



RESEARCH ARTICLE

Evidence of widespread movements from breeding to molting grounds by North American landbirds

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ABSTRACT

Precise locations for the complete feather molt of North American landbirds, relative to their breeding territories, remain undocumented for most species. We analyzed >760,000 records of 140 species at 936 bird-capture stations to assess probabilities of recording both molting landbirds at their breeding sites and breeding birds at molting sites, and to investigate latitudinal, longitudinal, and elevational shifts from breeding to molting grounds. We demonstrate widespread evidence for molt-migrations among a variety of North American landbirds, including many migratory species previously thought to molt on “breeding grounds.” Geospatial differences between breeding and molting grounds were detected in all 4 compass directions as well as both upslope and downslope in elevation, while individuals of some species appeared to disperse to specific molting locations not discriminated by spatial direction or elevation from breeding territories. Although western North American species and populations are reported to undergo more molt-migration than eastern species, our molt-movement probabilities were similar in western and eastern North America and were greater in the east than in the west for several species. Combining our results with those of these previous studies, we suggest that many landbird species in western North America move longer distances to molt, whereas many landbirds in eastern North America may equally or more likely move shorter distances between breeding and molting habitats, while remaining within the overall breeding ranges of the species. Heterogeneous molt-movement responses are suggested for many species, which may relate to breeding success, resource availability on breeding territories, weather events, and other factors. Researchers using stable-isotopic, genetic, and geolocator techniques need to consider potential molt-movement strategies, and to incorporate molting habitat requirements into full-annual-cycle conservation efforts.

Keywords: conservation, habitat, landbird, migration, molt, monsoon, upslope

Evidencia de movimientos generalizados desde sitios de cría a sitios de muda de aves terrestres de América del Norte

RESUMEN

Para la mayoría de las especies, aún se desconocen las ubicaciones precisas donde ocurre la muda completa de las plumas de las aves terrestres de América del Norte, con relación a sus territorios de cría. Analizamos >760,000 registros de 140 especies en 936 estaciones de captura de aves para evaluar las probabilidades de registrar tanto aves terrestres mudando en sus sitios de cría como aves criando en sitios de muda, y para investigar cambios latitudinales, longitudinales y de elevación desde sitios de cría a sitios de muda. Presentamos evidencia generalizada de migraciones de muda para una variedad de aves terrestres de América del Norte, incluyendo muchas especies migratorias que previamente se pensaba que mudaban en “sitios de cría.” Las diferencias geoespaciales entre los sitios de cría y los sitios de muda fueron detectadas en las cuatro direcciones de la brújula, así como hacia arriba y hacia abajo en elevación, mientras que los individuos de algunas especies parecieron dispersarse desde los territorios de cría a ubicaciones de muda específicas no discriminadas por la dirección espacial o la elevación. Aunque se reporta que las especies y las poblaciones del oeste de América del Norte experimentan más migración de muda que las especies de este, nuestras probabilidades de movimiento de muda fueron similares en el oeste y el este de América del Norte y fueron mayores en el este que en el oeste para varias especies. Combinando nuestros resultados con los de estos estudios previos, sugerimos que muchas especies de aves terrestres en el oeste de América del Norte se mueven distancias más largas para mudar, mientras que muchas aves terrestres del este de América del Norte pueden moverse distancias iguales o probablemente más cortas entre los hábitats de cría y muda, mientras que permanecen dentro de los rangos generales de cría de las especies. Se sugieren respuestas heterogéneas de movimiento de muda para muchas especies, las cuales pueden relacionarse con el éxito reproductivo, la disponibilidad de recursos en los territorios de cría, los eventos climáticos y otros factores. Los investigadores que usen técnicas de isótopos estables, genéticas y de geolocalización necesitan considerar estrategias potenciales de movimiento de muda e incorporar requerimientos de hábitat de muda en los esfuerzos de conservación para el ciclo anual completo.

Palabras clave: aves terrestres, conservación, hábitat, migración, monzón, muda, pendiente arriba

INTRODUCTION

Despite the evolutionary and energetic importance of annual, complete feather replacement, or definitive pre-basic molt, in birds (Humphrey and Parkes 1959, Murphy 1996), relatively little is known about where landbirds undergo this process (Gow and Stutchbury 2013, Nordell et al. 2016). In North America, the prebasic molt largely occurs in late summer following breeding (Pyle 1997), at which time molting landbirds become quiet, often retiring within dense vegetation, and have worn and damaged feathers. Such factors have resulted in the collection of few specimens by taxonomists upon which to assess molt location (Rohwer et al. 2005). Although the prebasic molt is reported to occur largely on the “breeding” or summer grounds (Pyle 1997, Rohwer et al. 2005), recent investigations on selected species indicate that landbirds can undergo movements from breeding grounds to specific molting grounds, for example from western North America to the monsoon region of northwestern Mexico (Rohwer et al. 2005, Pyle et al. 2009) or upslope into mountain ranges (Steele and McCormick 1995, Rohwer et al. 2008, Weigardt et al. 2017a, 2017b). These “molt-migrations” are presumed to take advantage of moister conditions or enhanced food resources in late summer to molt, before these individuals continue migration to wintering grounds (Rohwer et al. 2005, Pyle et al. 2009).

Despite this recent evidence for molt migrations, investigations modeling full-annual-cycle avian dynamics (Hostetler et al. 2015) and connecting summer and winter grounds through the use of stable-isotopic signals from feathers (Hobson et al. 2014, Pekarsky et al. 2015) largely assume, with little direct evidence, that most individual North American landbirds molt on or near their breeding territories. Dense cover providing protection for molting birds and specialized nutrients needed for feather production, however, may not be available on breeding territories, requiring birds to vacate breeding areas for specific molting habitats (Gow and Stutchbury 2013, Nordell et al. 2016). Thus, protection or management of these habitats may be critical to a species’ population stability (Leu and Thompson 2002, Chambers et al. 2011, Wiederholt et al. 2017), but conservation of North American landbirds has focused almost entirely on preserving breeding and wintering grounds rather than incorporating molting grounds within a full-annual-cycle approach (Hostetler et al. 2015). Without knowing locations or habitat requirements for the prebasic molt, conservation management of breeding and wintering grounds may be insufficient to reverse declining landbird trends.

Here we provide a broad-scale assessment of migration or dispersal from breeding territories to molt in North American landbirds. Our analyses leverage a spatially

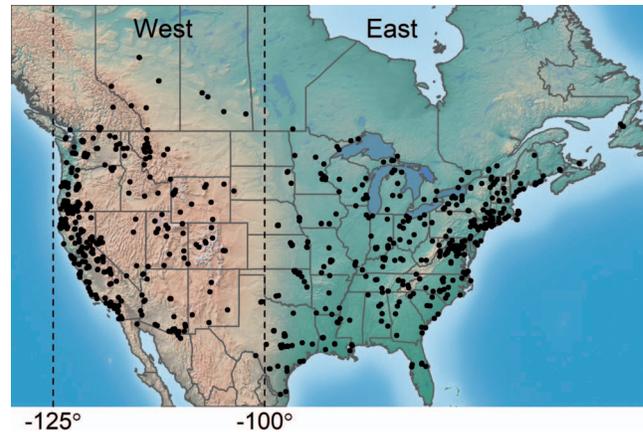


FIGURE 1. Bird-capture stations used in breeding and molting probability analyses. Dots indicate distribution of 936 Monitoring Avian Productivity and Survivorship (MAPS) stations and dashed lines indicate delineation of western and eastern North American regions for analyses.

extensive data set composed of >760,000 capture records of >530,000 adult landbirds at 936 mist-netting stations during the breeding and post-breeding periods, as part of the Monitoring Avian Productivity and Survivorship (MAPS) program (Figure 1; DeSante et al. 2015). We implemented multi-species hierarchical models to assess the probability of recapturing a molting individual at the same station at which it was captured as a breeding individual and, in turn, the probability of recapturing a breeding individual at the same station at which it was captured as a molting individual. Given broad-scale physiographic differences that appear to affect molt strategies (Voelker and Rohwer 1998, Rohwer et al. 2005), we conducted separate analyses for western and eastern North America (Figure 1). We examined molt probabilities in 140 species, 91 species in western North America and 80 species in eastern North America (Supplemental Material Table S1), 31 of which were of transcontinental species analyzed for both regions. We also assessed latitudinal, longitudinal, elevational, and stochastic shifts from breeding to molting grounds by examining spatial variation in the probabilities of capturing breeding and molting birds at each MAPS station.

METHODS

Bird Capture Data

Landbird capture data were collected as part of the Monitoring Avian Productivity and Survivorship (MAPS) program, a cooperative effort among public agencies, private organizations, and bird banders to provide long-term data on demographic parameters for landbird species of North America (Saracco et al. 2008, DeSante et al. 2015,

2017). We included data obtained during the 1992–2008 MAPS seasons, representing years in which all MAPS data had been thoroughly verified by a series of computer programs (DeSante et al. 2017). Data were collected at 936 discrete, long-term MAPS stations (Figure 1) in which 6–20 (usually ~10) twelve-meter mist nets were operated in similar habitats within an approximate 20 ha area. Stations were operated in a standardized manner, 6–12 times per year, for 6 hr beginning at local sunrise, with start dates between May 1 and June 10 and end dates between July 28 and August 28. Stations were operated for up to 17 consecutive years. Captured landbirds were marked with uniquely numbered leg bands and complete data were recorded on all recaptures of an individual.

For each capture, data obtained included station, date, band number, species, age, reproductive characteristics (cloacal protuberance and brood patch), and molt status of flight feathers (DeSante et al. 2017). Birds were aged as hatching-year or after-hatching-year (“adults”) based on the criteria of Pyle (1997); only adults were considered in our analyses. A cloacal protuberance indicated a male in breeding condition (Wolfson 1952, Pyle 1997) and was scored as none, small, medium, or large. A brood patch indicated a female (or, for some species, a male) in breeding condition (Jones 1971, Pyle 1997) and was scored as none, smooth, vascularized, heavy, wrinkled, or molting (DeSante et al. 2017). Symmetrical molt of flight feathers (primaries, secondaries, and/or rectrices) was recorded as present or absent (DeSante et al. 2017). In adult landbirds, symmetrical molt as opposed to adventitious loss of flight feathers (which was also recorded) is an indication of the complete prebasic molt, which takes place largely in July and August for most species (Figure 2; Pyle 1997).

Each marked landbird was scored as a breeding individual at a station if, at any time during its capture history, it was recorded with a medium or large cloacal protuberance or a vascularized or heavy brood patch. Additionally, to further exclude the chance of capturing transients or post-breeding migrants, we restricted certain analyses to individuals that had been captured at least twice spanning a period >10 days, a condition which excludes most or all migrants and transients (cf. Lain et al. 2017, Moore et al. 2017). The extensive MAPS database allowed us to use these conservative criteria to define breeding birds while still maintaining adequate sample sizes for analyses. An individual was scored as molting if, at any time during its capture history, it was recorded at the station undergoing symmetrical flight-feather molt. Once an adult landbird initiates symmetrical flight-feather molt, it typically does not move or migrate away from the area (molting grounds) until molt is complete, because flight is compromised by molting wing feathers (Murphy 1996, Rohwer et al. 2005).

Statistical Analyses

All models were implemented using Bayesian methods in JAGS (Plummer 2003) from the R statistical software (R Core Team 2015) using the R package jagsUI (Kellner 2015), and by obtaining posterior distributions using Markov chain Monte Carlo (MCMC) methods (Gilks et al. 1996). Additional model details and code are provided in [Supplemental Material Appendices A–C](#).

Probability that breeding birds were also captured molting. We estimated the probability that a breeding bird at a station was also captured molting at the station using samples of 243,264 records of 73,528 breeding adult landbirds captured at least once in breeding condition and at least twice spanning ≥ 10 days ([Supplemental Material Table S1](#)). We split data into 2 geographic regions with distinct groupings of MAPS stations (Figure 1) and contrasting physiographic, climatic, and ecological conditions reported to affect molt-location strategies for many species (Voelker and Rohwer 1998, Rohwer et al. 2005, 2011): (1) western North America (West; -125°W to -100°W) and (2) eastern North America (East; greater than -100°W). We excluded data from 50 stations located less than -125°W (primarily in Alaska) due to low sample sizes and differing seasonal dynamics. For one species, Painted Bunting (*Passerina ciris*), we assigned all individuals captured west of -90°W (rather than west of -100°W) to the western region to maintain continuity of breeding populations for this species (Thompson 1991a). This affected 3,110 captures of this species at 69 stations. We limited the dataset to individuals determined to be breeding according to the above criteria and we included for analysis only species with ≥ 20 adult individuals captured at ≥ 5 stations within a region. Our analysis for the West region included 148,599 captures of 43,159 breeding individuals of 91 species, at 460 stations, of which 6,675 individuals were also encountered molting. For the East region, our analysis included 94,665 captures of 30,369 individuals, of 80 species, at 496 stations, of which 3,522 were also encountered molting ([Supplemental Material Table S1](#)).

For each region, we used a hierarchical generalized linear mixed model to assess variation in probability of capturing a bird that bred at a station on another occasion in molting condition. Our analysis assumed that molting probability increased as a species-specific, logit-linear function of day of year, to account for the phenological transition from breeding to molt, and to allow prediction of molt probabilities for a date of August 1, by which date we expect most breeding to have been completed and most birds to have begun their prebasic molt (Figure 2). For $i = 1, \dots, N$ individuals, j in $1, \dots, S$ species, and k in $1, \dots, M$ sites, we defined the model as

$$\text{logit}(p_{i,j,k}) = \alpha_{0j} + \alpha_{1j} * \text{doy}_i + \beta * \text{lat}_k + \gamma * \text{ncap}_i,$$

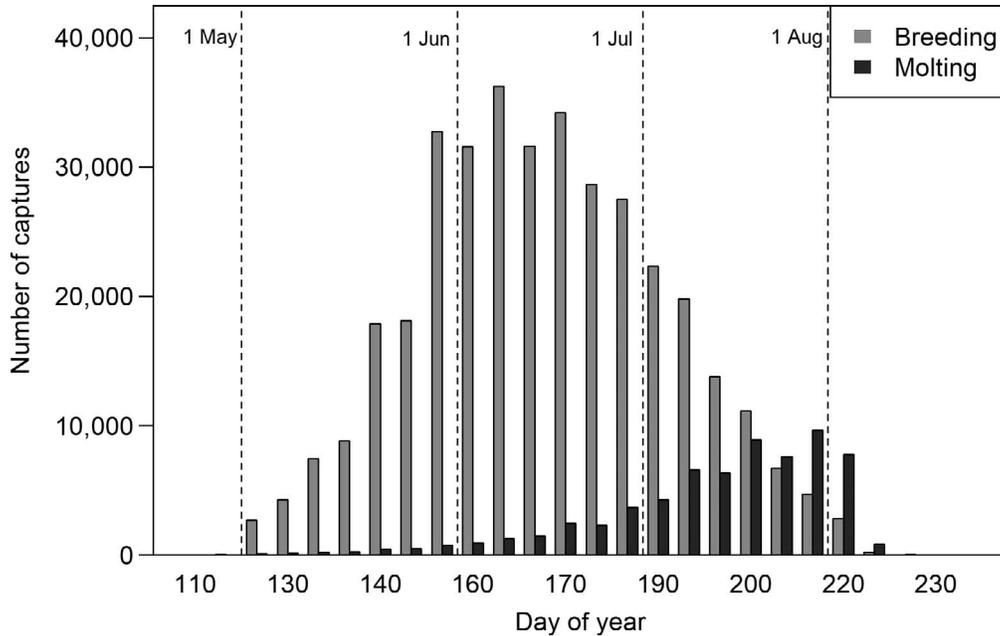


FIGURE 2. Captures of breeding and molting birds in relation to day of year. Birds in breeding condition peaked in June–July, while birds in molting condition were largely captured in July and August; no substantial differences in these patterns were noted between West and East regions.

whereby α_{0j} are random species intercepts, α_{1j} are species-specific effects of the maximum day of year of capture for individual i (doy), β are latitude effects for station k (lat_k), and γ is the effect of number of total captures of individual i ($ncap_i$). We considered the back-transformed (i.e. inverse logit) random species intercepts α_{0j} + the species-specific day-of-year effects at a maximum capture date of August 1, which represents the probability of capturing a breeding bird ($ncap_i$) at another time in molting condition, after controlling for the effects of a latitudinal gradient in molt (lat_k) to account for possible effects of earlier molting in more southern populations. We modeled species-level effects α_{0j} , α_{1j} as normally distributed with means μ_{a0} and μ_{a1} and variances σ_{a0} and σ_{a1} , respectively. We present post-stratified summaries of posterior distributions of our molt probabilities for species categorized in the literature (Pyle 1997, Rohwer et al. 2005) as either nonmigratory (Resident), migrants that are thought to molt on breeding grounds (Breed), or migrants thought to molt away from the breeding grounds (Nonbreed): we categorized 15 species as Resident, 51 species as Breed, and 25 species as Nonbreed in the West; and 12 species as Resident, 56 species as Breed, and 12 species as Nonbreed in the East (Supplemental Material Table S1). One of our subject species, Warbling Vireo (*Vireo gilvus*), was categorized as Nonbreed in the West region and Breed in the East region according to documented geographic variation in molt strategies (Voelker and Rohwer 1998).

Probability that molting birds were also captured breeding. To complement the molting probability analysis and to ensure inclusion of all molting birds in our analyses, we ran a second hierarchical multi-species model to assess the probability that a bird captured in molting condition was captured on another date at the same station in breeding condition. Due to lower sample sizes we defined breeding birds simply as those captured in breeding condition on at least one occasion, the same as for molting birds. Similar to our initial analysis, we included species with ≥ 20 molting individuals from ≥ 5 stations in a logit-linear model with a random species intercept. For the West region, our analysis included data from 35,325 molting individuals of 84 species from 432 stations; 11,519 of these individuals were encountered on another occasion at the same station in breeding condition. For the East region, our analysis included data from 21,646 molting individuals of 78 species from 473 stations, of which 6,835 individuals were encountered on another occasion in breeding condition. Due to lower sample sizes of molting birds and because sampling spanned the entire breeding season (Figure 2), we did not include day-of-year, latitude, or capture covariates in this analysis. As above, we categorized species into 3 groups according to reported molt-location strategies: Resident, Breed, and Nonbreed.

Spatial movement patterns between breeding and molting sites. We examined spatial patterns in molt compared to breeding for species with ≥ 500 captured

individuals of which ≥ 30 each of breeding and molting individuals were captured, at ≥ 25 stations each within a region. This included 62 species in the West and 54 species in the East. We first implemented weighted regressions with responses for latitude, longitude (decimal degrees), and elevation of a station modeled as a function of an indicator variable denoting whether one or more individuals was caught at that station either in molting or breeding condition. We weighted responses based on station capture rates (birds per net-hour) to account for uneven sampling among stations. Because stations were not sited randomly throughout the species' summer ranges (Figure 1), inferences may not necessarily be representative for a species as a whole. Nevertheless, because the same sites were sampled during both breeding and molting seasons, we inferred that variation in the distribution of breeding and molting sites likely reflect real differences for the species-region combinations considered.

For migratory species showing significant spatial (latitude/longitude) or elevational differences between breeding and molting captures we implemented spatial conditional autoregressive (CAR) models with responses representing (1) probability of an individual being captured in breeding condition, and (2) probability of capturing a bird in molting condition with a predicted maximum capture date of August 1 (Figure 2). Our goal was to highlight potential molt-migration patterns for individual species in each region. Based on a dataset consisting of all adult individuals of a particular species captured, we considered logit-linear models of 2 response variables: (1) probability of capturing a bird in breeding condition, and (2) probability of capturing a bird in molting condition. For each region we aggregated station-scale data for $j = 1, \dots, M$ grid cells of 1° resolution, and defined models of breeding probability of the form

$$\text{logit}(p_j) = p_0 + v_j,$$

where p_{ij} is the probability for an individual in grid cell j being captured at least once in breeding condition; p_0 is the mean breeding probability; and v_j indicate zero-mean random effects assumed to be spatially autocorrelated according to a CAR model. Here we consider the intrinsic version of the CAR model (Besag et al. 1991) for v_j :

$$v_j | v_{-j} = \text{Norm} \left(\frac{1}{n_j} \sum_{k \in N_j} v_k, \frac{\sigma^2}{n_j} \right),$$

where N_j denotes the neighborhood of spatial location j , which is the collection of identities of neighboring locations, and n_j is the number of neighbors of location j (i.e. $n_j = \dim [N_j]$). We defined N_j as a "queen's" neighborhood (sharing a corner or side with the central cell, N_j), such that each 1° cell had a maximum of 8 neighbors. For the molting probability response, we also

included a covariate representing the maximum day of year of capture for the individual. We also included latitude and capture-frequency covariates to predict molt probability for a capture date of August 1, corresponding to a time when most breeding has completed and molt has been initiated for many individuals (Figures 2 and 3).

RESULTS

Probabilities that Breeding Birds Molt on Breeding Territories, and Vice Versa

Overall, the probability of capturing an individual adult breeding bird on another occasion in molting condition increased sharply during July and August (reflecting the timing of molt), was higher at more southerly sites, and increased, expectedly, as a function of number of captures (Figure 3). The higher probability of molt on the breeding grounds at more southern latitudes could reflect earlier completion of breeding and initiation of molt to the south (increasing the capture probability of molting birds) or that molt migration is more prevalent in northern than in southern populations within the range of a species. Statistically accounting for these factors (Figure 3), bird species of both western and eastern North America showed a wide range of probabilities (Figure 4A). Although molt migrations are reported to be more prevalent in western than in eastern North America, we found that molt probabilities were similar in the West and East, when all target species were combined (Figure 4). Furthermore, among 31 species with adequate samples from both regions, 9 showed significantly higher molt probabilities (non-overlapping 95% credible intervals) in the West while only 3 showed higher molt probabilities in the East (Figure 5). In other words, more species showed higher probabilities for molt migration or dispersal within eastern populations than within western populations, although this effect was not notable when data from all species were combined. Species showing significantly higher molt probabilities in the West than in the East included House Wren (*Troglodytes aedon*), Hermit Thrush (*Catharus guttatus*), Gray Catbird (*Dumetella carolinensis*), American Goldfinch (*Spinus tristis*), Chipping Sparrow (*Spizella passerina*), and Song Sparrow (*Melospiza melodia*), whereas Warbling Vireo, Yellow Warbler (*Setophaga petechia*), and Yellow-breasted Chat (*Icteria virens*) showed significantly higher molt probabilities in the East than the West (Figure 5). In both regions, molt probabilities among species largely reflected molt locations reported in the literature (Figure 4B). However, in both regions, there were notable exceptions as well as a wide range of variation, especially among migratory species thought to molt on breeding grounds.

To further assess molt dispersal in these species and to incorporate all molting birds in results, we performed a

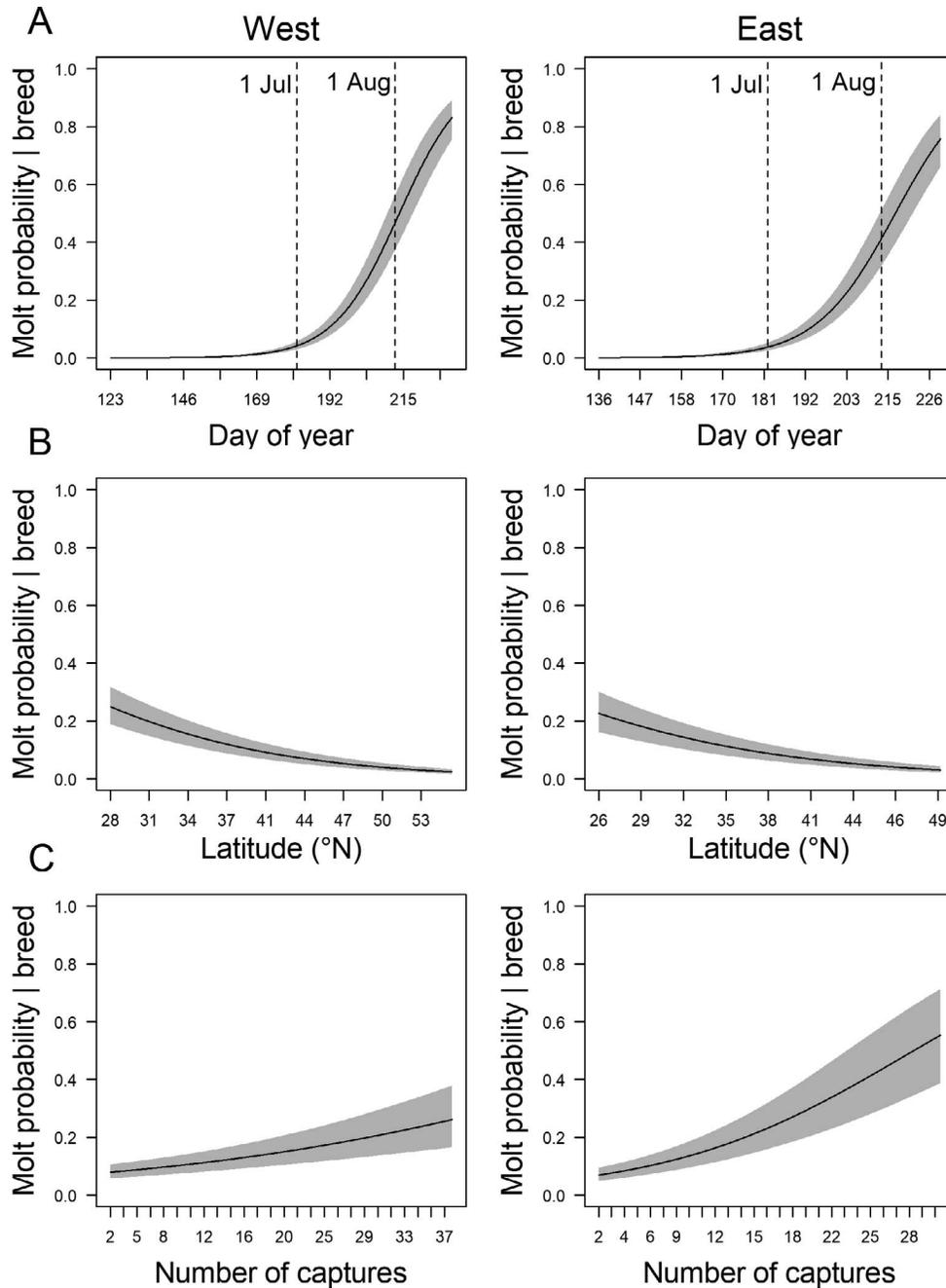


FIGURE 3. Covariate relationships for molt probability analyses. Predicted molt probabilities $\pm 95\%$ credible intervals (shaded regions), in relation to covariates for birds captured in breeding condition and at another time ≥ 10 days from initial capture, shown across the range of observed covariate values; all other covariates were held at mean values. Molt probability increased sharply during July and August (A); was higher at more southerly sites (B); and increased as a function of number of captures (C). Sample sizes are presented in [Supplemental Material Table S1](#).

complementary analysis to that shown in Figure 4, estimating the probability of capturing a molting individual at the same station on another occasion in breeding condition (Figure 6). As with the probability that a breeding bird would also be recorded molting at the same station (Figure 4), bird species of both regions showed a

wide range of probabilities that a molting bird would be recorded breeding at the same station, and breeding probabilities did not differ between the West and East regions when data from all species were combined (Figure 6A). Breeding probabilities in both regions also largely reflected migratory status and molt locations reported in

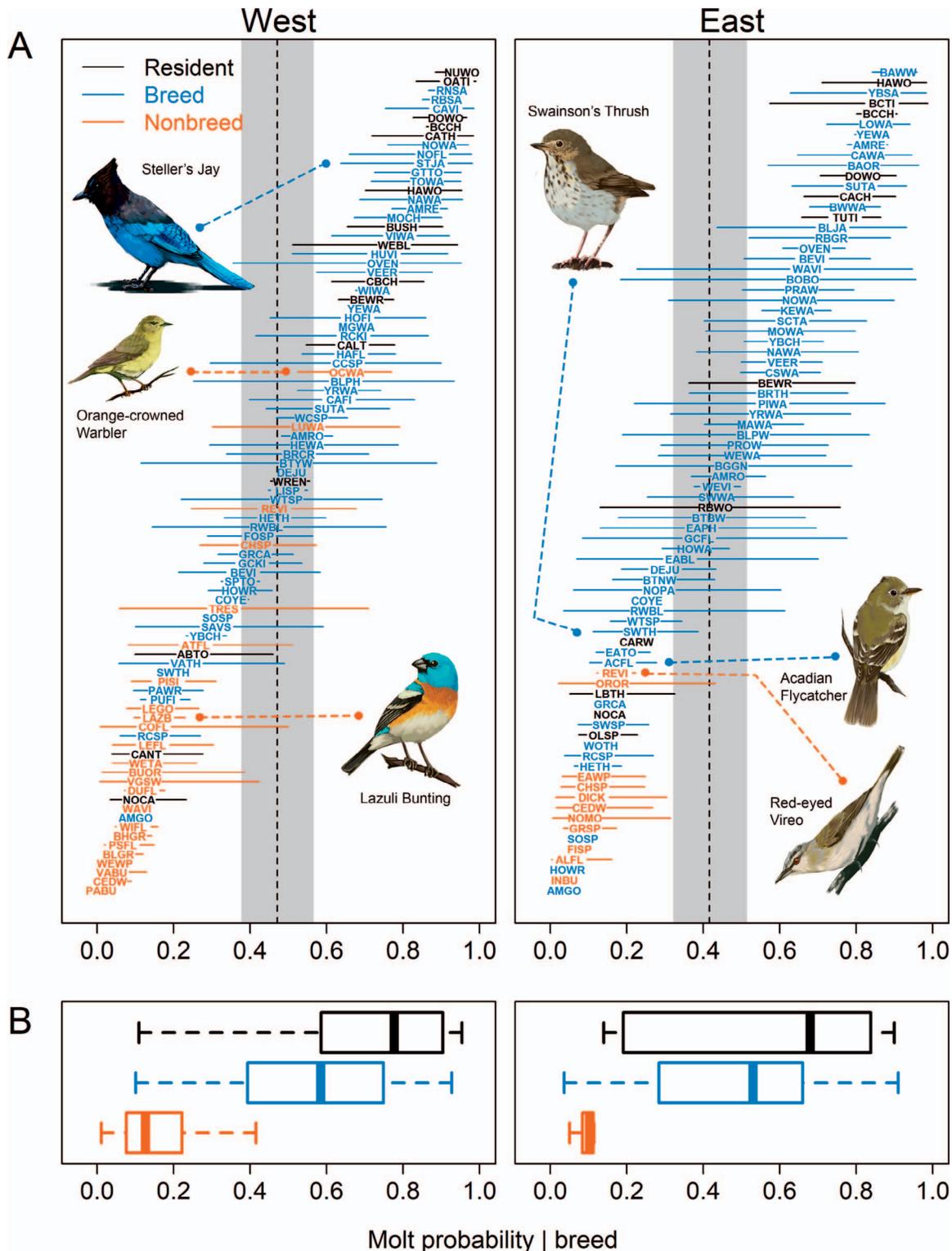


FIGURE 4. (A) Predicted probabilities that landbirds captured at their breeding sites would also be captured molting. Dashed lines show mean species predicted molt probabilities; shaded regions span $\pm 95\%$ credible intervals. The mean probability that a bird captured at its breeding site would be molting was similar in the West (0.47; 95% cred. int.: 0.38–0.57) and East (0.42; 95% cred. int.: 0.32–0.52). See [Supplemental Material Table S1](#) for sample sizes and 4-letter species alpha codes; 6 species showing evidence for directional or elevational movements to molt are illustrated. (B) Boxplots summarize distributions of predicted molt-probability means for species categorized according to the literature as nonmigratory (Resident; shown in black), migratory and reported to molt on the breeding grounds (Breed; shown in blue), or migratory and reported to molt away from the breeding grounds (Nonbreed; shown in orange).

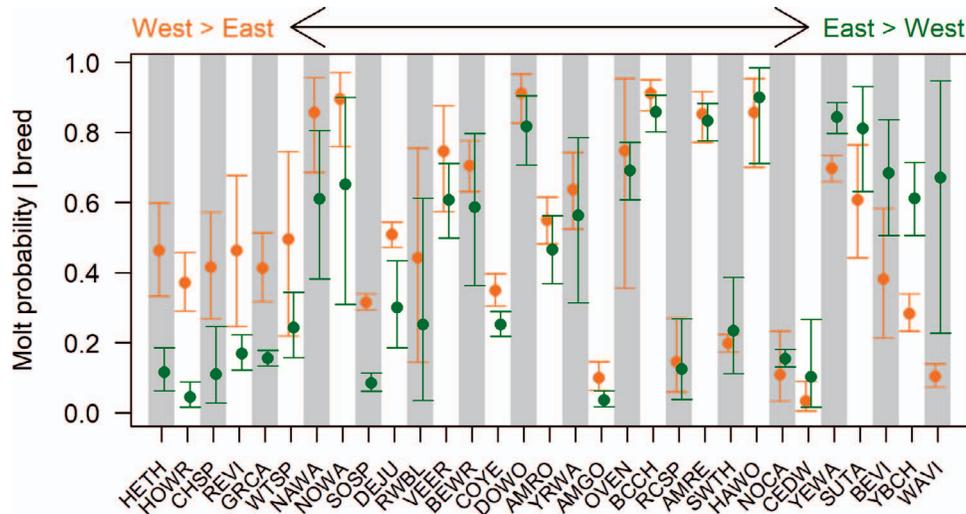


FIGURE 5. Variation in molt probabilities (see Figure 4), of transcontinental species, between western and eastern North America for species with adequate samples (≥ 20 breeding individuals captured at ≥ 5 stations per region: orange = West and green = East). Species are ordered based on the difference in posterior means between the West and the East. Sample sizes are given and 4-letter alpha codes are defined for each species in Supplemental Material Table S1.

the literature (Figure 6B), although more evidently in the West than in the East. We attribute the lower probabilities of capturing a molting bird breeding (Figure 6) than the opposite (Figure 4) as being related to our defining breeding but not molting criteria to include at least one recapture, increasing the molt probabilities in the latter analysis. A comparison of these complementary molt and breeding probabilities among species (Figure 7) indicated mutual support for molt movements in many species, while in some species the probabilities from the 2 analyses conflicted (see below). Overall, however, both molt and breeding probabilities were higher for residents and lower for species reported to breed away from molting grounds, supporting their validity in most cases.

Well-studied species, many with very robust sample sizes (Supplemental Material Table S1), thought to molt on breeding territories but showing evidence of molt migrations or dispersal (Figures 4, 6, and 7) included House Wren and American Goldfinch in both regions; Pacific Wren (*Troglodytes pacificus*) and Purple Finch (*Haemorrhous purpureus*) in the West; and Acadian Flycatcher (*Empidonax virescens*), Swainson’s Thrush (*Catharus ustulatus*), Gray Catbird, and Swamp Sparrow (*Melospiza georgiana*) in the East. Higher molt and breeding probabilities, suggesting that many individuals do molt on breeding territories, were indicated for other migratory species, including Veery (*Catharus fuscescens*), Yellow Warbler, and Summer Tanager (*Piranga rubra*) in both regions; Green-tailed Towhee (*Pipilo chlorurus*), MacGillivray’s Warbler (*Geothlypis tolmiei*), and Wilson’s Warbler (*Cardellina pusilla*) in the West; and Blue-winged Warbler (*Vermivora cyanoptera*), Swainson’s Warbler (*Limnethlypis*

swainsonii), and Kentucky Warbler (*Geothlypis formosa*) in the East (Figures 4, 6, and 7). Common resident species showing evidence for molt dispersal from breeding grounds included Northern Cardinal (*Cardinalis cardinalis*) in both regions (although sample sizes were low in the West; Supplemental Material Table S1) and Carolina Wren (*Thryothorus ludovicianus*) in the East.

Species with conflicting molt and breeding probabilities can be divided into 2 groups, those with higher relative probabilities that breeding birds were also recorded molting than the reverse (upper left quadrats in Figure 7) and those with higher relative probabilities that molting birds were also recorded breeding than the reverse (lower right quadrats in Figure 7). Species in the first group included Northern Flicker (*Colaptes auratus*), Cassin’s Vireo (*Vireo cassinii*), Bushtit (*Psaltriparus minimus*), Nashville Warbler (*Oreothlypis ruficapilla*), and Townsend’s Warbler (*Setophaga townsendi*) in the West, and Downy Woodpecker (*Picoides pubescens*), Hairy Woodpecker (*Picoides villosus*), Carolina Chickadee (*Poecile carolinensis*), Black-crested Titmouse (*Baeolophus atricristatus*), and Baltimore Oriole (*Icterus galbula*) in the East (Figure 7). Those in the second group include Swainson’s Thrush, Common Yellowthroat (*Geothlypis trichas*), Yellow-breasted Chat, Spotted Towhee (*Pipilo maculatus*), and Song Sparrow in the West, and Hermit Thrush, Wood Thrush (*Hylocichla mustelina*), Olive Sparrow (*Arremonops rufivirgatus*), Field Sparrow (*Spizella pusilla*), and Song Sparrow in the East (Figure 7). Notably, sample sizes for molting birds were higher than those of breeding birds for all 10 of the species/regions of the first group (Supplemental Material Table S1; mean 661% higher, range 78–1,481%), whereas sample sizes for breeding birds were higher than those of

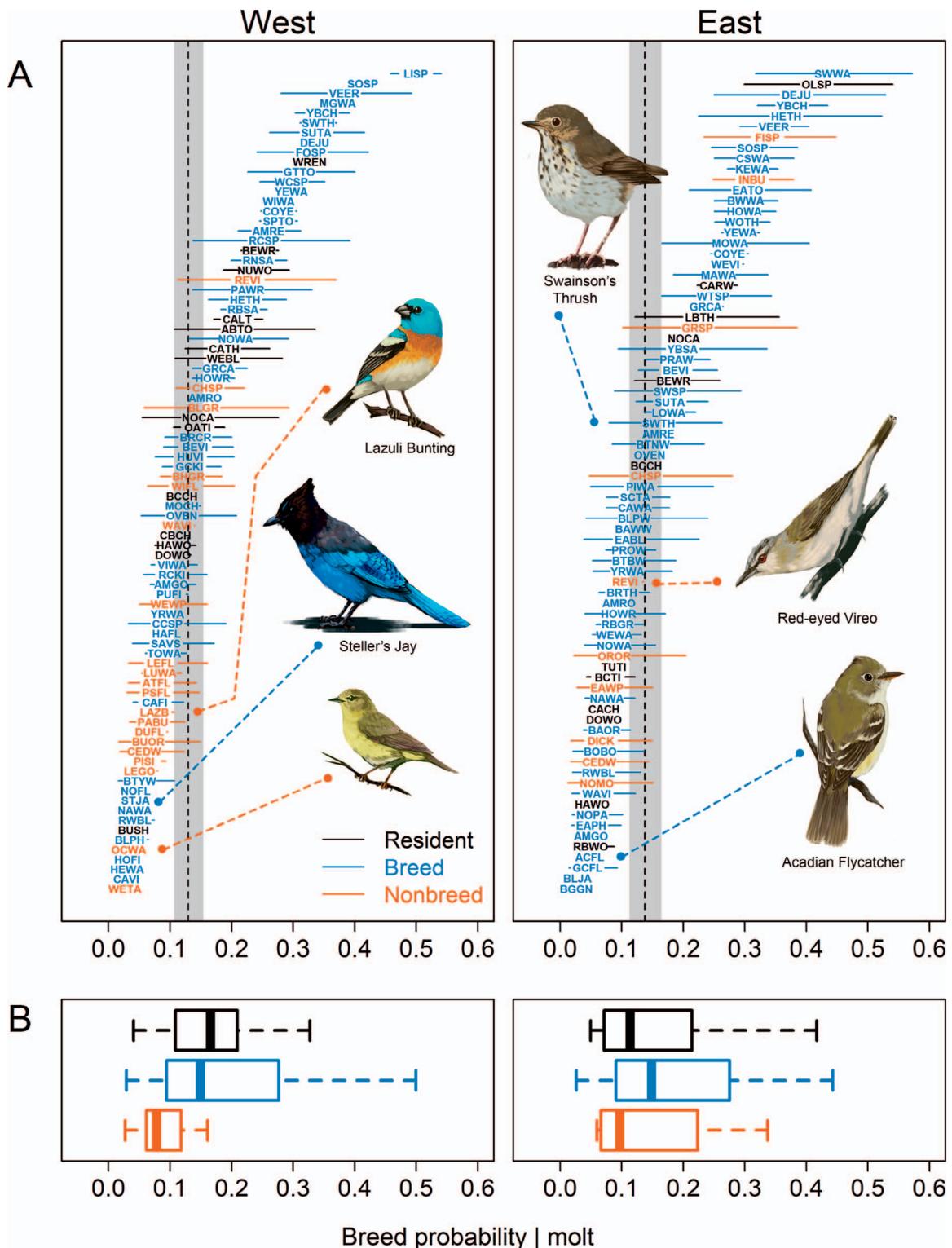


FIGURE 6. (A) Probabilities that molting landbirds were captured at the same location on another occasion in breeding condition, (B) boxplots of posterior breed-probability means are shown for species as categorized in the literature as nonmigratory (Resident; shown in black), migratory and reported to molt on the breeding grounds (Breed; shown in blue), or migratory and reported to molt away from the breeding grounds (Nonbreed; shown in orange). See caption to Figure 4 for additional details. The mean probability of capturing a bird at its molting site on another occasion in breeding condition was similar in the West (0.13; 95% cred. int.: 0.11–0.15) and East (0.14; 95% cred. int.: 0.11–0.16).

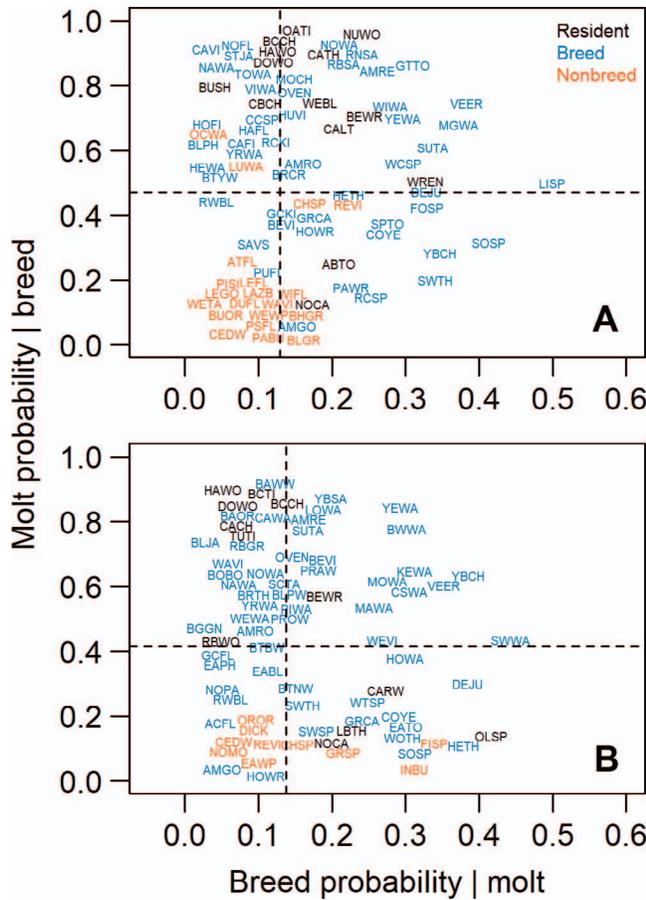


FIGURE 7. Contrasting molt (see Figure 4) and breeding (see Figure 6) probabilities in (A) western and (B) eastern North America. The x axis represents the probability that a bird captured at its breeding site would also be captured molting, whereas the y axis represents the probability that a bird captured molting would also have been captured at that site in breeding condition. Species located in the lower left quadrat show greater evidence of molt-migration according to both analyses; those in upper right quadrat show greater evidence of molt on breeding territories. Species in the upper left and lower right quadrats show contrasting probabilities (see text for discussion of these species). Sample sizes are given and 4-letter alpha codes are defined for each species in Supplemental Material Table S1. Species are categorized according to the literature as nonmigratory (Resident; shown in black), migratory and reported to molt on the breeding grounds (Breed; shown in blue), or migratory and reported to molt away from the breeding grounds (Nonbreed; shown in orange). Species labels with very similar positions in the plot were shifted slightly to avoid overlap and facilitate interpretation.

molting birds for all 10 of the species/regions of the second group (mean 338% higher, range 55–928%).

Spatial Differences between Breeding and Molting Sites

To assess differences between breeding territories and molting grounds, we (1) examined spatial (latitude and

longitude) and elevational differences between stations where birds were captured in breeding and molting condition, and (2) implemented 1° resolution, spatial-conditional autoregressive models with responses representing probabilities of capturing breeding individuals in May–August and molting individuals on August 1. In western North America, several species showed contrasting spatial molt and breeding probabilities consistent with previously documented southward molt migrations to the northwestern Mexican monsoon region; e.g., for Lazuli Bunting (*Passerina amoena*) (Figure 8A), as well as Ashthroated Flycatcher (*Myiarchus cinerascens*), Warbling Vireo, Lesser Goldfinch (*Spinus psaltria*), Chipping Sparrow, Western Tanager (*Piranga ludoviciana*), Black-headed Grosbeak (*Pheucticus melanocephalus*), and Bullock’s Oriole (*Icterus bullockii*) (Supplemental Material Figure S1). Most of these species also molt in Mexico, south of our study area. Painted Buntings (*Passerina ciris*) also showed similar patterns although low sample size of molting birds (likely due to most birds’ molting in Mexico) prevented our undertaking the spatial autocorrelation analysis. Species showing evidence of upslope dispersal to molt in western North America included Orange-crowned Warbler (*Oreothlypis celata*) (Figure 8B), along with Lesser Goldfinch and Nashville Warbler (Supplemental Material Figure S1). Some high-elevation and other breeding species also showed evidence for downslope movements to molt in western North America; e.g., American Goldfinch (Figure 8C) along with Warbling Vireo, Steller’s Jay (*Cyanocitta stelleri*), Mountain Chickadee (*Poecile gambeli*), and Western Tanager (Supplemental Material Figure S1). Southward and/or eastward differences between breeding and molting grounds were detected for most migrants to the Mexican monsoonal region, as expected; a northward shift in molting grounds was detected for Steller’s Jay and Purple Finch; eastward shifts in molting grounds were detected for Black Phoebe (*Sayornis nigricans*) and Nashville Warbler; and westward shifts in molting grounds were detected for Orange-crowned Warbler, Purple Finch, and American Goldfinch (Figure 8 and Supplemental Material Figure S1).

In eastern North America, individuals of several species showed westward as well as southward differences between breeding and molting grounds. For example, Swainson’s Thrushes that breed in montane and subalpine regions of New England and Canada appeared not to molt in these regions, whereas this species was recorded molting outside of the breeding areas in the Mississippi Valley (Figure 8D). Evidence for similar southward and/or westward patterns in molting vs. breeding grounds were noted for Great Crested Flycatcher (*Myiarchus crinitus*); Blue-gray Gnatcatcher (*Polioptila caerulea*); and Worm-eating (*Helmitheros vermivorum*), Black-and-white (*Mnio-*

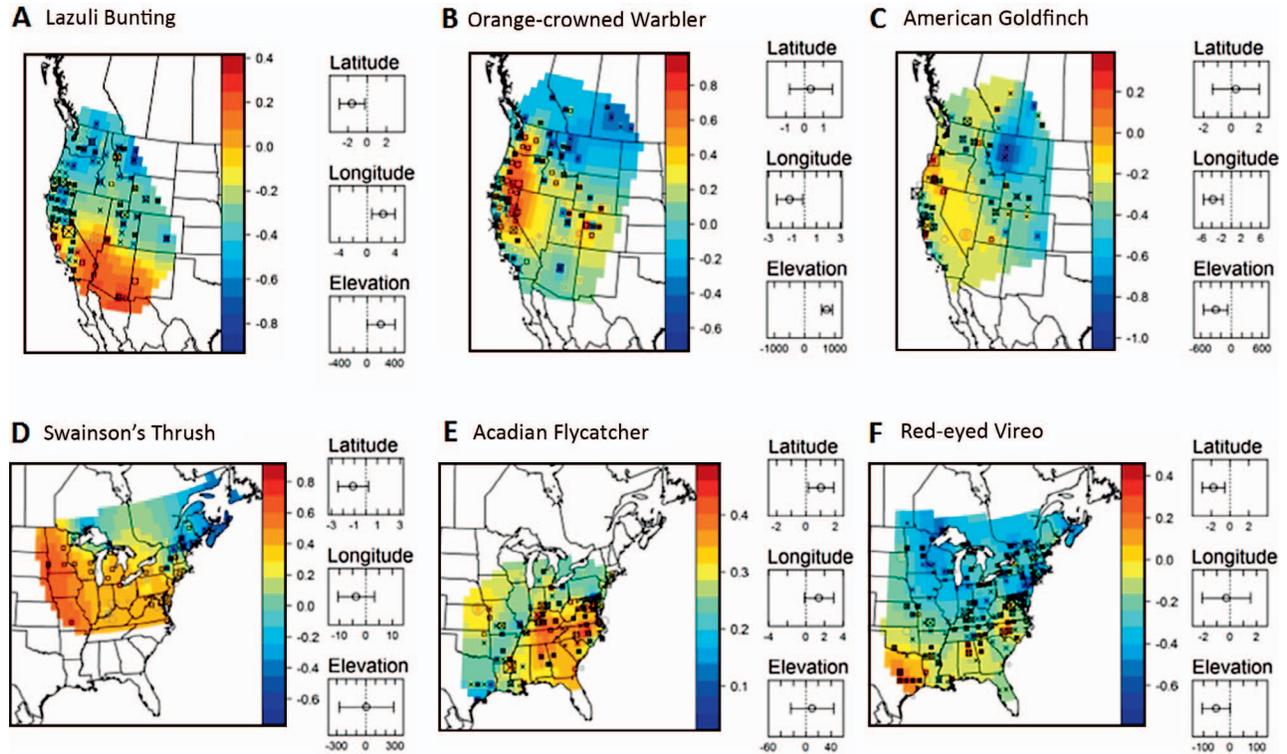


FIGURE 8. Examples of spatial (latitude and longitude) and elevational shifts from breeding to molting locations for selected species. Sample sizes are given for each species in [Supplemental Material Table S1](#). Maps were developed by implementing 1° resolution, spatial-conditional autoregressive models with responses representing differences between probabilities of captured individuals being in breeding condition during May–August and being in molting condition if captured on August 1. Bluer areas represent relatively high breeding probabilities relative to molting probabilities; redder areas represent relatively high molt probabilities relative to breeding probabilities. Breeding locations aggregated within 1° cells are indicated with black “x” symbols; molting locations are indicated with black open squares; symbol sizes are scaled according to numbers of captures in breeding or molting condition, respectively. Locations in which all captures lacked both breeding or molting condition are shown with gray open circles scaled to total numbers of captures. Latitude, longitude, and elevation plots represent differences in each response variable (mean \pm 95% confidence intervals) between stations where birds were captured in molting relative to breeding condition. See also [Supplemental Material Figures S1 and S2](#).

tilta varia), and Nashville warblers ([Supplemental Material Figure S2](#)). We also found evidence for a northeastward shift in molting grounds for Acadian Flycatcher (Figure 8E), a downslope and southward shift to molting grounds for Red-eyed Vireo (*Vireo olivaceus*) (Figure 8F) and Nashville Warbler ([Supplemental Material Figure S2](#)), and a southeastward shift in molting grounds for Chestnut-sided Warbler (*Setophaga pensylvanica*) ([Supplemental Material Figure S2](#)).

In both regions, our probability analyses indicated movements to molt for some species (Figures 4, 6, and 7) that showed little evidence of geospatial differences, suggesting that individuals may disperse to specific molting habitats not discriminated by spatial direction or elevation from breeding territories. Such species included House Wren, Pacific Wren, Swainson's Thrush, Savannah Sparrow, and House Finch (*Haemorhous mexicanus*) in western North America and Eastern Phoebe (*Sayornis*

phoebe), Blue Jay (*Cyanocitta cristata*), Gray Catbird, American Goldfinch, Northern Parula (*Setophaga americana*), Swamp Sparrow, Rose-breasted Grosbeak (*Pheucticus ludovicianus*), and Baltimore Oriole in eastern North America.

DISCUSSION

We demonstrate widespread evidence for movements between breeding territories and molting grounds for a variety of North American landbirds, including many species previously thought to molt on “breeding” or summer grounds (Pyle 1997, Rohwer et al. 2005). Geospatial differences between breeding and molting grounds were detected in all 4 compass directions, including unexpected northward movements in some species, and both upslope and downslope in elevation. We interpret at least some of these differences to directional geospatial

shifts from breeding to molting grounds, although in species with significant portions of breeding or molting ranges outside of the core MAPS-station area, the differences could represent the responses of different subpopulations rather than direct movements, including effects of earlier molting in southern than in northern breeding subpopulations (Figure 3). Some species also showed evidence to move from breeding territories to molting grounds but not consistently by geospatial direction or elevation. Our results largely accord with previous anecdotal inferences on the general molting locations, especially regarding resident species and those reported to molt away from breeding grounds (Pyle 1997, Rohwer et al. 2005), supporting their validity in most cases.

A few species showed conflicting results between our 2 (molt and breeding) probability analyses (Figure 7), but sample sizes for the independent variable in all cases were higher for the resultant lower probability value (whether that breeding birds were also recorded molting or molting birds were also recorded breeding), indicating more robust evidence for molt migration or dispersal in these species. That these sample sizes for breeding vs. molting birds differed for these species is of interest and may indicate different behavioral patterns leading to divergent capture probabilities during the breeding and molting periods for these species. For example, higher captures of molting than breeding woodpeckers, other resident species, Cassin's Vireo, and Baltimore Oriole (upper left quadrats of Figure 7) could indicate that these species are relatively sedentary during breeding but show more movement during the molting period, perhaps including foraging lower to the ground to be captured in mist nets. Species showing higher captures during breeding than molting, including thrushes, Common Yellowthroat, Yellow-breasted Chat, and sparrows (lower right quadrats of Figure 7), may need to forage more during breeding and less during molting periods. Our statistical adjustments for capture probability at least partially account for such differences in our probability calculations. Other reasons for these contrasting molt and breeding probabilities could include heterogeneity of responses among populations, individual variation in molt strategies, or that our probabilities for some species may not be robust due to lower sample sizes.

Our results accord with those documenting molt-migration to the Mexican monsoon region in many species (Figures 4–8 and [Supplemental Material Figure S1](#); Rohwer and Manning 1990, Thompson 1991b, Young 1991, Butler et al. 2002, 2006; Rohwer et al. 2005, Barry et al. 2009, Pyle et al. 2009, Contina et al. 2013, Siegel et al. 2016). In our study, some individuals of these species were also captured molting on breeding territories (Figure 4A and [Supplemental Material Table S1](#)) while others showed differing longitudinal and elevational shifts between breeding and molting locations (Figure 8A and

[Supplemental Material Figure S1](#)), indicating a variety of responses among molt-migrants to the Monsoon region. In general, this indicates that prevalent molt-migration patterns should not be assumed to occur uniformly in all species or for all individuals within a species. Rather, these patterns may involve variable and heterogeneous movement responses, suggesting annual decisions at both the species and the individual levels based on immediate food-resource conditions or success during the previous breeding season (Pyle et al. 2009, Gow and Stutchbury 2013), despite the fact that a large proportion of birds do follow an overall monsoonal molt-migration strategy. We suggest that yearling (one-year-old, or second-calendar-year) birds, failed breeders, or those that breed on lower-quality territories may migrate or disperse to the monsoon region or elsewhere to molt, whereas successful breeders or those with high-resource breeding territories may remain on the breeding grounds to molt, at least during years of favorable food availability (Pyle et al. 2009). Our data suggest that movements to molt may also occur in resident species, including Northern Cardinal and Carolina Wren (Figure 7), although we infer that such movements are likely much shorter in distance than those undertaken by migratory species.

Our results also accord with the conclusions of other previous studies, for example, that eastern Swainson's Thrushes can show molt-migration into the Mississippi Valley (Figure 8D; Cherry 1985, Winker et al. 1992), that American Redstarts (*Setophaga ruticilla*) appear to molt primarily near (Reudink et al. 2008) rather than away from (Norris et al. 2004) breeding territories (Figure 7), and that Lucy's Warblers (*Oreothlypis luciae*), which showed intermediate probabilities in both of our analyses, could exhibit a mixture of molt-migration strategies in the West (Figure 7; Voelker and MacFarland 2002, Rohwer et al. 2007, Pyle et al. 2009). Such mixed results in Lucy's Warbler could also relate to an expansion of breeding range due to irrigation in the Mexican monsoonal region (Rohwer et al. 2015). In some cases, molting areas for eastern species may be bounded by the Gulf of Mexico, as has been found in swallows (Yuri and Rohwer 1997, Rohwer et al. 2011) and hummingbirds (Weidensaul et al. 2013). Mixed results between our 2 probability analyses are also consistent with studies suggesting a variety of molt strategies for Wood Thrushes, including molt on or near breeding territories for some individuals and long-distance molt-migration for others (Vega Rivera et al. 1998, Stutchbury et al. 2010, Gow et al. 2012, Gow and Stutchbury 2013). It is possible that molting Wood Thrushes are more sedentary as compared with other species, explaining the much higher captures of breeding (2,012) than molting (386) individuals in our data set ([Supplemental Material Table S1](#)). Eastward upslope migration has also been documented for Orange-crowned

Warbler from California into the Sierra Nevada mountains (Steele and McCormick 1995, Weigardt et al. 2017b); that our data suggest a westward upslope shift (Figure 8A) also indicates that populations of this species may migrate into this mountain range from the Great Basin region as well.

In some cases, our results contrast with those of other studies. For example, high probabilities for both molting on breeding grounds and vice versa in the western Veeries appears to contrast with direct evidence that some individuals of this species migrate up to hundreds of kilometers to stopover locations between breeding and southbound migration, presumably to molt (Hobson and Kardynal 2015). Our results showing downslope movement to molt in Western Tanagers, at least within the MAPS region north of the Mexican border, contrasts with those inferred by Butler et al. (2002) based on specimen data. We also found little evidence for upslope or eastward migration for western populations of Cassin's Vireo, Swainson's Thrush, MacGillivray's Warbler, or Wilson's Warbler, as found in other studies (Rohwer et al. 2008, Weigardt et al. 2017a, 2017b), although we did find weak evidence for upslope migration in western Yellow-rumped Warblers (*Setophaga coronata auduboni*), as also found by Weigardt et al. (2017b). These contrasts in evidence for molt-migration strategies may have resulted from local vs. regional patterns, from differences in the robustness of statistical methods, especially those regarding capture probability, or simply from the variable and heterogeneous molt-movement responses by individuals within species and populations of species, as mentioned above.

Overall probabilities of movements from breeding grounds to molt were similar in both western and eastern North America, despite evidence that molt-migrations occur more frequently in western than eastern populations of some transcontinental species (Rohwer et al. 2005, 2011), including Warbling Vireo (Voelker and Rohwer 1998), as also supported by our results (Figure 5). That Nashville Warblers appeared to move upslope to molt in the West, but downslope to molt in the East, further supports such regional-specific differences in molt-migration strategies within North America. Several species, for example Red-eyed Vireo, House Wren, Hermit Thrush, Gray Catbird, Common Yellowthroat, and Song Sparrow, showed greater probabilities of leaving breeding grounds to molt in the East than in the West, opposite to that of other species (Voelker and Rohwer 1998, Rohwer et al. 2005, 2011). Combining our results with those of these previous studies, it appears that many landbird species in western North America move much longer distances to molt whereas many landbirds in eastern North America may equally or more likely move shorter distances between breeding and molting habitats, while remaining within the overall breeding ranges of the species.

Our results indicate previously unknown migrations or spatial shifts to molt by North American landbirds and invite additional studies on molting location relative to breeding territories, especially for those migrant species reported to molt on breeding grounds but showing evidence herein for molt migration or dispersal. Understanding molting strategies of North American landbirds is critical for the conservation of declining species. Stable-isotopic (Hobson et al. 2014, Perkasky et al. 2015, Nordell et al. 2016), genetic (Reugg et al. 2014), and geolocator (Stutchbury et al. 2009, Contina et al. 2013, McKinnon et al. 2013, Hobson and Kardynal 2015, Siegel et al. 2016) technology, or ideally 2 or more of these tools simultaneously (Rundell et al. 2013, Pillar et al. 2015), can be used not only to study migratory connectivity in birds and better incorporate post-breeding effects in full-annual-cycle models (Barta et al. 2008, Hostetler et al. 2015), but can be used to increase our ability to identify and conserve habitats required by molting landbirds. Researchers using these technologies need to consider potential molt-movement strategies when designing their studies, and to investigate specific habitat requirements needed for molt.

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Data depository: Data used for analyses have been archived as summarized in the [Supplemental Material](#).

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