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Connectivity of Migratory Bird Populations Breeding on Department of Defense Lands

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TABLE OF CONTENTS

Executive Summary 3

Introduction 4

Migration Defined 4

Role of Population Connectivity 4

Migration Strategies 5

Stable Isotopes as Tool for Migration Study 6

Focus and Purpose of this Study 7

Methods 8

Figure 1 – DoD installations where feathers were collected 9

Results and Discussion 11

Figure 2 – Non-breeding area with similar feather stable-hydrogen isotope values 13

Figure 3 – American Redstart migratory connectivity 15

Figure 4 – Black-and-white Warbler migratory connectivity 16

Figure 5 – Northern Parula migratory connectivity 18

Figure 6 – Ovenbird migratory connectivity 19

Recommendations for DoD Installations 20

References 21

EXECUTIVE SUMMARY

Neotropical-Nearctic migratory birds spend the majority of the year in tropics, but management decisions usually occur on breeding grounds. Development of best management practices that consider the complete annual cycle of these species has been limited by our inability to follow individuals year-round and determine the degree of connectivity among winter and breeding populations. Determining movement patterns and population connectivity of individuals between their breeding and wintering grounds is critical for understanding how limiting factors (e.g. habitat destruction, climate change, etc.) operate in different parts of the annual cycle and how this affects population size and local abundance. Department of Defense (DoD) personnel are responsible for managing lands on military installations to protect suitable breeding areas for migratory birds. Because migratory birds spend most of the year on their non-breeding grounds in the tropics, it is equally likely that events in the tropics, off of military bases, are also important drivers of population abundance of these birds. To close this knowledge gap, we used stable-hydrogen isotopes as a marker of geographic origin to link birds breeding on military installations with their winter areas in the tropics for four species: American Redstart (*Setophaga ruticilla*), Ovenbird (*Seiurus aurocapilla*), Northern Parula (*Setophaga americana*), and Black-and-white Warbler (*Mniotilta varia*). We detected strong patterns of connectivity, but found few generalities among species, indicating a need for installation management efforts aimed at particular species. Installations should focus habitat management on those breeding species that are connected to the core of the winter range, where abundances are likely to be high. These results will help DoD personnel develop a model to better manage populations of migratory birds. This research was funded in part by the United States DoD Legacy Resource Management Program.

IINTRODUCTION

MIGRATION DEFINED

Migration is the persistent, directional movement from breeding to non-breeding areas that exceeds the temporal and spatial scale of typical daily activity. In most species, migration is part of an annual cycle of round-trip, seasonal movements that recur throughout life. This form of migration has evolved repeatedly and independently over evolutionary time. Among the chordates, migration has arisen in at least 43% (6/14) of extant Classes and many other times at higher levels of taxonomic organization. Migration is therefore spectacularly varied, involving journeys that cross hemispheres, span multiple generations, traverse thousands of meters of altitude, or bridge terrestrial and aquatic life stages. Despite the diversity of these phenomena, migration remains poorly understood. While researchers have made substantial progress in understanding the redundant navigation mechanisms and environmental cues that facilitate migration, advances in ecological and conservation knowledge have lagged behind owing to the difficulty of tracking individual animals across the entire year.

ROLE OF POPULATION CONNECTIVITY

Understanding how different periods of the annual cycle interact to influence both population dynamics and conservation decisions requires knowing how populations are connected spatially and temporally (Marra et al. 1998; Studds et al. 2008). Thus, the degree to which populations of migratory animals are connected is a fundamental and challenging question facing biologists (Webster et al. 2002). Successfully conserving migratory species also requires knowing how populations are geographically linked to determine the influence that factors such

as climate change and habitat destruction have within distinct stages in the annual cycle. Yet before such advances are possible, it is necessary to first describe patterns of migratory connectivity.

Migratory connectivity can be classified along a weak to strong gradient. Breeding populations that exhibit weak migratory connectivity mix extensively on their non-breeding grounds and therefore show little population structure. Organisms with small breeding ranges and those that exploit ephemeral resources for reproduction are expected to show weak connectivity because the entire population may converge within a narrow geographic area. Examples of animals that display weak connectivity include monarch butterflies that breed throughout North America and winter almost exclusively at two sites in Mexico and wildebeest that congregate in southern Tanzania during the rainy season. Alternatively, breeding populations that exhibit strong migratory connectivity migrate to unique non-breeding areas. Numerous ecological and evolutionary processes may generate strong connectivity. In some whales and birds, genetic similarity among related individuals helps maintain strong connectivity.

MIGRATION STRATEGIES

Biologists recognize two distinct migration strategies that migratory birds employ at the broadest spatial scale: leap-frog and chain migration. Under leapfrog migration, northern wintering populations breed in southern portions of the breeding range, and southern wintering populations breed in the northern portions of the breeding range. This strategy results in differential migration distance between populations, where northern wintering populations migrate a comparatively short distance and southern winter populations migrate to northern

latitudinal extremes. Alternatively, under chain migration, northern wintering populations breed in the northern portion of the breeding range and southern wintering populations breed in the southern portion of the breeding range. Migration distance, therefore, is similar between populations. In both cases, the result may have profound implications for life history strategies, the ecology of migratory species, and successful conservation measures.

STABLE ISOTOPES AS A TOOL FOR MIGRATION STUDY

Stable isotopes are powerful tool for identifying geographic origins of populations (Hobson 1999, Marra et al. 1998, Chamberlain et al. 2000, Rubenstein et al. 2002, Norris et al. 2006). Stable isotopes are naturally occurring elements that vary in their atomic weights, and higher order consumers reflect this variation through assimilation of isotopes into their diets (van der Marwe et al. 1990; Wassenaar and Hobson 1998; Hobson and Wassenaar 1997; Marra et al. 1998). The turnover rate of isotopes in animal tissues (e.g. feathers, toenails, blood, muscle) depends upon their metabolic stability and can, therefore, be used as a marker to reveal the location of where the isotope was incorporated into the organism. In North America, stable-hydrogen isotope ratios in growing season precipitation (δ^2H_P) show a strong north-south gradient and correlate strongly with the δ^2H of locally grown tissues, especially in the eastern region of the continent (Hobson and Wassenaar 1997).

Neotropical-Nearctic migratory songbirds represent an ideal system to estimate migratory connectivity by using stable isotopes. These species spend about three months of the year on their North American breeding grounds, six to eight months on their tropical wintering quarters, and two months on migration. Mark-recapture approaches, including continental-scale banding efforts such as the MAPS program, have yielded extremely low return rates despite years of

effort (Webster et al. 2002). Satellite transmitters are too large for small-bodied passerines to carry during migration, and newer daylight level geolocators have not yet been deployed or recovered at a sufficient rate to estimate connectivity at a broad spatial scale. In addition, genetic markers have also been of limited use because there is little continent-wide structure in the species studied to date (Clegg et al. 2003, Lovette et al. 2004). Chamberlain et al. (1997) and Hobson and Wassenaar (1997) showed that δ^2H values in feathers of Nearctic-Neotropical migrants were highly correlated with δ^2H values in growing season precipitation at locations across North America. Because feathers molted at or near their breeding grounds become metabolically inert after feather growth has ceased, feathers sampled from individual birds on their wintering grounds reflect the isotopic composition of their growth location.

FOCUS AND PURPOSE OF THIS STUDY

In this study, we examined migratory connectivity between temperate breeding and tropical non-breeding areas for four species of Neotropical-Nearctic migratory bird: American Redstart (*Setophaga ruticilla*), Black–and-white Warbler (*Mniotilta varia*), Northern Parula (*Setophaga americana*), and Ovenbird (*Seiurus aurocapilla*). These species are common and widespread on both their breeding grounds in eastern North America and non-breeding areas in the Caribbean Basin and are generally common on Department of Defense (DoD) installations with significant natural resources. These considerations allowed us to collect a large number of samples across an extensive geographical area in eastern United States and the Caribbean Basin and to maximize the ability to detect migratory connectivity between DoD installations and non-breeding populations. We sampled over 1200 tail feathers from 10 countries in the Caribbean Basin and at 18 locations across eastern North America and analyzed their stable-hydrogen

isotope values (δ^2H). We grouped individuals of each species across Caribbean locations with similar δ^2H and then use maximum likelihood assignment tests to assess migratory connectivity among breeding and non-breeding populations. This approach allowed our analyses to reveal how breeding populations of focal species on DoD installations are connected to winter regions in the Caribbean Basin.

METHODS

Feather samples were collected from 1995-2010 during both the tropical non-breeding period in the Caribbean Basin and the temperate breeding season in the eastern United States. Samples from the non-breeding period were taken at 20 sites from 10 countries, encompassing the majority of the known winter range for each of the five focal species. Dominant vegetation varied across sites, but included mangrove forest, thorn-scrub, mixed broadleaf, wet limestone forest, coffee farms that ranged in elevation from 5-200 m. Breeding season sampling took place at 18 sites in eastern North America, including at 8 United States Department of Defense (DoD) installations (Fig. 1). Vegetation types included bottomland hardwoods, coastal plain forest, northern hardwoods, and spruce-fir forest at elevations from 5-1000 m. Birds were captured in mist nets, aged and sexed using criteria from Pyle (1997), banded with a United States Geological Survey (USGS) aluminum leg band, and released. One tail feather was removed from each bird before release and stored in a paper envelope. We performed isotope analyses on 843 feathers from the non-breeding season and 228 feathers from the breeding season.

Isotope analyses were done at the Stable Isotope Mass Spectrometry Facility of the Smithsonian Institution in Suitland, MD. Feathers were washed in a 2:1 chloroform:methanol solution to remove surface oils and air-dried under a fume hood for 48 hours. After transport to

the lab, feathers were allowed to equilibrate with the local atmosphere for 72 hours. A small sample of each feather (0.30–0.35 mg) was packed into a silver capsule, combusted at 1350°C in

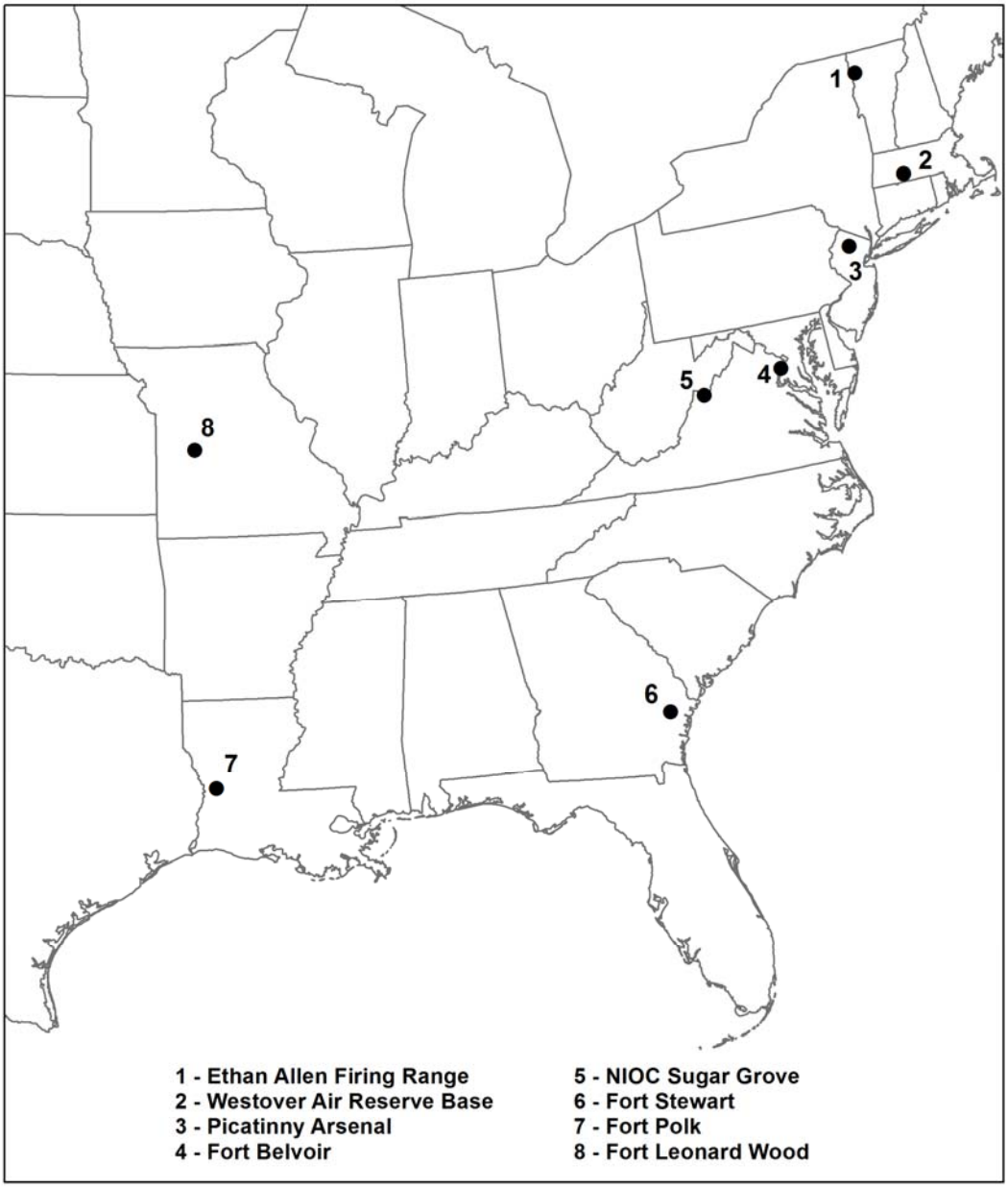


Figure 1. Geographic distribution of United States Department of Defense (DoD) installations where feathers were collected in 2009-2010. Feather samples were used to convert a continental-scale spatial grid of stable-hydrogen isotope values in growing season precipitation (δ^2H_P; Bowen et al. 2005) to one that predicted stable-hydrogen isotope values in feathers of the four focal species. This new grid helped assess the likelihood that feathers sampled on non-breeding sites in the Caribbean were grown on DoD installations.

an elemental analyzer (Thermo TC/EA), and introduced online to an isotope ratio mass spectrometer (Thermo Delta V Advantage) via a Conflo IV interface. Four in-house keratin standards were run for every 10 unknowns to account for exchangeable and nonexchangeable H in feather samples. Nonexchangeable H was determined by linear regression with keratin standards (Wassenaar and Hobson 2003). We report δ^2H_F of nonexchangeable H in per mil units (‰) relative to the Vienna Standard Mean Ocean Water-Standard Light Antarctic Precipitation (VSMOW-SLAP) scale. Duplicate samples run for one in five feathers (n = 228) indicated that analytical error (± 1 SD) was 2 ‰.

We assigned the δ^2H values of feathers collected in the non-breeding season to potential breeding locations to a map of geospatial isotope patterns in North America (Bowen et al. 2005). Metabolic tissues such as feathers preferentially store the lighter fraction of H, causing isotopic values that are more negative relative to isotopic values in growing season precipitation where feathers were grown. To account for this pattern, we constructed a δ^2H_F isoscape by fitting a linear-mixed model with δ^2H_F values of feathers from know locations in North America as a dependent variable and the δ^2H_P value predicted by the Global Network of Isotopes in Precipitation (GNIP) model for each location as an independent variable. We fit models with random intercepts, random slopes, and both random slopes and intercepts for each species then evaluated which calibration equation best the data. Using the Spatial Analyst extension in ArcGIS 10.1 (ESRI, Redlands, CA, USA), we applied this equation to the δ^2H_P surface, yielding a new surface of expected δ^2H_F for each species.

Prior to assigning winter-collected feathers to putative origins in North America, we first determined the locations in the non-breeding range that could be grouped for each species. This approach allowed us to more robustly determine the non-breeding areas that supported breeding

populations breeding on DoD installations. We fit a hierarchical Bayesian model where parameters for each non-breeding site were drawn from a normal distribution with a mean corresponding to the mean δ^2H_F of each non-breeding site and a standard deviation lambda. Hyperparamters for lambda were modeled as a gamma distribution with shape and rate parameters for each non-breeding site. We computed the median and associated 85% credible intervals from posterior distributions for each nonbreeding site and used this information to define a set of non-breeding sites where each species overlapped in their δ^2H_F.

We used a model developed by Royle and Rubenstein (2004) to assign 843 feathers from the non-breeding season to their breeding origin where the likelihood that each δ^2H_F value, $y*$, originated from a given breeding location is

$$f(y^* \mid \mu_b, \sigma_b) = \frac{1}{\sqrt{2\pi\sigma_b}} \exp\left[-\frac{1}{2\sigma_b^2} (y^* - \mu_b)^2 \right]$$

and μ_b and σ_b are the mean and standard deviation of expected δ^2H_F values in each location. The model thus explicitly incorporates information about isotopic variation across the landscape to predict a probability of origin for each δ^2H_F measurement.

RESULTS and DISCUSSION

Few studies have examined migratory connectivity across the annual cycle of migratory birds. Using a combination of stable isotopes and neutral genetic markers, Kelly et al. (2005) found that Swainson's Thrush (*Catharus ustulatus*) connectivity was consistent with leapfrog migration, with birds from northern parts of the winter range migrating relatively short distances to southern breeding sites and birds from the southern sections of the winter range migrating comparatively longer distances to northern breeding sites. In contrast, Norris et al. (2006) found

that American Redstarts underwent chain migration in which individuals from northern winter sites migrated to far northern breeding sites and birds from southern winter sites migrated to southern breeding sites. However, no study has yet investigated migratory connectivity patterns for multiple species that occupy similar breeding and nonbreeding ranges. Our results show that there are few generalities among species, suggesting that annual range geography alone does not determine migratory connectivity. Instead, data on individual species is necessary to successfully document year-round migratory connectivity.

Of the five species considered, American Redstart showed the strongest migratory connectivity across the across their annual range, patterns that were evident as a function of both winter latitude and longitude (Fig. 2A). In general, western non-breeding populations migrated to the northern reaches of the breeding range, while non-breeding populations further to the east migrated to breeding sites further south. Isoptope values of redstart populations overwintering in Mexico were consistent with breeding sites near the border between the United States and Canada to the west of the Continental Divide (Fig. 3A). Non-breeding redstarts in the Bahamas and Florida were assigned to breeding locations in southern part of the breeding range west of the Continental Divide and to the far north of the eastern portion of the breeding range (Fig. 3B). Isotope values of redstarts overwintering in Jamaica, Dominican Republic, and Puerto Rico indicated that these populations bred primarily in the northeastern United States (Fig. 3C). These islands therefore are likely the primary overwintering area of redstarts breeding at Ethan Allen Firing Range (Fig. 3C – 1) and Westover Air Reserve Base (Fig. 3C – 2). Redstart non-breeding populations in St. Martin and Dominica bred in the eastern United States from New York in the north to Georgia in the south (Fig. 3D). These non-breeding locations are thus the most likely

source of redstarts breeding at Fort Belvoir (Fig. 3D – 4), NIOC Sugar Grove (Fig. 3D – 5), and Fort Leonard Wood (Fig.3D – 8).

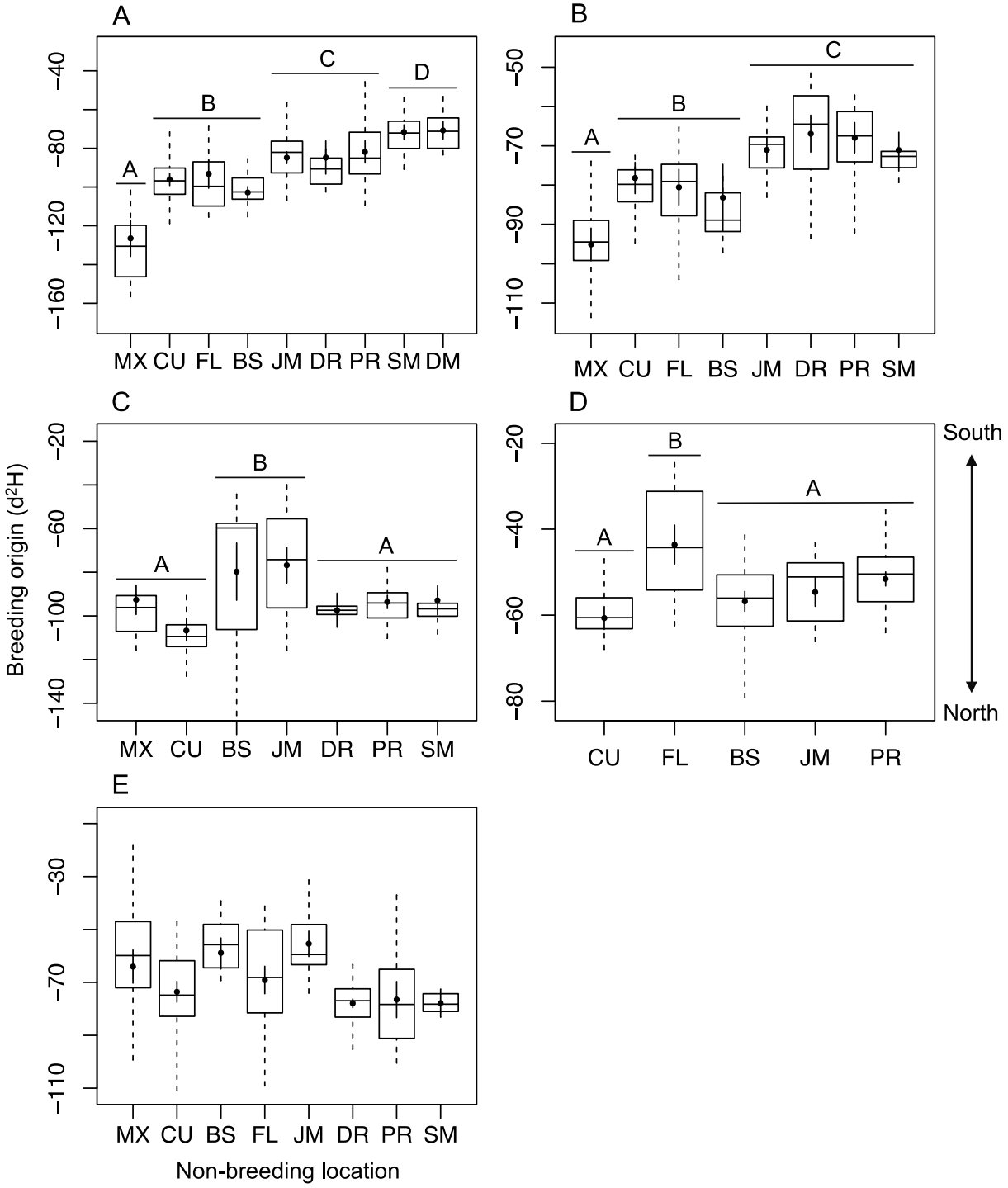


Figure 2. Boxplots illustrating groupings of non-breeding areas with similar stable-hydrogen isotope feather values (δ^2H_F) for A) American Redstart, B) Black-and-white Warbler, C) Northern Parula, D) Prairie Warbler and E) Ovenbird. Points and associated errors show means and 85% credible intervals, boxes depict medians and interquartile ranges, and dashed vertical lines are the data range.

Black-and-white Warblers demonstrated similar patterns of connectivity to redstarts, with western non-breeding populations migrating further north and west compared to eastern non-breeding populations (Fig. 2B). Black-and-white Warblers overwintering in Belize, Mexico, and Nicaragua had δ^2H values that suggested breeding locations in the northern center of the breeding range in Canada (Fig. 4A). Non-breeding populations in Bahamas, Cuba, and Florida were assigned to similarly northern breeding locations but further to the east (Fig. 4B). This region is the most likely origin of Black-and-white-warblers breeding at Ethan Allen Firing Range (Fig. 4B – 1) and Westover Air Reserve Base (Fig. 4B – 2). Isotope values of non-breeding populations in Dominican Republic, Jamaica, Puerto Rico, and St. Martin were consistent with breeding sites in the northeastern United States, slightly to the south of those overwintering in Bahamas, Florida, and Cuba (Fig. 4C). This region is the most likely overwintering area for breeding populations at Fort Belvoir (Fig. 4C – 4), NIOC Sugar Grove (Fig. 4C – 5), and Fort Leonard Wood (Fig. 4C – 8).

Together connectivity patterns for both American Redstart and Black-and-white Warbler are indicative of chain migration, as all birds migrated approximately the same distance between breeding and non-breeding locations. Although their breeding and non-breeding ranges in these overlap extensively, these two species occupy different breeding habitats. Therefore, it is unlikely that the distribution of breeding habitat played a role in determining observed patterns of migratory connectivity.

Figure 3. Likelihood of migratory connectivity among tropical non-breeding and temperate breeding areas for American Redstart (*Setophaga ruticilla*). Predicted breeding range distribution differs for birds overwintering in A) Mexico; B) Bahamas, Florida, and Cuba; C) Dominican Republic, Jamaica, and Puerto Rico; and D) Dominica and St. Martin. The approximate non-breeding range is shaded grey. Black points in the inset show non-breeding locations where birds were sampled. Numbers are DoD installations where birds were sampled and correspond to the list shown in Fig. 1.

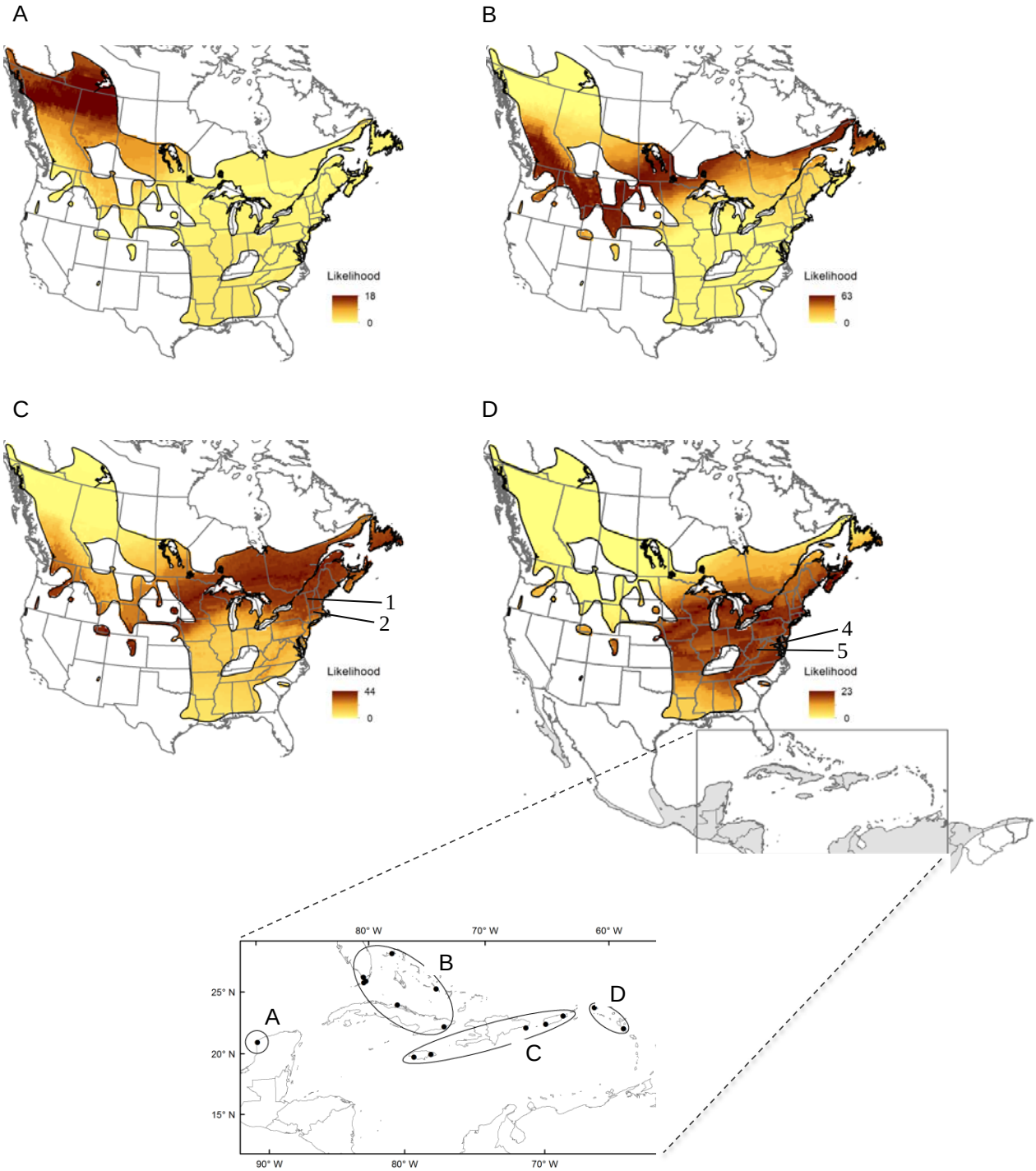
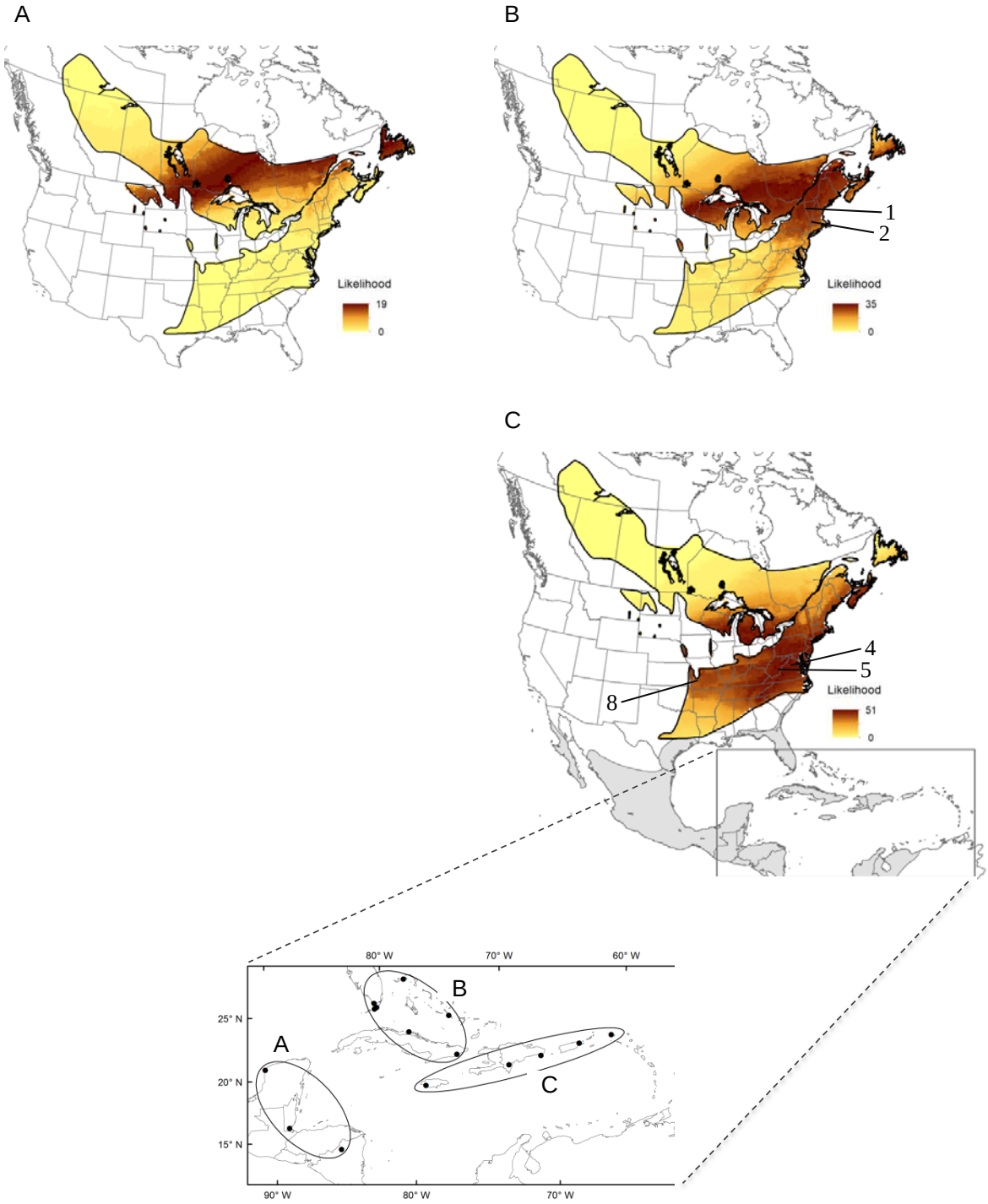


Figure 4. Likelihood of migratory connectivity among tropical non-breeding and temperate breeding areas for Black-and-white Warbler (*Mniotilta varia*). Predicted breeding range distribution differs for birds overwintering in A) Mexico, Belize, and Nicaragua; B) Bahamas, Florida, and Cuba; C) Dominican Republic, Jamaica, Puerto Rico, and St. Martin. The approximate non-breeding range is shaded grey. Black points in the inset show non-breeding locations where birds were sampled. Numbers are DoD installations where birds were sampled and correspond to the list shown in Fig. 1.



Northern Parula also exhibited strong patterns of migratory connectivity, yet these were apparent more as a function of winter longitude than latitude (Fig. 2C). Isotope values of non-breeding populations at the center of the nonbreeding-range in Bahamas and Jamaica indicated that they migrated relatively short distances to the most southern breeding sites (Fig. 5B). Conversely, non-breeding populations further to both the west in Mexico and the east in Cuba, Dominican Republic, Puerto Rico and St. Martin migrated relatively long distances to the extreme northern part of the breeding range (Fig. 5A). These islands are the most likely non-breeding area for Northern Parula breeding at Fort Stewart (Fig. 5B – 6), Fort Polk (Fig. 5B – 7), and Fort Leonard Wood (Fig. 5B – 8).

Thus, unlike Black-and-white Warbler and American Redstart, which appeared to exhibit chain migration, connectivity patterns for Northern Parula are consistent with leapfrog migration, where southern non-breeding population passing over more northern ones during spring migration to breeding sites. One explanation for the contrasting pattern among these species is the breeding range of Northern Parula extends farther into the southern U.S., and these species may therefore gain greater advantage by wintering near to their breeding site.

Patterns of connectivity for Ovenbird were anomalous relative to the other three species considered. Unlike American Redstart and Black-and-white Warbler, in which western non-breeding populations migrated further north to breed, Ovenbird generally showed the opposite trend, with western non-breeding populations breeding in more southern locations (Fig. 2E). Isotope values of non-breeding populations across a large area extending from Mexico in the southwest to the Bahamas in the northeast were consistent with breeding locations in the southern third of the breeding range (Fig. 6A). These non-breeding areas are likely to be the

Figure 5. Likelihood of migratory connectivity among tropical non-breeding and temperate breeding areas for Northern Parula (*Seophaga americana*). Predicted breeding range distributions differ for birds overwintering in A) Cuba, Dominican Republic, Mexico, Puerto Rico, and St. Martin; and B) Bahamas and Jamaica. The approximate non-breeding range is shaded grey. Black points in the inset show non-breeding locations where birds were sampled. Numbers are DoD installations where birds were sampled and correspond to the list shown in Fig. 1.

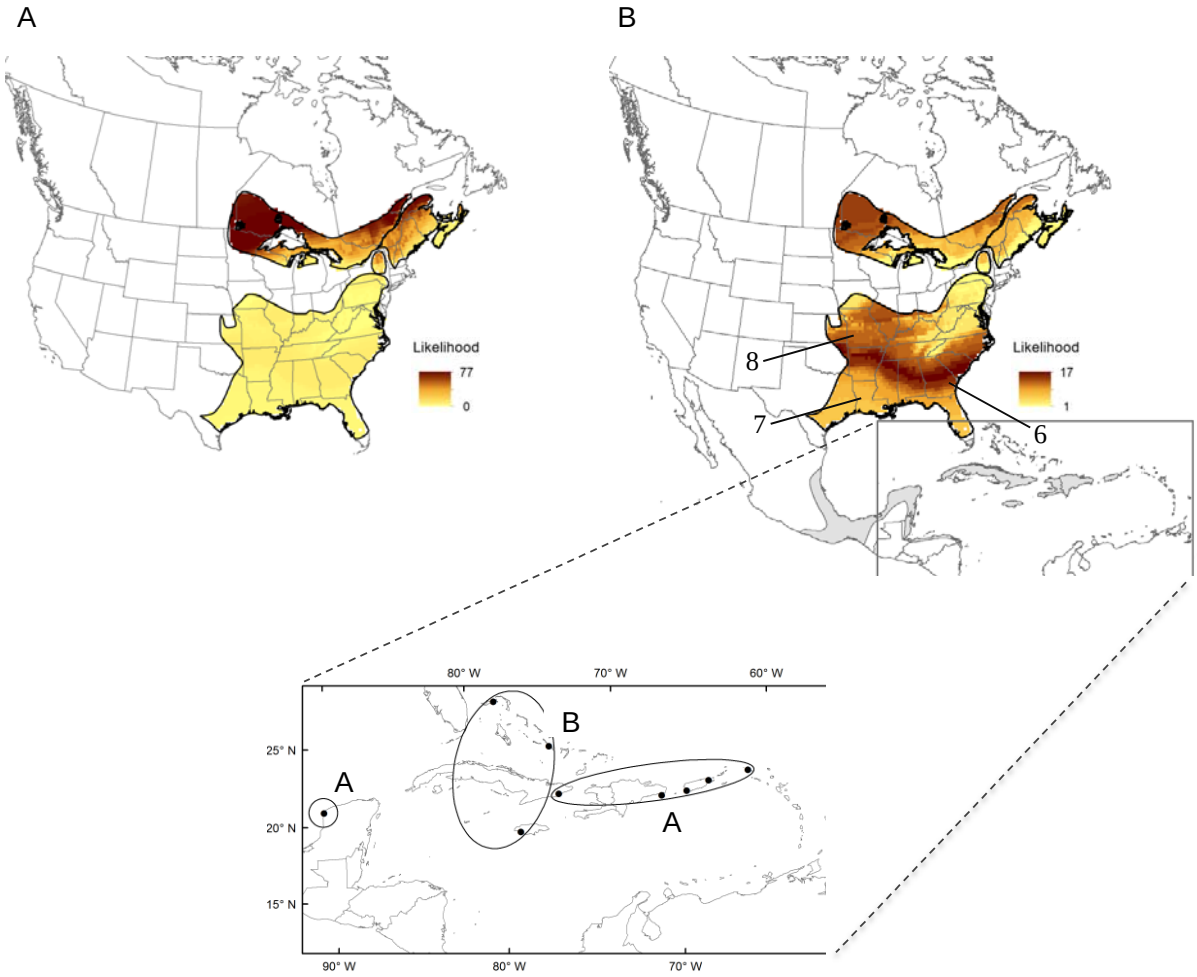
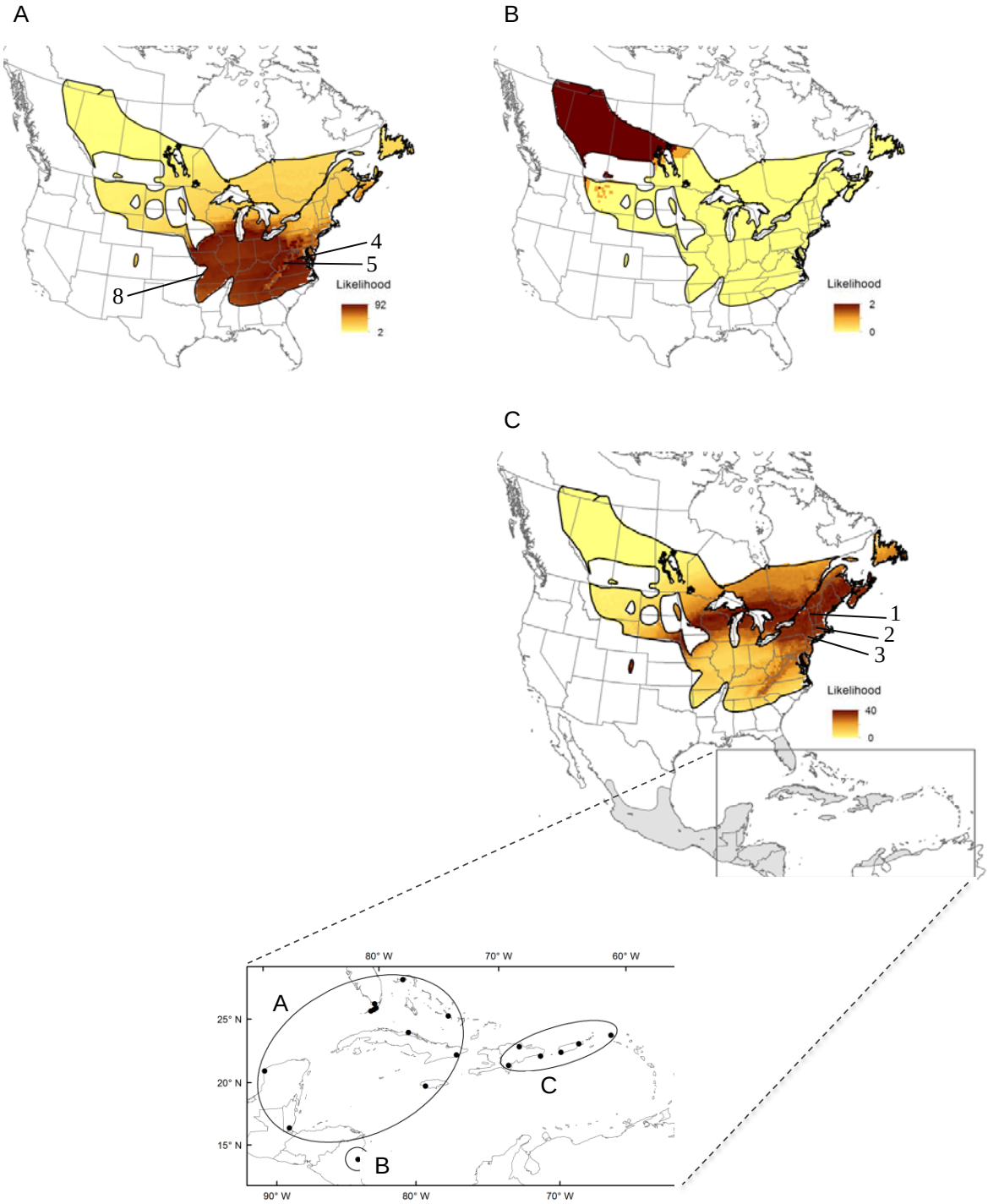


Figure 6. Likelihood of migratory connectivity among tropical non-breeding and temperate breeding areas for Ovenbird (*Seiurus aurocapilla*). Predicted breeding range distributions differ for birds overwintering in A) Bahamas, Belize, Cuba, Florida, Jamaica, and Mexico; B) Nicaragua; and C) Dominican Republic, Puerto Rico, and St. Martin. The approximate non-breeding range is shaded grey. Black points in the inset show non-breeding locations where birds were sampled. Numbers are DoD installations where birds were sampled and correspond to the list shown in Fig. 1.



source of Ovenbirds breeding at Fort Belvoir (Fig. 6A – 4), NIOC Sugar Grove (Fig. 6A – 5), and Fort Leonard Wood (Fig. 6A – 8). Non-breeding populations in Nicaragua were an exception to the trend for western non-breeding populations to migrate to southern breeding areas; δ^2H values for these individuals suggested breeding locations at the far northwestern portion of the breeding distribution (Fig. 6B). Ovenbirds overwintering in the eastern part of the non-breeding grounds in Dominican Republic, Puerto Rico, and St. Martin were assigned to the northeastern part of breeding range (Fig. 6C). These islands are the most likely overwintering areas for birds breeding at Ethan-Allen Firing Range (Fig. 6C – 1) Westover Air Reserve Base (Fig. 6C – 2), and Picatinny Arsenal (Fig. 6C – 3).

RECOMMENDATIONS FOR DoD INSTALLATIONS

Neotropical-Nearctic migratory birds spend about three months on DoD installations, and approximately twice that time on tropical non-breeding areas. To provide effective planning and to maximize conservation investments, installations must consider the limiting factors these birds may encounter in the tropics. Connectivity maps such as those presented in Fig. 3-6 can allow natural resource managers at DoD installations to identify the tropical non-breeding areas used by locally breeding species, creating the potential for regional management efforts. Ethan Allen Firing Range and Westover Air Reserve Base receive breeding American Redstart from the core of the non-breeding range in the West Indies. Ethan Allen Firing Range, Westover Air Reserve Base, Fort Belvoir, and NIOC Sugar Grove together contain a substantial part the Black-and-white Warbler non-breeding range. Fort Stewart and Fort Leonard Wood receive breeding populations of Northern Parula from the center of the winter distribution in the Bahamas and Jamaica. Finally, Ethan Allen Firing Range, Westover Air Reserve Base, Picatinny Arsenal, Fort

Belvoir, NIOC Sugar Grove, and Fort Leonard Wood together support breeding individuals from a large fraction of the Ovenbird non-breeding range.

These installations could maximize their conservation efforts by enhancing breeding habitat for these species because management may generate positive outcomes over the largest possible non-breeding distribution. Because of the high variation in migratory connectivity among species, it is unlikely that our results can be applied to other species. However, for the four focal species, the migratory connectivity maps we present can be used to by DoD installations other than the ones we sampled. In addition, these connectivity maps will allow resource managers to assess environmental conditions such as drought or habitat loss at connected non-breeding sites when evaluating the success of breeding habitat management plans. Such knowledge of migratory connectivity between breeding and non-breeding populations also could eventually provide a template for further collaboration between biologists and managers at other organizations in temperate and tropical regions.

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