may explain the opposite relationships between the degree of habitat specialization and dispersal for birds vs.

some invertebrate groups, if those invertebrate groups typically have short movement ranges relative to the distances among their habitat patches.

Even within endotherms, the direction of the relationship between the degree of habitat specialization and dispersal distance might vary geographically. For example, the relationship could be opposite for temperate and tropical bird species. Gap-crossing studies provide preliminary support for the prediction that habitat generalist tropical birds move farther than habitat specialist tropical birds, showing lower rates of gap-crossing by tropical forest specialists than generalists (Kennedy and Marra 2010, Ibarra-Macias et al. 2011). However, to our knowledge, this relationship has not been shown in multi-species studies with empirical estimates of the degree of habitat specialization and dispersal. If the relationship is in fact opposite for temperate and tropical species, we speculate that this could be due to an effect of landscape structure on the evolution of the habitat-specialization–dispersal relationship, using a modified version of the arguments presented by Jocque et al. (2010). In a stable tropical landscape, where local extinction events are rare, the higher costs of movement for habitat specialists should drive selection for less dispersal. However, in a more dynamic temperate landscape (Báldi 1996, Saigusa et al. 2008), the need to disperse to escape locally declining conditions and recolonize after local extinctions may be greater than the costs of dispersal. In these temperate landscapes, the degree of habitat specialization may drive selection for greater dispersal distances, because specialists need to move farther to locate resources than generalists. Thus habitat specialist birds in the more dynamic temperate regions may evolve to disperse farther than generalists, while habitat generalists in the more stable tropical regions may evolve to disperse farther than specialists. We emphasize that this is only speculation and needs to be tested.

Relationships between the degree of habitat specialization and migration status

We found that full migrant species had more specialized breeding habitat requirements than partial migrants and resident species. This may occur because residents in temperate regions adapt to fluctuations in resource availability by becoming habitat generalists, whereas migrants do not have to become generalists within their breeding ranges because they avoid declines in local resource availability through migration (Cox 1985, Holt and Fryxell 2011). Interestingly, such relationships between the degree of habitat specialization and migration status have not been observed for species in their overwintering ranges (Wunderle and Waide 1993, Ivande and Cresswell 2016), where seasonal resource fluctuations are less extreme.

One might speculate that the positive relationship between the degree of habitat specialization and migration status could be driven by the association between habitat specialization and dispersal distance, if migratory species disperse farther than resident species. However, we found no support for a relationship between a species' migration status and its mean natal or breeding dispersal distance (Appendix S5). This is similar to the findings of other studies of dispersal–migration relationships in birds (e.g., Sutherland et al. 2000,

Stevens et al. 2014). Thus mark–recapture data can reveal short dispersal distances for migratory species, despite their ability to move long distances during migration, if individuals of that species tend to return to breed in a location near to their natal (or previous breeding) site rather than dispersing to breed in a distant location.

Our finding of greater degrees of habitat specialization in migratory species is opposite to what was reported by Reif et al. (2016) for European breeding birds. This difference most likely results from differences in the methods used to classify and relate habitat specialization and migration status in the two studies. In particular, Reif et al. (2016) estimated SSI based on published habitat associations (e.g., species occurrence) in a bird guidebook, rather than using empirical estimates of abundance in different land cover types. They also classified migration status based on the migratory behavior of all populations across Europe, whereas we classified migration status for U.K. species based only on the populations found in Britain. Finally, Reif et al. (2016) treated migration status as a continuous variable (1, resident; 2, partial migrant; and 3–4, full migrant), which assumes an equal and quantifiable difference between migration categories. Supplementary analyses support this explanation. When we used an occurrence-based SSI, Europe-wide estimate of migration status, and treated migration as a continuous variable during analysis, we found that resident and partial migrant species had a greater degree of habitat specialization than full migrant species, as in Reif et al. (2016; Appendix S6). One might also speculate that differences in the direction of relationship between the degree of habitat specialization and migration status could be explained by differences in the covariates included in the analyses. However, the direction of the SSI–migration-status relationship was the same in multivariate and univariate analyses in both our study and in Reif et al. (2016). Thus the difference between our finding and that of Reif et al. (2016) is most likely due to differences in study methods. Future research is needed to clarify how the degree of habitat specialization is related to migration status.

Conclusions

This is the first large-scale, multi-species study to demonstrate that habitat specialists can be stronger dispersers than habitat generalists. Our result for temperate breeding birds is opposite to previous results for invertebrates (Bonte et al. 2003, Entling et al. 2011, Sekar 2012, Carnicer et al. 2013, Dapporto and Dennis 2013, Stevens et al. 2014, Dahirel et al. 2015). This suggests that a trade-off between the degree of habitat specialization and dispersal distance may not be consistent across taxa. We speculate that differences in the habitat-specialization–dispersal relationship among species groups occur because other species traits (e.g., endothermy vs. ectothermy) or landscape attributes (spatial or temporal resource availability) affect the evolution of the habitat-specialization–dispersal relationship.

It is often thought that species with narrower habitat requirements and limited dispersal should receive higher conservation priority, because they are most sensitive to human landscape change (e.g., Julliard et al. 2003, Garrard

et al. 2012). Our results caution against making the assumption that prioritizing conservation actions for species with narrower habitat requirements will necessarily protect the most dispersal-limited species. While these traits may sometimes be negatively correlated, our results suggest that these two traits can also be positively related, as we found here for temperate birds. This means that efforts aimed at conserving habitat-specialist temperate bird species will not lead to conservation of the most dispersal-limited species. Whether one prioritizes based on degree of habitat specialization or dispersal ability will depend on the relative importance of these two traits for species' risk in human-dominated landscapes.

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SUPPORTING INFORMATION