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Migration and Wintering Locations of Breeding eastern Willet (*Tringa semipalmata semipalmata*) in the Western Gulf of Mexico

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Abstract.—Knowledge of the geographic linking of individuals or populations between different annual life cycle stages is essential for effective conservation decision making. The Willet (*Tringa semipalmata*) is composed of two distinct subspecies that are separated by breeding habitat in North America, with eastern Willets breeding in estuarine marshes along the Atlantic and Gulf Coasts and western Willets breeding in wet grasslands and prairies in the interior west of North America. We studied the migratory paths and wintering locations of Texas Gulf Coast breeding eastern Willets from 2015 to 2019 using light-level geolocators. Data analysis from 9 retrieved geolocators indicated that all birds departed Texas 5–26 July, made a 2–5-day flight, and arrived on the wintering grounds 8–30 July. All birds wintered on the Pacific coasts of Central and South America. In spring, the birds departed the wintering location 9–24 March, made a 3–4-day flight and arrived on the breeding grounds 12–27 March. These results are in contrast to previous work which showed that Atlantic breeding eastern Willets overwintered on the Atlantic coast in northern South America. This work has implications for shorebird conservation planning, which currently considers all Willets overwintering on the Pacific coast to be western Willets.

Key words.—breeding, geocator, migratory connectivity, nonbreeding, Texas, *Tringa semipalmata*, western Gulf, Willet.

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We are still learning about the paths North American migratory bird species take, the stops they make along the way, and where specific populations spend their non-breeding season. Knowledge of migratory connectivity—the geographic linking of individuals or populations between different annual life cycle stages (Webster *et al.* 2002)—is essential for effective conservation decision making because the threats that populations experience throughout the annual cycle can then be better assessed and managed. However, we have not established these linkages for most species and have only monitored many populations at one end of migration or the other. Understanding all phases of the life cycle of migrant birds is critical for determining conservation needs related to successful reproduction, recruitment, and assessing population trends (Marra *et al.* 2015).

The Willet (*Tringa semipalmata*) is composed of two distinct subspecies that are separated morphologically, vocally, and by breed-

ing habitat in North America (Oswald *et al.* 2016). The eastern Willet (*T. s. semipalmata*) breeds in estuarine marshes along the Atlantic and Gulf Coasts from Newfoundland south to northern Tamaulipas and in the West Indies, while the western Willet (*T. s. inornata*) breeds in wet grasslands and prairies in the interior west of North America (Lowther *et al.* 2020). On the Atlantic and Gulf coasts of North America, western Willets replace eastern Willets during the nonbreeding season. Because western Willets are present in North America during both the breeding and nonbreeding seasons, their presence is well documented there during both of those life cycle phases. However, where eastern Willets spend the nonbreeding season has not been fully investigated. Connectivity for breeding eastern Willets is important because factors influencing conservation strategies may differ by nesting location, overwintering range or migratory route.

The conservation status of the Willet is an emerging concern for several reasons.

First, the future of Willet breeding habitat is uncertain. Coastal wetlands, by their nature, are limited in extent and although many salt marshes in the eastern U.S. have protected status, their future may be in jeopardy as the effects of sea level rise due to climate change become increasingly apparent (Kirwan and Megonigal 2013). Eastern Willet nests are susceptible to tidal flooding events and sea level rise will only exacerbate this problem. Additionally, salt marsh breeding birds are subject to several human caused disturbances including habitat loss through development, oil spills and recreational disturbance that results in nest failure. For these reasons, the Willet has a North American Bird Conservation Initiative (NABCI) concern score of 14, which categorizes it as a species at risk of extinction unless its decline is reversed and threats are lessened (NABCI 2016). Additionally, because of differences in morphometric and vocal characteristics of eastern and western Willets, this species is under consideration to be split into two subspecies (Oswald *et al.* 2016).

The continental Willet population is estimated at 250,000, with 90,000 of those being eastern (Morrison *et al.* 2001; Andres *et al.* 2012). Some ornithologists believe the eastern number is an overestimate because of the difficulty of separating the two subspecies that can be simultaneously present on the Atlantic and Gulf coasts (O'Brien 2006). However, information from a saltmarsh survey along the Atlantic coast of the USA from Virginia to Maine (Wiest *et al.* 2016) estimated a breeding population of 117,000. If this information tracks with breeding populations outside this region on the Atlantic and Gulf coasts, the eastern population may be closer to 175,000 (B. Andres., pers. commun.). At any rate, breeding eastern Willets are susceptible to a host of threats from sea level rise that do not impact breeding western Willets.

The study of migratory connectivity has been advanced by new tracking technology including the advent of light-weight, inexpensive archival light-level geolocators (hereafter geolocators). These devices can be carried by birds to record their location as

they travel between breeding and wintering areas (Stutchbury *et al.* 2009) and have been used successfully on many shorebirds (Conklin and Battley 2010; Minton *et al.* 2010; Niles *et al.* 2010). Migratory connectivity studies of Atlantic coast breeding eastern Willets (hereafter, Atlantic Coast Willet) using these geolocators indicate that those birds spend the nonbreeding season along the Atlantic coast of northern South America, primarily in northern Brazil (Smith *et al.* 2020). However, to date no one has investigated where Gulf breeding eastern Willets (hereafter, Gulf Coast Willet) spend the nonbreeding season. Banding data provides no insights. There have been 1669 Willets (both eastern and western) banded from 1960 to 2019 with only 30 reported encounters outside of the breeding grounds of those banded birds. None of these were from birds banded along the Gulf Coast (USGS Bird Banding Laboratory 2020).

To build upon the previous tracking work on Atlantic Coast Willets and set the stage for a clearer understanding of threats faced by willets throughout the annual cycle, we studied the migration of breeding eastern Willets on the Texas Gulf coast from 2015 to 2019. The objectives of this study were to determine the timing, routes, nonbreeding locations, and migratory connectivity of eastern Willets breeding in the western Gulf of Mexico.

METHODS

Study Area

We worked on a 14.2 ha study site (48° 31' 40.59" N, 70° 14' 16.28" W) at San Bernard National Wildlife Refuge in Matagorda County, Texas (Fig. 1). Located only 448 m from the Gulf of Mexico, our site includes wetlands that are estuarine, emergent, intertidal, and irregularly flooded (USFWS 2020). These wetlands are divided into two distinct zones by their differing elevations. Approximately 59.6% of the site is dominated by *Distichlis spicata*. The remaining 40.4% is slightly higher in elevation and dominated by Gulf Cordgrass (*Spartina spartinae*).

Geocator Deployment and Retrieval

From 2015–2019, we located Willet nests by use of search images or behavioral cues, or by pulling a two-person dragline constructed of clothesline through

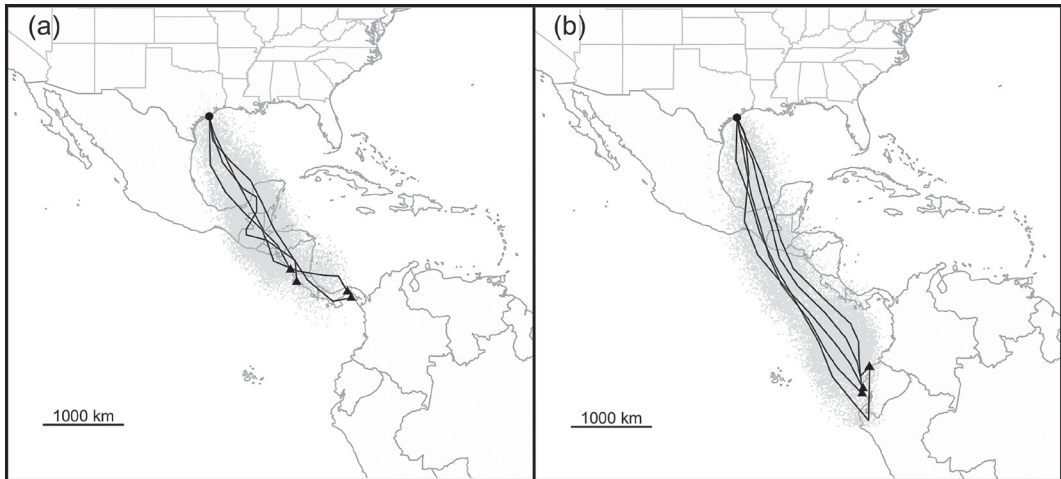


Figure 1. Southbound migratory paths (black lines) and associated error (grey polygons) for nine eastern Willets (*Tringa semipalmata semipalmata*) tracked with light-level geolocators wintering in Central America (a) and South America (b). Known breeding locations and estimated wintering locations are shown with a closed circle and closed triangles respectively. Migratory paths were defined as the mean path of the posterior distribution from the MCMC analysis. For visual clarity, winter locations are shown as a single point by taking the closest coastal site to the centroid of the 95th quantile of all estimated wintering locations. This process resulted in two pairs of birds sharing the same location.

the salt marsh. For all nests, we noted the number of eggs and marked the area with small diameter dowel rods placed 5 m away on two sides of the nest with the top of the rod angled away to indicate nest placement relative to the dowel. For nests containing 3–4 eggs, we returned a minimum of one hour later and lowered a 12 m, 127 mm mesh mist net suspended between two poles over the nest. We then approached the nest to flush the incubating bird into the net. Once captured, we applied a USFWS aluminum band, two color bands (light blue, orange, red, green, or yellow) or a unique alphanumeric leg flag to facilitate identification, and a leg-mounted Migrate Technology Intigeo C65 geolocator supported by one of the color bands (Minton *et al.* 2010). The geolocator weight was 1.83 g when accounting for leg flag attachment, and all markers combined weighed either 2.8 g when color band identifiers were used, or 3.45 g for leg flag applications. Relative to our individual bird weights, these markers comprised no greater than 1.86% of the body mass (range 0.73–1.86%, $n = 22$). We measured wing chord (mm), culmen (mm) and weight (g). We returned at a different time of day (either morning or afternoon) to trap the uncaptured pair member as there is evidence that incubation is temporally spaced in Willets (Bulla *et al.* 2016). We always attempted capture of both pair members each year but sometimes failed due to nest completion, nest termination, or bird wariness. When we captured both pair members (70% of all pair capture attempts), we used overall size and comparison of pair members to determine sex as males are smaller (Lowther *et al.* 2001). In subsequent years, we retrieved geolocators by locating the nests of returning birds and trapping on these nests or using noose carpets to capture tagged birds (Bub 1991).

Analysis of light-level data

Light data from the geolocators was analyzed with the Solar/Satellite Geolocation for Animal Tracking package (Wotherspoon *et al.* 2013; Sumner *et al.* 2009), for Program R (R Core Team 2017). This package uses Markov Chain Monte Carlo (MCMC) simulations to estimate both the geographic locations and their associated error. We followed the general protocol outline by Lisovski *et al.* (2019). First, we imported light data using the package “GeoLight” (Lisovski and Hahn 2012). Then, we used functions within “TwGeos” (Lisovski *et al.* 2016) to convert light data to twilight times and identify outliers. We removed all twilight times that were more than 35 minutes earlier or later than twilights on the two days before or after each day. Next, we used functions within TwGeos to determine the appropriate breeding ground zenith angle and to define the error distribution for the whole year. For this step we used a 2–4-week period shortly after geolocator deployment when individuals were known to be on the breeding grounds. The exact timing and duration of this period varied for each bird because we excluded periods when light profiles indicated that incubation had interfered with collection of light data (i.e., when complete darkness was recorded during daylight hours; Tonra *et al.* 2019). We used the Hill-Ekstrom calibration to estimate the zenith angle during the nonbreeding period and took the average of breeding and wintering zenith angles to estimate the zenith angle during migration (Cooper *et al.* 2017; Lisovski *et al.* 2019). Using these zenith angles, we used the thresholdPath function in SGAT to create a preliminary set of locations for each individual that would later be used as an informed prior in the MCMC

analysis. Finally, we specified a model that included: 1) the preliminary locations derived above, 2) a distribution of errors between known and estimated breeding ground locations, and 3) a plausible flight speed distribution. We ran each individual's model with three independent chains 60,000 times for burn-in and tuning, and another 15,000 times to define the posterior distribution.

We determined the timing of migration and stationary nonbreeding periods by determining when the mean path from the posterior distribution indicated that birds had departed and arrived at a stationary site without return. Using this timing information, we estimated the location of the nonbreeding sites by plotting the 95th quantiles of positions during the nonbreeding season (Cooper *et al.* 2017). Due to known inaccuracy in latitudinal estimation with geolocators during the spring and fall equinoxes, we removed all position estimates 40 d before and after each equinox when estimating the location of the wintering site. Strong overlap in time between spring migration and the spring equinox prevented us from accurately estimating migratory paths in spring. However, we were able to roughly estimate the timing of spring migration using changes in longitude.

RESULTS

We located 40 nests from which we banded 30 birds and deployed 24 geolocators. From 2016 to 2019 we retrieved 10 geolocators (Table 1). Nine birds were recaptured on nests and one was caught using noose carpets (Bub 1991). Four of the retrieved geolocators contained data for at least one year, five contained data for southbound migration and part of the nonbreeding period, and the tenth one incurred saltwater intrusion which resulted in corruption of all data.

Individuals departed the Texas coast breeding site from 5–26 July ($n = 9$, $\bar{x} =$ July 14 ± 2.9 d). Eight of 9 individuals (89%) made a direct flight from the breeding grounds to the wintering grounds, while 1 individual (11%) appeared to make a one-

day stopover somewhere on the Atlantic coast of Mexico in the states of Tabasco or Campeche (Fig. 1a,b). Southbound migration lasted 2–5 days ($\bar{x} = 4 \pm 0.3$ days; Table 2), with individuals arriving at their wintering sites from 8–30 July ($\bar{x} =$ July 17 ± 2.9 d). Wintering sites were along the Atlantic or Pacific coasts of Central America and the Pacific coast of northern South America. Five individuals wintered on the coast of Ecuador or northern Peru, with two individuals wintering on the coasts of Nicaragua or Costa Rica and two individuals wintering on the coasts of Panama or northern Colombia (Fig. 2). Four tags stopped collecting light data prior to the onset of northbound migration. Four of the remaining five individuals departed the wintering grounds from 9–24 March ($\bar{x} =$ 17 March ± 3.2 d). Given their close proximity to the spring equinox, we could not accurately estimate the paths of their migrations, but they appeared to spend 3–4 days migrating back to the breeding grounds, arriving in Texas from 13–27 March ($\bar{x} =$ 21 March ± 3.1 d). One individual remained on the wintering grounds (i.e. over-summered, McNeil *et al.* 1994) in Ecuador at least through 8 June of the following breeding season when its tag stopped collecting light data. This individual returned to the breeding grounds for the 2017 breeding season during which the geolocator was retrieved and this bird was documented returning all subsequent seasons (2017–2019).

Interestingly, one of our mated pairs (M568 and X059) from which we recovered geolocators did not travel together or over-winter in the same country following their southbound migration: the female M568 departed on 11 July and arrived in Ecuador or northern Peru on 15 July, while the male X059 departed on 9 July and arrived in Nicaragua or Costa Rica on 11 July. Both tags died prior to their return migration, but the pair returned to the breeding site and nested together the following year. This is the only data recovered for simultaneous time periods from both pair members in our study. We are unable to speculate how commonly this occurs.

Table 1. Number of nests located, birds banded, and geolocators (geos) applied and retrieved 2015–2019.

	2015	2016	2017	2018	2019	Total
Nests located	9	4	9	11	8	40
Birds banded	10	3	8	8	1	30
Geos applied	10	3	8	3	0	24
Geos retrieved	N/A	1	2	4	3	10

Table 2. Dates of departure from breeding grounds and arrival on wintering grounds, length of migration in days and non-breeding (winter) sites derived from geolocator data for eastern Willets recaptured 2016–2019 (“SD” = standard deviation).

Season	Winter Site	Geolocator	Departure	Arrival	Duration (days)
Fall	C. America	BM866	8 Jul 2018	13 Jul 2018	5
	C. America	X059	9 Jul 2017	11 Jul 2017	2
	C. America	J018	10 Jul 2015	15 Jul 2015	5
	C. America	W582	26 Jul 2016	29 Jul 2016	3
	S. America	J090	5 Jul 2015	9 Jul 2015	4
	S. America	W585	5 Jul 2017	8 Jul 2017	3
	S. America	M568	11 Jul 2017	15 Jul 2017	4
	S. America	J093	22 Jul 2015	26 Jul 2015	4
	S. America	BM863	26 Jul 2018	30 Jul 2018	4
			mean (SD)		4 (0.3)

DISCUSSION

Our study provides the first evidence that there is likely little range overlap throughout the annual cycle between Atlantic Coast Willets and western Gulf Coast Willets on the wintering grounds or any other phase in the annual cycle. The evidence to date regarding wintering ranges indicates that Atlantic coast-breeding eastern Willets winter primarily along the Atlantic coast of northern South America (Smith *et al.* 2020), with small

numbers occurring as far south as Argentina (Martinez-Curci *et al.* 2014). In contrast, At least some Gulf Willets winter on the coasts of Central America and the Pacific coast of northern South America. In both regions, it appears that eastern Willets are wintering in mangrove-dominated estuaries with large tidal ranges that have, in many cases, been previously identified as important sites for shorebirds (Duncan 2006; Morrison and Ross 1989).

Although they occupy similar coastal habitats, Willets wintering on the Pacific coast of Central and South America may face different types and magnitudes of threats than those wintering on the Atlantic coast in the Guianas and Brazil. For example, in Brazil, although wetland conversion to shrimp aquaculture looms as a threat (Rovai *et al.* 2012), the core wintering areas remain relatively undeveloped (Goldberg *et al.* 2020). Conversely, on the Pacific coast, considerable development has already occurred. The coastline of Ecuador, where the majority of the Willets we tracked wintered, has experienced extensive conversion of coastal habitats into shrimp farm ponds over the last 50 years (Hamilton 2020). Shrimp farms are the dominant landcover in half of Ecuador’s major estuaries and occupy more space than mangroves in $\frac{3}{4}$ of these estuaries. Even in the most pristine estuary, 28% of the landcover is occupied by shrimp farms (Hamilton 2020).

This level of habitat loss for feeding and roosting shorebirds may ultimately re-

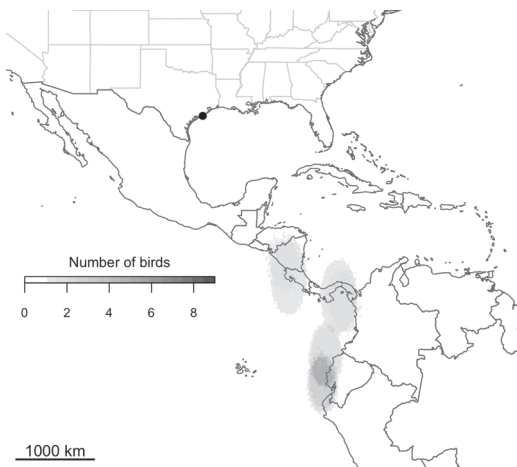


Figure 2. Estimated wintering locations shown for nine eastern Willets (*Tringa semipalmata semipalmata*) tracked with light-level geolocators. Wintering locations were estimated by taking the 95th quantile of positions estimated during the nonbreeding season but excluding the 40 d surrounding the equinoxes. Greyscale indicates where the estimated locations of wintering sites overlap in space.

duce population carrying capacity and the remaining habitats may not reflect the full natural range of habitat availability. In addition, they may be reduced in quality due to the effects of contaminants, excessive nutrients and other chemicals in shrimp farm effluent (AFSI 2015). Observations over the past five years indicate that Willets and other shorebirds wintering along the Pacific coasts of Central and South America are forced to use the dikes next to empty ponds for roosting due to loss of natural habitats from shrimp farming (Morales *et al.* 2019). This is a concern because of the use of exploding gunpowder as a non-lethal control mechanism to scare away shrimp predators such as cormorants and gulls which also roost on the dikes (Morales *et al.* 2019). Additionally, alterations associated with shrimp aquaculture have undoubtedly altered estuarine hydrology and the effects of this are unknown (Morales *et al.* 2019).

Beyond the threat of shrimp farming, coastal habitats in the neotropics are threatened by commercial, industrial, residential, and agricultural development (AFSI 2015) which may now be expanded due to changes in the Native Vegetation Protection Law in Brazil (Grasel *et al.* 2019). Shorebird hunting is also a concern in the Caribbean and northern South America (AFSIHWG 2016). There are also issues with diffuse pollutants from agriculture, aquaculture and cities which contaminate the tidal waters used for foraging by shorebirds (Morales *et al.* 2019).

These wintering ground threats may have disproportionate impacts on the Gulf-breeding eastern Willet population because our results show that individuals spend eight months of the year in wintering areas, have no significant stopover areas and make rapid direct flights between breeding and wintering sites. Furthermore, a significant portion of the population may remain at wintering sites for the entire year (Lowther *et al.* 2020). Several studies have shown that a significant portion of the juvenile population of long-distance migrant shorebirds spend the first and possibly several subsequent breeding seasons over-summering on the wintering grounds (Tavera *et al.* 2020; O'Hara *et al.*

2005). In our study, one adult over-summered on the wintering grounds subsequent to tagging but then returned to breed in following years indicating that some proportion of adult breeding willets remain on the wintering grounds as well. Martínez-Curci *et al.* (2014) documented over-summering individuals in South America of both eastern and western Willets. A primary mechanism proposed for over-summering of breeding-age adults is that poor body condition delays the timing of molt and other physiological changes necessary for northbound migration, so that increasing rates of adults over-summering may be related to degrading habitat conditions in wintering and stopover areas (Martínez-Curci *et al.* 2020).

While Atlantic Coast Willets and Texas Gulf Coast Willets do not have overlapping winter ranges, individuals we tracked did overlap with overwintering western Willets on the Pacific coast of central and South America. The presence of eastern Willets along the Pacific coast of central and South America has not previously been recognized. Current shorebird plans treat all wintering Pacific Coast Willets as westerns (National Audubon Society 2016; Agreda 2017; Morales *et al.* 2019), so an adjustment to shorebird plans is necessary to account for this new information on the distribution of eastern Willets. Distribution and population assessment of eastern and western Willets continues to be hampered by inconsistent subspecies assignment during shorebird survey efforts on the wintering grounds and stopover sites. The differing wintering locations for Texas Gulf Coast versus Atlantic Coast Willets points towards the need for distinguishing between the subspecies and subpopulations when generating population assessments and conservation planning efforts. However, we should note that we only sampled Gulf Coast Willets in Texas and more tracking data are needed from other populations breeding along the Gulf Coast to clarify the nonbreeding distribution of Gulf Coast breeding willets more generally.

Our findings suggest that eastern and western Willets mix on Pacific Coast wintering areas which offers an intriguing oppor-

tunity to disentangle the role of breeding vs wintering ground impacts on population trajectories because eastern and western Willets occupy the same wintering habitat but use distinct breeding habitats. If populations occupying the same wintering sites have different trajectories, then breeding habitat may be implicated as a driver of population declines.

These results indicate that shorebird plans and survey techniques inclusive of nonbreeding Willets on the Pacific coasts of Central and South America should be adjusted to consider the possibility of eastern Willets in these areas. Additionally, if the species is split, eastern Willet conservation efforts must include nonbreeding individuals on the Pacific coast. Also because the population size of eastern Willets seems to be in question, surveys should be conducted to determine the size of this population. Finally, additional work is needed on the Gulf Coast to determine where the dividing line is between eastern Willets spending the nonbreeding season on the Pacific coast and those spending it on the Atlantic coast.

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All applicable ethical guidelines for the use of birds in research have been followed including those presented in the Ornithological Council's "Guidelines to the Use of Wild Birds in Research" (Fair *et al.* 2010). All banding was conducted under U.S. Geological Survey banding permits 20224 and 23712.

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