Strong migratory connectivity indicates Willets need subspecies-specific conservation strategies

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ABSTRACT

By combining all available banding and tracking data, we found that Willets (*Tringa semipalmata*) have a strong migratory connectivity between breeding and nonbreeding locations at the range-wide and subspecies levels, exposing two subspecies to varying threats such as hunting for the eastern subspecies (*T. s. semipalmata*) and climatically-altered coastal habitats for both subspecies. We found that western Willets (*T. s. inornata*) primarily used nonbreeding habitats along the Pacific Coast of the United States, although their reported nonbreeding range extends to the U.S. Atlantic and Gulf Coasts and the Pacific Coast of Central and South America. Eastern Willets wintered in Central and South America, which covers much of the subspecies' known nonbreeding range. By quantifying migratory connectivity within and between two subspecies, we could suggest subspecies-specific threats and potential limiting factors in the breeding and nonbreeding periods of the annual cycle of a declining migratory shorebird. Effective management of the species will likely require a range of conservation strategies across the diverse nonbreeding regions the two subspecies occupy within the United States, Central America, and South America. However, more data are needed from Willets breeding in mid-continental North America to understand the complete extent of overlap of the two subspecies throughout the annual cycle. The strong migratory connectivity documented here highlights the need to manage Willets by subspecies and protect a diversity of breeding and nonbreeding habitats, which will benefit the conservation of other shorebird species that overlap with Willets throughout the annual cycle.

Keywords: annual cycle, conservation, migration, migratory connectivity, shorebirds, subspecies, *Tringa semipalmata*, Willet

LAY SUMMARY

- The eastern and western subspecies of Willets (*Tringa semipalmata*) are both declining and have little overlap in breeding and nonbreeding ranges.
- Tracking and banding data show that Western Willets from Canada and the western United States wintered in California and Central America. Eastern Willets from the Atlantic Coast wintered in northern South America and those from the Gulf Coast wintered on the Pacific Coasts of Central America and Ecuador.
- Both subspecies are threatened by habitat loss from climate change and development and the eastern subspecies has additional threats from hunting.
- Strong migratory connectivity estimates between and within subspecies verify that subspecies-specific management actions are needed and indicate that population-specific actions are needed as well.
- More information is needed on the migration of individuals in the center of the species range and where and when the two subspecies overlap to better understand where the two subspecies are relying on the same habitats and encountering the same threats.

La fuerte conectividad migratoria indica que *Tringa semipalmata* necesita estrategias de conservación específicas para las subespecies

RESUMEN

Al combinar todos los datos de anillamiento y seguimiento disponibles, descubrimos que *Tringa semipalmata* tiene una fuerte conectividad migratoria entre los lugares reproductivos y no reproductivos a nivel de todo el rango de distribución y de las subespecies, revelando que dos subespecies están sujetas a diversas amenazas, como la caza para la subespecie *T. s. semipalmata* y la presencia de hábitats costeros climáticamente alterados para ambas subespecies. Encontramos que *T. s. inornata* usó principalmente hábitats no reproductivos a lo largo de la costa del Pacífico de los Estados Unidos, aunque su rango no reproductivo reportado se extiende hasta las costas del Atlántico y del Golfo de los EEUU y la costa del Pacífico de América Central y del Sur. *T. s. semipalmata* invernó en América Central y del Sur, lo que cubre gran parte del rango no reproductivo conocido de la subespecie. Al cuantificar la conectividad migratoria dentro y entre las dos subespecies, podríamos sugerir amenazas específicas para las subespecies y potenciales factores limitantes en los períodos reproductivos y no reproductivos del ciclo anual de un ave playera migratoria en declive. El manejo efectivo de la especie probablemente requerirá una variedad de estrategias de conservación en las diversas regiones no reproductivas que ocupan las dos subespecies dentro de los Estados Unidos, América Central y América del Sur. Sin embargo, se necesitan más datos sobre la reproducción de *T. semipalmata* en el centro continental de América del Norte para comprender el alcance completo de la superposición de las dos subespecies a lo largo del ciclo anual. La fuerte conectividad migratoria documentada aquí destaca la necesidad de manejar a *T. semipalmata* por subespecie y de proteger una diversidad de hábitats reproductivos y no reproductivos, lo que beneficiará la conservación de otras especies de aves playeras que se superponen con *T. semipalmata* a lo largo del ciclo anual.

Palabras clave: aves playeras, ciclo anual, conectividad migratoria, conservación, migración, subespecies, *Tringa semipalmata*

INTRODUCTION

Understanding the ecology of animals throughout their full annual cycles is necessary for conservation of threatened and common species (Marra et al. 2015). Among migratory species, shorebirds perform some of the longest migrations, moving between distant habitats where they experience varied threats throughout their annual cycle (Niles et al. 2010, Battley et al. 2012). Many shorebird populations are declining due to habitat loss, predation, climate change, human disturbance, hunting, and factors yet to be determined, and these threats can affect shorebirds at any point in their annual cycle (Andres et al. 2012, Galbraith et al. 2014, Rosenberg et al. 2019). Shorebirds are especially at risk, because they use specialized habitats during breeding, nonbreeding, and migration that are simultaneously being developed and negatively affected by climate change (Galbraith et al. 2014, Studds et al. 2017, Haig et al. 2019). These rapid and significant changes to their habitats (Iwamura et al. 2013, Navedo et al. 2017, Murray et al. 2018), as well as varying levels of protection throughout the annual cycle (Watts and Turrin 2016), present urgent challenges to shorebird conservation (e.g., Senner et al. 2016).

It is critical to understand the geographic and temporal linkage of populations throughout phases of the annual cycle (i.e., migratory connectivity; Webster et al. 2002, Marra et al. 2018), because threats can have disproportional effects across a species' range depending on how populations are connected (Somveille et al. 2021). For example, strong migratory connectivity, in which there is little mixing of populations throughout the annual cycle, can lead to differential population trends that require population-specific management actions. This aligns with flyway-based management, which is currently done for many waterfowl and shorebird species (Blohm et al. 2006, Atlantic Flyway Shorebird Initiative 2015, Weiser et al. 2015). By contrast, weak migratory connectivity, in which there is a high degree of mixing, can indicate that the species should be managed similarly across the entire range. Studies have increasingly assessed levels of migratory connectivity between breeding and nonbreeding grounds (Haig and Oring 1988, Johnson et al. 2010, Brown et al. 2017, Cooper et al. 2018, Tonra et al. 2019), and more recently, during migration (Cohen et al. 2018b, Bégin-Marchand et al. 2021, Knight et al. 2021). Progress has also recently been made in understanding the fundamental processes that drive observed patterns of migratory connectivity (Somveille et al. 2021), but scientists and conservationists still lack detailed descriptions of migratory connectivity for most species (Cohen et al. 2018a, Tonra et al. 2019, Knight et al. 2021).

Like other migratory shorebirds, Willets (*Tringa semipalmata*) experience various threats throughout the annual cycle, including habitat loss and conversion, climate change, and both legal and illegal hunting (Galbraith et al. 2014, Watts and Turrin 2016). Willets breed on the coasts and interior wetlands of North America, with the eastern subspecies (*T. s. semipalmata;* hereafter Eastern Willets) breeding in salt marshes of the Atlantic and Gulf Coasts of the United States and the western subspecies (*T. s. inornate;* hereafter Western Willets) breeding in interior wetlands and prairies of western North America (Oswald et al. 2016). Previous studies indicate that Western Willets breeding in the Great Basin use the California Coast during the nonbreeding season (Haig et al. 2002). By contrast, Eastern Willets breeding on the Atlantic Coast of the United States use the northern coast of South America (Smith et al. 2020), whereas Gulf Coast breeding birds use the Pacific Coast of Central and South America during the nonbreeding season (Heath et al. 2022). These differences in breeding and nonbreeding areas appear to result in disjunct ranges, which likely results in them experiencing different threats and needing population-specific conservation planning (Galbraith et al. 2014, Senner et al. 2016, Lowther et al. 2020). While both subspecies have been tracked and their migration patterns described, this study combines range-wide Willet migratory connectivity data to quantify and compare patterns across and within subspecies for the first time.

Long-term monitoring indicates that Willets have declined by 23.3% since 1970 (90% credible interval [CI]: 9.2–34.6%; Rosenberg et al. 2019). These declines are occurring in pockets throughout the breeding range, affecting both subspecies (Sauer et al. 2020). In the early 1900s, Eastern Willets were overhunted and extirpated throughout much of their breeding range (Bent 1927). They recolonized their breeding range over the course of the 20th century (Weyl and Potter 1930, Craig 1990), before commencing current population declines. Describing and quantifying Willet migratory connectivity, both within and between subspecies, is a critical first step in understanding population declines. The eastern and western subspecies of Willets differ in their behavior, habitat use, and ranges during both the breeding and nonbreeding seasons (Oswald et al. 2016), and thus the magnitude and causes of the declines likely differ.

The objective of this study was to combine all Willet location data to comprehensively describe and quantify migratory connectivity and identify differences in threats that may require different conservation strategies throughout the annual cycle. Based on published wintering locations (Haig et al. 2002, Smith et al. 2020, Heath et al. 2022), we expected strong range-wide migratory connectivity, resulting in little, if any, overlap between Eastern and Western Willets on the nonbreeding grounds. We expected more mixing within the two subspecies, which would result in weaker migratory connectivity. The results of this study are important for the management of Willets and other shorebirds throughout the annual cycle and can be used to guide research to fill remaining knowledge gaps.

METHODS

Data Collection

To quantify migratory connectivity, we gathered location data from published studies that used radio transmitters (Haig et al. 2002) and light-level geolocators (Smith et al. 2020, Heath et al. 2022), as well as re-encounter data from the US Geological Survey (USGS) Bird Banding Laboratory. Between 1996 and 1999, radio transmitters and color bands (n = 146) were deployed on Willets breeding in inland California and Oregon and later resighted at nonbreeding sites along the California Coast (Haig et al. 2002). Nonbreeding locations for these individuals were determined using telemetry and band resighting. Geolocators (n = 40) were recovered between 2010 and 2014 from Willets breeding in Maine, Massachusetts, and New Jersey, and between 2016 and 2019 from Willets breeding in on the Gulf Coast in Texas (Smith et al. 2020, Heath et al. 2022). In addition to tracking data, we used all band re-encounters (1932–2018; n = 30) from the USGS Bird Banding Laboratory. We filtered out any recoveries within the same 10-minute block or during the same season resulting in 15 breeding and nonbreeding locations, defined by annual cycle dates from eBird (below).

To visualize overlap of the two subspecies throughout the annual cycle, we retrieved all eBird observations of Willets that were identifiable to subspecies (eastern n = 41,223; western n = 57,018; Cornell Lab of Ornithology 2020). Observations that occurred between 2007 and 2020 were binned into breeding (May 31 to June 28), fall migration (July 6 to October 19), nonbreeding (October 26 to March 15), and spring seasons (March 22 to May 24) using annual cycle dates from eBird. Breeding phenology varies widely by location but these dates are fairly conservative to avoid inclusion of migrating individuals during stationary periods of the annual cycle.

Analysis

Breeding and nonbreeding locations were determined through direct observation for banded and radio-tagged birds. Breeding locations of individuals tracked with light-level geolocators were recorded as the site of capture, but we used light-level data to estimate nonbreeding locations (see Smith et al. 2020 and Heath et al. 2022 for details of geolocator analysis). Raw light level data were analyzed in the R packages *GeoLight* (Lisovski et al. 2012), *TwGeos* (Wotherspoon et al. 2016), and *Solar/Satellite Geolocation for Animal Tracking* (SGAT; Sumner et al. 2009). The centroid of each individual's estimated nonbreeding season distribution was used as the estimate for the nonbreeding location. We used the *MigConnectivity* package (Hostetler and Hallworth 2017) function *estMC* in R version 4.1.0 (R Core Team 2021) to quantify migratory connectivity (Cohen et al. 2018a). This function requires breeding and nonbreeding regions, a distance matrix between regions, a variance/covariance matrix for geolocator data, and relative abundance in breeding regions.

Breeding and nonbreeding regions were defined by the state or country of observation (Figure 1). Breeding and nonbreeding region polygons were created using the geographic boundaries of the state or country for all regions except New England (which combined Massachusetts, New Hampshire, Maine, and New York) and Brazil, for which a minimum convex polygon was constructed around the seasonal observations. We then clipped the regions to the species range, which helped restrict regions to only areas where the species occurs. When observations fell outside of a region polygon, which sometimes occurred because centroids of geolocator wintering distributions were located on water, the polygon was buffered by several kilometers to include all observations. This did not affect relative distance between regions, as the centroid of each region remained the same.

When discussing population-level results within each subspecies, we refer to the breeding regions defined for the migratory connectivity analysis. A total of 6 breeding regions were defined for Eastern Willets and 3 regions for Western Willets. We defined 8 nonbreeding regions for the eastern subspecies and 3 for the western subspecies.

We estimated Willet relative abundance from eBird data using the R package *ebirdst* (Auer et al. 2020). The *ebirdst* package uses eBird observations to estimate year-round distribution and abundance across a regular grid while controlling for variation in detectability (Fink et al. 2020). Abundance values were extracted from the region polygons used to define each breeding region (see above) and then scaled to sum to 1, a requirement of the *estMC* function. We then estimated migratory connectivity for the species as a whole, for each subspecies separately, and for the Eastern subspecies excluding observations from the Gulf Coast.

RESULTS

We acquired breeding and nonbreeding observations of 40 radio-tagged and banded Western Willets (23 telemetry observations and 17 visual observations), 40 geolocator-tagged Eastern Willets, and 15 banded and re-encountered Willets (10 eastern, 5 western). USGS bird banding data included both resightings and recoveries. Of recovered individuals, 8 of 15 (53%) were individuals killed by hunters between 1938 and 1979 in Guyana (n = 2), French Guiana (n = 1), Brazil (n = 3), Mexico (n = 1), and Costa Rica (n = 1). Individuals breeding in the Great Basin in California, Oregon, and Nevada all wintered on the California Coast. Individuals banded in the Prairie Pothole region wintered in western Mexico and on the Gulf Coast. Geolocator-tagged individuals from the U.S. Atlantic Coast wintered throughout the Atlantic Coast of northern South America, while those tagged on the Gulf Coast wintered on the Pacific Coast of Central America (Figure 2).

Using eBird observations, we found that the western subspecies range overlapped spatially but generally not temporally with the eastern subspecies range for all seasons, except for some overlap in Central America (Figure 3). Observations of the eastern subspecies were restricted to the Atlantic and Gulf Coasts of the United States during the breeding season. Eastern Willets appeared to entirely leave the United States during the nonbreeding season. Western Willets used much of the eastern subspecies breeding range during the nonbreeding season, meaning the Atlantic and Gulf Coasts are occupied by Willets year-round. The Pacific Coasts of Mexico, Central America, and South America are also occupied year-round, which eBird and connectivity data indicate are mostly Western Willets.

Our estimate of migratory connectivity for the species as a whole was 0.90 ± 0.029. The migratory connectivity of the western subspecies was 0.78 ± 0.102, and the migratory connectivity of the eastern subspecies was 0.66 ± 0.0995. When excluding individuals from the Gulf Coast, the migratory connectivity of Willets breeding on the Atlantic Coast was 0.24 ($\pm$ 0.208).

DISCUSSION

Overall, we found that Willets had strong range-wide migratory connectivity, with different breeding regions showing minimal overlap on the nonbreeding grounds. Consistent with our hypotheses, much of this structure was driven by differences in nonbreeding locations between the two subspecies—Eastern and Western Willets in our study showed little overlap in nonbreeding regions, with the exception of Gulf Coast breeding Eastern Willets, which used parts of the nonbreeding range of Western Willets in South and Central America. Subspecies-specific migratory connectivity was also quite strong, except when considering just the Atlantic Coastal populations of the eastern subspecies, which had weak migratory connectivity with almost complete mixing on the nonbreeding grounds regardless of breeding location.

Subspecies-specific Threats

The strong connectivity we documented between the eastern and western subspecies indicates that managers may need to monitor and conserve the two subspecies differently, particularly when it comes to hunting. Most Western Willets winter in the United States where hunting has been effectively ended since passage of the Migratory Bird Treaty Act in 1918. Eastern Willets, by contrast, are actively hunted on their nonbreeding grounds, including Guyana, Suriname, French Guiana, and Brazil (Watts and Turrin 2016, Atlantic Flyway Shorebird Initiative Harvest Working Group 2020), and Suriname has the highest harvest of migratory shorebirds in the western hemisphere (Atlantic Flyway Shorebird Initiative Harvest Working Group 2020). Several geolocator-tagged Willets wintered in Suriname and most of the eastern breeding population stopped over there before moving to Brazil (Smith et al. 2020), but the actual proportion that stopover and winter there may be underestimated by archival tracking technology, like geolocators, if the mortality rate is much higher there due to hunting (Rushing et al. 2021). Although exactly how hunting pressure for Eastern Willets varies by nonbreeding location is not fully understood (Atlantic Flyway Shorebird Initiative Harvest Working Group 2020), Watts et al. (2015) found that both subspecies, and particularly Eastern Willets, had low sustainable harvests compared to other shorebirds, and thus were particularly sensitive to hunting. Atlantic Coast breeding Eastern Willets appear to be at greater risk during migration than Gulf Coast breeding Willets because the former travel through the Caribbean and then winter in northern South America where they are exposed to high levels of harvest (Watts and Turrin 2016; see also McDuffie et al. 2022).

Current international treaties regulate hunting to some degree throughout the western hemisphere, but more legal protections are needed in the form of domestic laws in countries not included in the Migratory Bird Treaty Act to reverse declining populations in Willets (Watts and Turrin 2016). Increased public awareness, education, and incentives to stop hunting will also be necessary to alter the culture of unsustainable shorebird harvest (Atlantic Flyway Shorebird Initiative 2015). However, without more accurate information on actual harvest levels for Willets and other shorebird species, it remains difficult to know how large of a role hunting plays in recent population declines (Watts et al. 2015). With our new migratory connectivity information, managers should re-estimate sustainable harvest levels by region and subspecies. These estimates could provide the basis for new region- and subspecies-specific efforts aimed at reducing harvests to sustainable levels.

In addition to hunting pressure, Eastern and Western Willets may also experience other threats differently depending on their nonbreeding locations. Although Western Willets use some of the same nonbreeding sites in Central America as the eastern subspecies, a large portion of the population winters in the United States, where a primary threat is habitat development, especially in the San Francisco Bay (Haig et al. 2002, Stralberg et al. 2011). Similar to other shorebird species, nonbreeding Western Willets have declined 15% in the San Francisco Bay region over the past 30 years (Warnock et al. 2021). Shorebirds on the Pacific Flyway are also threatened by climate change, disturbance from off-leash pets and recreational activities, aquaculture, and wetland modification (Senner et al. 2016). Continuing to recognize and assess the diversity and magnitude of threats throughout the Atlantic (Atlantic Flyway Shorebird Initiative 2015) and Pacific Flyways (Senner et al. 2016) separately is important for implementing conservation effectively for both subspecies of Willets. This will benefit other shorebirds, as many nonbreeding sites and habitat types used by willets are also important for other species, including Whimbrels (Watts et al. 2021), Lesser Yellowlegs (McDuffie et al. 2022), and Red Knots (Niles et al. 2010).

Among Eastern Willets, the strong migratory connectivity of Gulf and Atlantic Coast breeding birds suggests that managers may need to develop different monitoring and conservation plans even within the eastern subspecies. All Atlantic Coast breeding Willets in our study wintered along the northeastern coast of South America from Guyana to Brazil, and among these countries, habitat threats vary greatly. Northern Brazil, for example, is relatively undeveloped, with legislation that preserves approximately 70% of the country's mangroves (Ferreira and Lacerda 2016). Other countries like Guyana, Suriname, and French Guiana are less protected and the coastlines are increasingly being developed (Anthony and Gratiot 2012). Ecuador, where many Gulf Coast breeding Willets winter, is experiencing large-scale degradation of mangroves, saltmarsh, and mudflat habitat due to shrimp farming (Beitl 2017). With proper management, shrimp farming practices can create opportunities for resting and foraging (Navedo et al. 2017), and aquaculture developments may even be attractive to Western Willets. However, most shorebirds appear to avoid shrimp farms and therefore managers will need to balance species-specific vs. community-wide habitat goals (Kelly et al. 1996, Senner et al. 2016).

Range-wide Threats

Although Willets may face different threats depending on their migration routes and nonbreeding locations, some threats are likely to have range-wide impacts. Across the nonbreeding range, the species is likely to encounter loss of tidal mudflats and mangroves. Both habitat types, which are necessary for the species, are concentrated in only a few countries and have been declining in recent decades (Thomas et al. 2017, Murray et al. 2019). Though the subspecies nonbreeding ranges are generally disjunct, they rely on the same habitat types during the nonbreeding portion of the annual cycle. Due to their dependence on these habitats, the loss of tidal mudflats in North America from sea level rise is predicted to negatively affect shorebird populations (Galbraith et al. 2002). With each breeding population relying on unique portions of the nonbreeding range, managers will likely need to maintain diversity of nonbreeding sites to manage both subspecies effectively. Current plans to protect and manage existing shorebird habitat (Atlantic Flyway Shorebird Initiative 2015, Senner et al. 2016) can be used alongside the results presented here to ensure that wintering areas for each population of Willets are protected, benefiting Willets and other shorebirds (Butler et al. 2001).

Limitations and Directions for Future Research

It is important to note that we do not have complete migratory information from all breeding regions, and therefore our estimates of migratory connectivity may change with the addition of more information. Most importantly, although many Western Willets breed in the interior of the United States, we relied on just a few band re-encounters to document migratory connectivity from this region. eBird data indicate that the interior breeding population winters in coastal areas, but we do not know if they use some of the same coastal nonbreeding areas as other Western Willets or if they exclusively winter further east as our few band re-encounters indicate. If this pattern were to hold true with more data, it would improve the evidence for strong migratory connectivity at the range-wide and subspecies level. Further study of mid-continent Willets is a high priority because that population may be encountering unique threats such as wind turbines and unpredictable water resources with climate change in the Prairie Pothole Region (Niemuth et al. 2013, Steen et al. 2018). Additionally, we are missing data on individuals of the eastern subspecies that breed along the Gulf Coast outside of Texas. These individuals may winter in parts of the nonbreeding range outside of our observations, such as the Pacific Coast of Mexico, the Caribbean, or Central America. Tracking individuals from these regions is a high priority to further understand migratory connectivity and associated threats at a range-wide scale.

Even with the distinct nonbreeding locations for each subspecies revealed by our data, there is a need to understand when and where the two subspecies overlap in the annual cycle. eBird data show that Western Willets are found in the Eastern Willet breeding range during all parts of the annual cycle, but limited band encounters from the central continent portion of the western range do not show movement to the eastern United States. There is some indication that the western subspecies individuals that are found in the eastern subspecies range during the breeding season are juveniles that over-summer in the eastern range and are not reproductively active (Oswald et al. 2016). If this is the case, there is a need to track other age classes as well. This behavior is common among shorebirds, many of which over-summer in their nonbreeding ranges (Martínez-Curci et al. 2020), and has been documented in one Willet that bred on the Gulf Coast and likely spent a full year in Ecuador (Heath et al. 2022). Further study of age-based differential migration and over-summering in nonbreeding regions may help to reveal how much the western subspecies makes use of the Eastern Willet range. If Eastern and Western Willets overlap along the Atlantic Coast, it highlights the need for year-round protections and habitat conservation efforts.

Conclusion

By combining radio-tracking, light-level geolocator, and banding data our study provides the most comprehensive information available on Willet migratory connectivity and allows identification of threats facing both subspecies in migratory and nonbreeding locations. Our data reveal clear migration patterns for Willets on the Atlantic, Pacific, and Gulf Coasts of the United States, but more tracking data are needed from birds in the middle of the continent. There is also a need to determine the origin of individuals that winter along the Atlantic and Gulf Coasts of the United States by collecting data from additional sites. This new migratory connectivity information should be used to estimate more accurate sustainable harvest limits between and within subspecies and implement strategies to reduce harvest as needed. Additionally, breeding and nonbreeding ground protections should continue to be implemented for populations that occur exclusively in the Atlantic and Pacific flyways to ensure that a diversity of habitats are maintained for the two subspecies. These results illustrate how establishing migratory connectivity within and among populations can help better define population-specific conservation threats and potential limiting factors throughout the annual cycle that in turn can yield more focused conservation strategies and research agendas.

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Figure 1. States and countries clipped to species range used to define breeding and nonbreeding regions for eastern and western willet subspecies in analysis. Gray area represents range of the species where no connectivity data have been collected. Range map created using eBird observations (Cornell Lab of Ornithology 2020).

Figure 2. Breeding to nonbreeding connections, colored according to breeding region used in the migratory connectivity analysis. Solid lines (green, blue, and purple) are eastern subspecies and dashed lines (pink, red, orange) are western subspecies. Range map created using eBird observations (Cornell Lab of Ornithology 2020).

Figure 3. eBird observations for eastern and western subspecies of Willets for breeding and nonbreeding seasons of the annual cycle (Cornell Lab of Ornithology 2020).

Figure 1

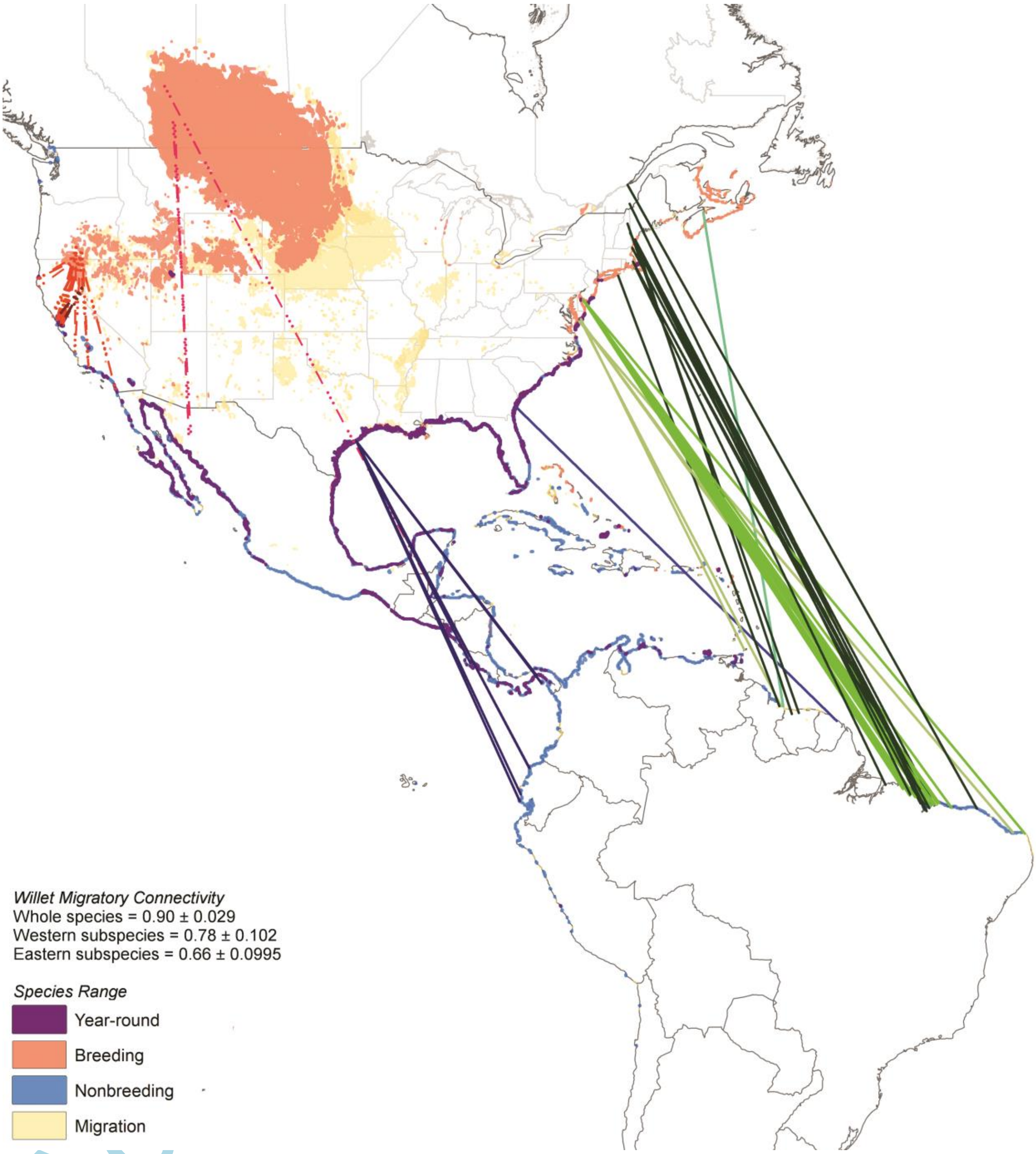

Willet Migratory Connectivity
Whole species = 0.90 ± 0.029
Western subspecies = 0.78 ± 0.102
Eastern subspecies = 0.66 ± 0.0995
Species Range
Year-round
Breeding
Nonbreeding
Migration

Figure 2

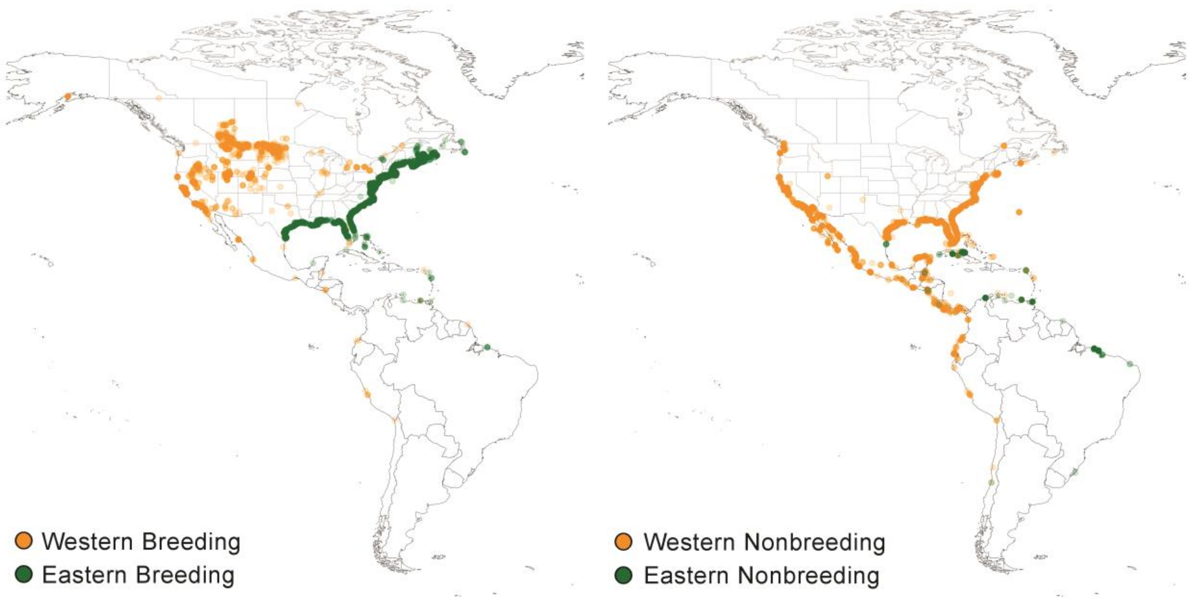
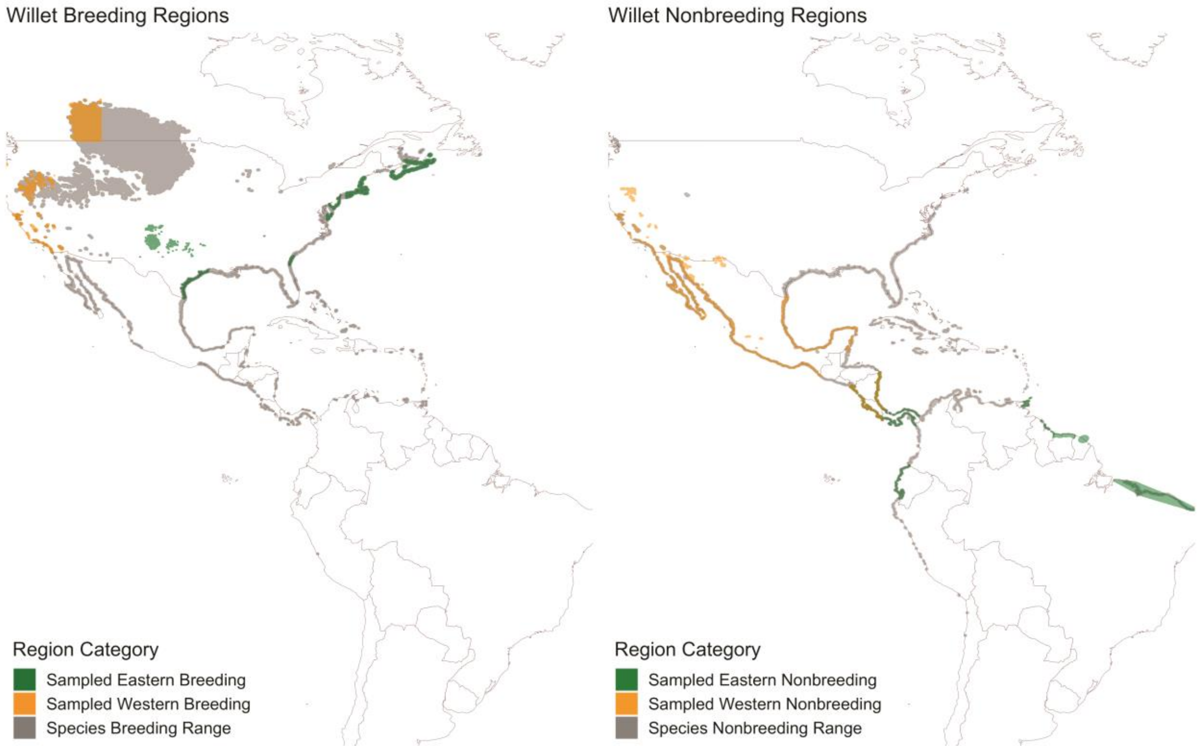

Western Breeding
Eastern Breeding
Western Nonbreeding
Eastern Nonbreeding

Figure 3


Willet Breeding Regions
Region Category
Sampled Eastern Breeding
Sampled Western Breeding
Species Breeding Range
Willet Nonbreeding Regions
Region Category
Sampled Eastern Nonbreeding
Sampled Western Nonbreeding
Species Nonbreeding Range