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Letters

A bridge between oceans: overland migration of marine birds in a wind energy corridor

Juliet S. Lamb, David J. Newstead, Lianne M. Koczur, Bart M. Ballard, M. Clay Green and Patrick G. R. Jodice

J. S. Lamb (http://orcid.org/0000-0003-0358-3240) (jslamb@clemson.edu) and P. G. R. Jodice, Dept of Forestry and Environmental Conservation, Clemson Univ., Clemson, SC, USA. JSL also at: South Carolina Cooperative Fish and Wildlife Research Unit, Clemson, SC, USA. PGRJ also at: U.S. Geological Survey South Carolina Cooperative Fish and Wildlife Research Unit, Clemson, SC, USA. – D. J. Newstead, Coastal Bend Bays and Estuaries Program, Corpus Christi, TX, USA. – L. M. Koczur, B. M. Ballard and DJN, Caesar Kleberg Wildlife Research Inst., Texas A&M Univ.-Kingsville, Kingsville, TX, USA. – M. C. Green, Dept of Biology, Texas State Univ., San Marcos, TX, USA.

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Located at the shortest overland route between the Gulf of Mexico and the Pacific Ocean, Mexico's Tehuantepec Isthmus is a globally important migratory corridor for many terrestrial bird species. The Pacific coast of the Isthmus also contains a significant wetland complex that supports large multi-species aggregations of non-breeding waterbirds during the boreal winter. In recent years, extensive wind energy development has occurred in the plains bordering these wetlands, directly along the migratory flyway. Using recent studies of movement patterns of three marine-associated bird species – reddish egrets *Egretta rufescens*, brown pelicans *Pelecanus occidentalis*, and red knots *Calidris canutus* – from the northern Gulf of Mexico, we assess the use of the isthmus as a migratory corridor. Our data provide evidence that marine birds from the Gulf region regularly overwinter along the Pacific coast of Mexico and use the isthmus as a migratory corridor, creating the potential for interaction with terrestrial wind farms during non-breeding. This study is the first to describe migration by marine-associated bird species between the Gulf of Mexico and Pacific coast. These data contribute new information toward ongoing efforts to understand the complex migration patterns of mobile marine species, with the goal of informing integrated conservation efforts for species whose year-round habitat needs cross ecoregional and geopolitical boundaries.

Introduction

Although avian migration is a readily observable phenomenon, its outward simplicity masks a complex reality. Species, populations, and individuals vary in their migratory behavior based on a complex suite of internal and external factors that vary across space and time (Alerstam et al. 2003, Vardanis et al. 2011). At the same time, understanding the broader principles governing migration patterns and habitat connectivity is a

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critical component of conservation planning (Webster et al. 2002). As human activity alters natural environments with unprecedented rapidity, species' migratory patterns may come under threat due to changes in resource availability relative to migration timing (Saino et al. 2011), loss of crucial migratory stopover habitat (Weber et al. 1999), or physical barriers along migration routes (Masden et al. 2009). Understanding why, when, and how birds make their migratory decisions is not only a matter of biological interest, but a conservation necessity (Martin et al. 2007).

One of the most significant international bird migration corridors in the Americas is Mexico's Tehuantepec Isthmus (Cabrera-Cruz et al. 2017). Classified as an Important Bird Area (IBA) based on its concentration of three of the four major North American migratory flyways (Devenish et al. 2009), the isthmus links North American breeding habitat to Central and South American wintering grounds for millions of migratory birds each year (Winker 1995, Bildstein 2006, Cabrera-Cruz et al. 2013). The isthmus, a saddle between the Sierra Madre de Oaxaca and Sierra Madre de Chiapas mountain ranges, concentrates crosswinds from the north and creates a tailing wind for southward migrants during the boreal autumn (Romero-Centeno et al. 2003; Fig. 1). The forceful and predictable wind conditions that create favorable migratory paths have also made the region a focus of infrastructure development for wind energy. Since 2010, the southern portion of the Isthmus has experienced intense wind energy development, and in 2013 the Tehuantepec Isthmus was designated an IBA in Danger due to development-related habitat deterioration (BirdLife International 2015).

In addition to its importance as a migration corridor, the Tehuantepec region is also a key wintering area for waterbirds of unknown breeding origin. The Lagunas del Istmo, a vast, remote wetland complex on the Pacific coast of the isthmus, supports large numbers of shorebirds, wading birds, and nearshore seabirds representing a variety of species (Aid et al. 1997, Rioja-Paradela et al. 2014). Since many of the nearest breeding aggregations of coastal birds in the region are located along the coast of the Gulf of Mexico, observers have suggested that marine-associated bird species may cross the Tehuantepec Isthmus to winter in the Lagunas (Binford 1989). However, migration of marine birds between the Gulf of Mexico and the Pacific coast has yet to be directly quantified. It is important to understand movement patterns and habitat use in the region in order to estimate the extent to which individuals may be exposed to collision risk at new and proposed wind turbine sites

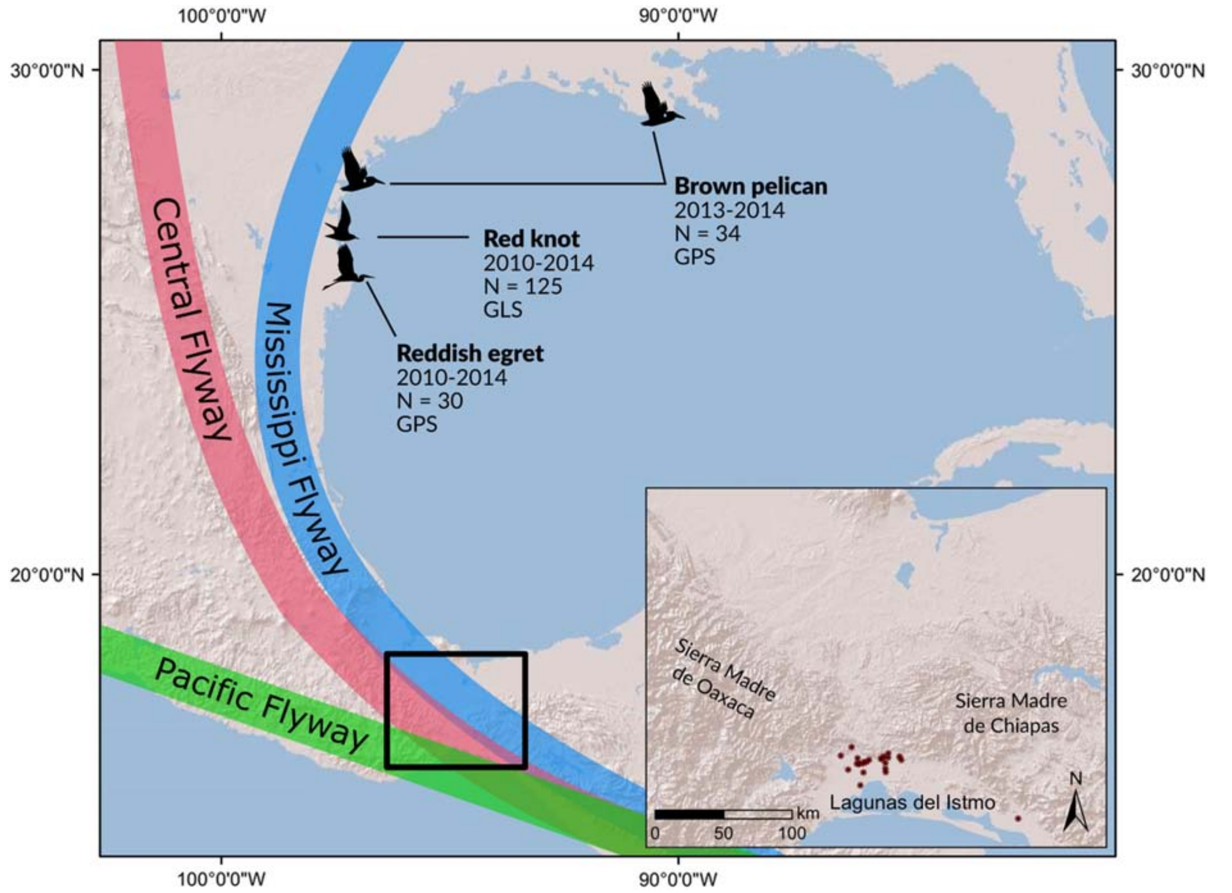

Figure 1. Capture locations and dates of individual tracking studies in the northern Gulf of Mexico (2010–2014), relative to the Isthmus of Tehuantepec (inset). Wind farm locations are indicated by brown stars in the inset map.

(Furness et al. 2013), which could affect mortality rates and, thus, long-term population parameters in long-lived marine birds (Croxall et al. 2012).

Mark–recapture data from individual leg bands (Calvo and Furness 1992) provide one means of illuminating connectivity between populations and habitats; however, these data alone offer limited information about when or how individuals travel between locations (Gillespie 2001), and the difficulty of re-encountering marked individuals in remote, inaccessible areas may result in underestimation of key habitat areas and risk factors for marine birds (Montevecchi et al. 2012). Recently, miniaturized tracking technologies have allowed collection of year-round individual movement data for many species whose nonbreeding movement patterns were previously unknown (Wakefield et al. 2009). Individual tracking of long-distance migrants has helped to reveal complex migratory patterns that cross geopolitical and ecoregional boundaries (Webster et al. 2002, Jodice and Suryan 2010), to elucidate sources and patterns of adult mortality (Montevecchi et al. 2012, Klaassen et al. 2014), and to identify previously unknown migration routes (Gillespie 2001). Although sample sizes from telemetry studies are often small, they can be combined with mark–recapture data to yield important insights into population connectivity and conservation of wide-ranging marine bird species.

To determine the extent to which marine birds migrate between the Gulf of Mexico and the Pacific coast, and whether movement pathways intersected with wind energy installations, we compared band encounter records and individual tracking data collected from marine-associated waterbird species in the northwestern Gulf of Mexico (Garrison and Martin 1973). We focused our analysis on the only three species in the region for which both mark–recapture records and year-round tracking data were available, each of which also represented a distinct taxa group: a wading bird (reddish egret *Egretta rufescens*), a nearshore seabird (brown pelican *Pelecanus occidentalis*), and a shorebird (red knot *Calidris canutus*). All three species are of conservation concern: both the reddish egret and red knot are listed as Near Threatened by the IUCN Red List, and the brown pelican was listed as Endangered under the United States Endangered Species Act until 2009 and is currently a species of concern at the state level. Our study provides insight into risk factors along a previously unknown migration route for marine birds, as well as assessing the comparative value of marking and tracking to evaluate movement pathways and risk factors for migratory marine birds.

Methods

Study area

Two hundred kilometers wide at its narrowest point, the Tehuantepec Isthmus represents the shortest overland distance between the Gulf of Mexico and the Pacific Ocean. The northern portion of the isthmus is located in the state of Veracruz, Mexico, and the southern portion, including the Lagunas del Istmo, in the states of Oaxaca and Chiapas, Mexico. Between 2010 and 2014, wind infrastructure in the region has increased from 225 turbines in five complexes to 1451 turbines in sixteen complexes (Wind Power 2014). Wind energy installations in the area are primarily concentrated in a 3000 km^2 area around the town of Juchitán de Zaragoza in Oaxaca (Fig. 1). The area currently accounts for approximately 84% of Mexico's total wind energy production (Wind Power 2014). The Lagunas del Istmo cover an area of ca 785 km^2 on the Pacific coast of the Isthmus over seven principal lagoons.

Mark–recapture

For the three focal species (Table 1), we accessed data on individual leg band (ring) re-encounters from the U.S. Bird Banding Lab (BBL) database, which contains records of birds marked from 1973 to 2017. We determined the number of individuals banded in northwestern Gulf Coast states (Alabama, Mississippi, Louisiana, and Texas) and later re-encountered along the Pacific coast of the Tehuantepec isthmus, as a percentage of all individuals from the same region re-encountered. Each individual was counted only once; thus, we excluded multiple re-encounters of the same individual. For red knots, small teams of 3–5 biologists also conducted opportunistic resighting of uniquely-numbered leg flags during annual visits to the Lagunas del Istmo in January and February of 2012 through 2016. Resighting efforts were focused primarily on the northwestern edge of Laguna Superior (Fig. 1), near the town of Santa Maria Xadani.

Individual tracking

We conducted Global Positioning System (GPS) tracking of breeding reddish egrets and brown pelicans captured at nests during incubation and early chick-rearing in the northwestern Gulf of Mexico (Fig. 1). We fitted individuals with solar-powered Platform Terminal Transmitters (GPS-PTTs) (reddish egrets: 22 g, Microwave Telemetry, n = 30; brown pelicans: 65 g, GeoTrak, n = 34). GPS-PTTs collect precise locations on a regular schedule using global

Table 1. Number of individuals of target species originally banded in the northern Gulf of Mexico and later resighted. Percentages of individuals involved in movements between the Gulf of Mexico and the Pacific are calculated as a percentage of total resightings.

Species	Total banded	Total resighted in Pacific	Proportion of all resights
Reddish egret	2211[1]	6	0.08
Brown pelican	20432[1]	14	0.01
Red knot	553[2]	5	0.01

[1]Individuals banded in the northwestern Gulf of Mexico (United States: Texas, Louisiana, Mississippi, and Alabama), 1973–2017. Source: U.S. Geological Survey Bird Banding Lab.
[2]Individuals banded with colored leg flags, Texas only.

positioning system satellite networks; locations are then stored on board the device and transmitted every few days to the Argos satellite network (Witt et al 2010). Transmitters were attached using backpack-style, Teflon ribbon harnesses. Transmitters collected 6–12 locations d^{-1} and locations were downloaded weekly from the Argos system (argos-system.org). Horizontal error of GPS locations was approximately 3–5 m. Since vertical error of GPS locations is generally much larger, however (Ladetto et al. 2000), we chose not to use altitude measurements obtained from GPS-PTTs. We estimated migratory routes using straight-line distances between consecutive GPS points, and inferred missing points using bilinear interpolation. We defined 'wind energy installations' as all wind farm areas included in the Wind Power (2014) database. We used ArcGIS 10.2 (ESRI) to measure distances between migratory routes (represented as lines) and wind energy installations (represented as polygons).

Additionally, we conducted Global Location Sensor (GLS) tracking of red knots staging in the northwestern Gulf of Mexico (Fig. 1). GLS tracking systems sense and store information on light levels, which can then be interpreted to estimate latitude and longitude based on sunrise and sunset times (Phillips et al. 2004). A total of 553 red knots were captured on Mustang and North Padre Island (Texas) beaches using cannon nets between fall 2009 and fall 2014. Each bird was banded with a U.S. Geological Survey metal ring on one leg and a lime green plastic flag with a unique alphanumeric code on the opposite leg. Light-level geolocators (BAS MK10 and MK12, and Migrate Technology Intigeo-W65, two locations d^{-1}) mounted on a small leg flag were attached to the upper leg opposite the coded flag on 125 individuals. Error of raw GLS locations was $\leq$ 200 km. We conducted initial data analysis using software provided by GLS manufacturers, with additional refinement of locations using methods described in Porter and Smith (2013) to reduce location error. Since the reduction in error provided by these adjustments is unknown, we considered GLS trajectory estimates to be accurate to within 200 km.

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.1m12h> (Lamb et al. 2017).

Results

Mark–recapture

Of the three focal species, six Gulf-banded reddish egrets and 14 Gulf-banded brown pelicans were later encountered on the Pacific coast of the isthmus within 500 km of its narrowest point (Fig. 2), representing 8 and 1% respectively of all reported re-encounters of individuals of each species from the Gulf of Mexico. Five uniquely marked red knots from the Gulf of Mexico (1% of all individuals banded) were reported from Laguna Superior between 2012 and 2016 (Fig. 2). Two individuals were observed in the Lagunas in two separate years: one in 2012 and 2015, and another in 2013 and 2016.

Individual tracking

Of 30 marked reddish egrets, five (17%) crossed the Tehuantepec Isthmus and wintered along the Pacific coast in Oaxaca and/or Chiapas (Fig. 3a). Three individuals were tracked for a single fall migration and two were tracked for three complete migratory cycles, for a total of 15 migratory trips across the Isthmus. Distance to the nearest wind energy installation from the estimated migratory path ranged from 0 to 120 km ($\bar{x}=16 \pm 33$ km), and three of the five individuals passed through wind energy installations on nine occasions.

Of 34 brown pelicans tracked through a full migratory cycle, two (6%) wintered along the Pacific coast of the Tehuantepec Isthmus (Fig. 3b), including one breeder from Louisiana tracked through a single annual cycle, and one from Texas tracked through two annual cycles. Migratory routes for both pelicans crossed the isthmus within a longitudinal span of 250 km from its narrowest point, and each individual crossed wind energy installations on at least one route. Distance to the nearest wind energy installation from the estimated migratory path ranged from 0 to 59 km ($\bar{x}=27 \pm 30$ km).

Of 26 red knots from which geolocators were recovered between fall 2010 and spring 2014, four (15%) wintered along the Pacific coast of Central America and South America, and all four crossed Mexico during migration. The margin of error of geolocator data ($\leq$ 200 km) is too wide to identify precise migratory pathways; however, one individual, which stopped for five days in the area of the Lagunas del Istmo, likely crossed the Isthmus on northbound migration from wintering habitat in Chile. Flight tracks for the remaining individuals indicate crossings slightly east of the isthmus and as far as the Yucatan region (Fig. 3c). Mean distance to wind energy installations from the estimated migration tracks was 320 km.

Timing and conditions of migration

Fall migrations for the three focal species occurred from September through December, with average dates between late October and late November. Spring migrations occurred from March through May, with average dates falling between late March and early April (Table 2). Among reddish egrets, travel through the isthmus occurred both during daylight hours (23% of trips) and overnight (77% of trips). Each overland migration consisted of a single trip without apparent stopovers. Brown pelicans traveled only during daylight hours: fall migrations occurred within a single day, while spring migrations spanned 2–3 d of daylight travel and overnight stops. Reddish egrets and brown pelicans that passed through wind energy installations did so either at the end (fall) or beginning (spring) of their migration flights (Fig. 3).

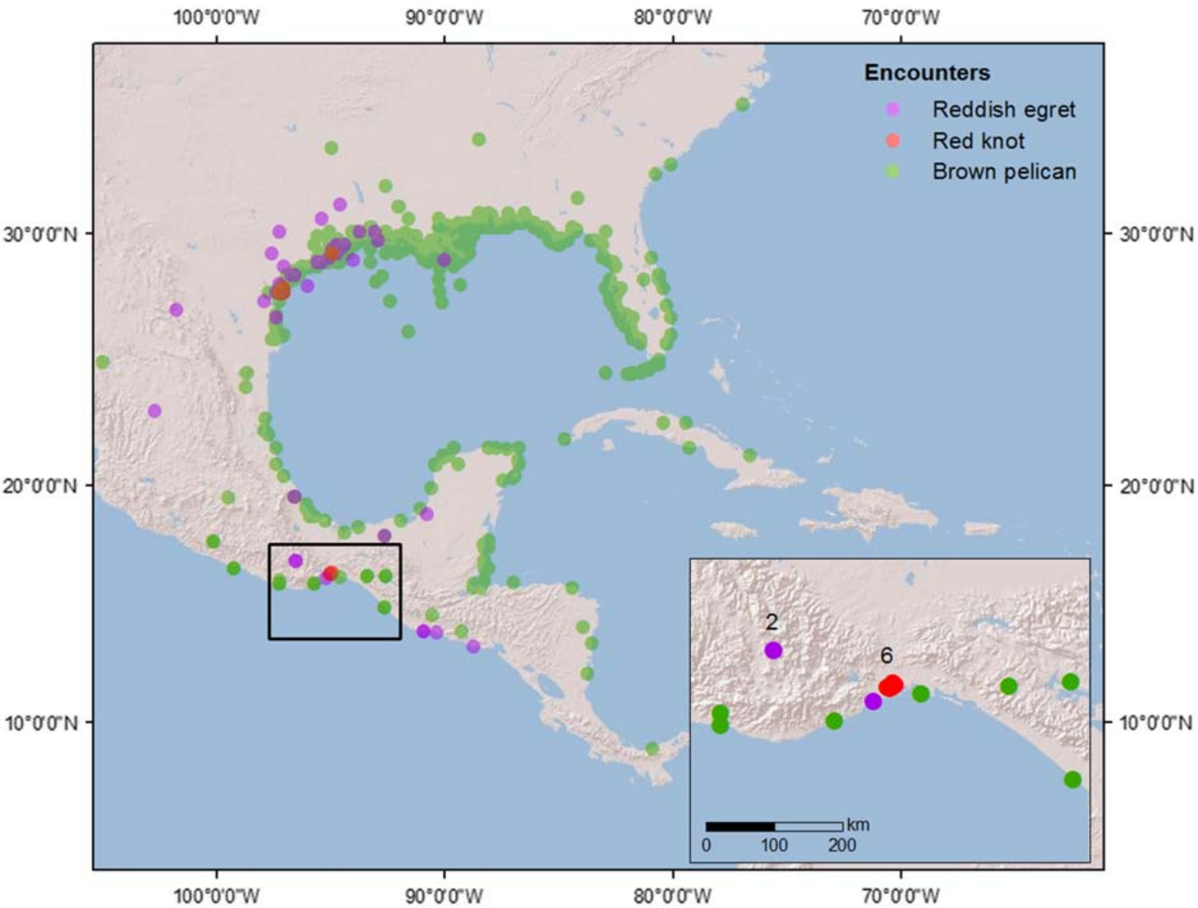

Figure 2. Re-encounter locations of reddish egrets, brown pelicans, and red knots originally marked in the northwestern Gulf of Mexico (USA), 1973–2017. Inset shows detailed locations in the Laguans del Istmo area, with numbers indicating the total number of overlapping individuals.

Red knots crossed the isthmus region in the midst of nonstop, multi-day migration flights; the specific timing of crossings cannot be determined from geolocator data. Fall migrations of reddish egrets occurred on days with wind speeds exceeding mean monthly values by 39%, while brown pelicans conducted fall migrations under lower-than average wind speeds (–58%). Migrations for all other seasons and species fell within 10% of average wind speeds (Table 2).

Discussion

Although the Tehuantepec Isthmus has previously been identified as a potential migration route through which marine bird species breeding on the east coast of North America might cross to the Pacific (Binford 1989), regular inter-oceanic migrations of marine birds across Central America have not previously been described, with the exception of a single red-necked phalarope *Phalaropus lobatus* tracked from Scotland (Smith et al. 2014). Using a combination of mark–recapture and tracking data from three marine bird species, we found that 1–17% of marked individuals originally encountered in the Gulf of Mexico commuted over land to the Pacific Ocean. The proportion of each species involved in inter-oceanic movements ranged from 1 to 8% based on raw mark–recapture data and 6 to 17% based on individual tracking data. Molecular data suggest that Central America is a significant barrier to gene flow for marine birds (Steeves et al. 2005, Friesen et al. 2007); however, the use of this migratory route suggests that Atlantic and Pacific populations may overlap in non-breeding areas.

We found that a combination of bird-borne telemetry and mark–recapture data provided more complete insights into movement patterns than either technique alone. The two methods have complementary strengths: mark–recapture data can be collected from large numbers of individuals, but are highly restricted in space and time, while bird-borne telemetry offers a continuous time series of data from a small subset of individuals across their entire ranges (Hazen et al. 2012). Like previous work in marine systems (Montevecchi et al. 2012), our study suggests that estimates of the percent of a population involved in long-distance movements based on mark–recapture data may be lower than those generated through individual tracking; however, given the differences

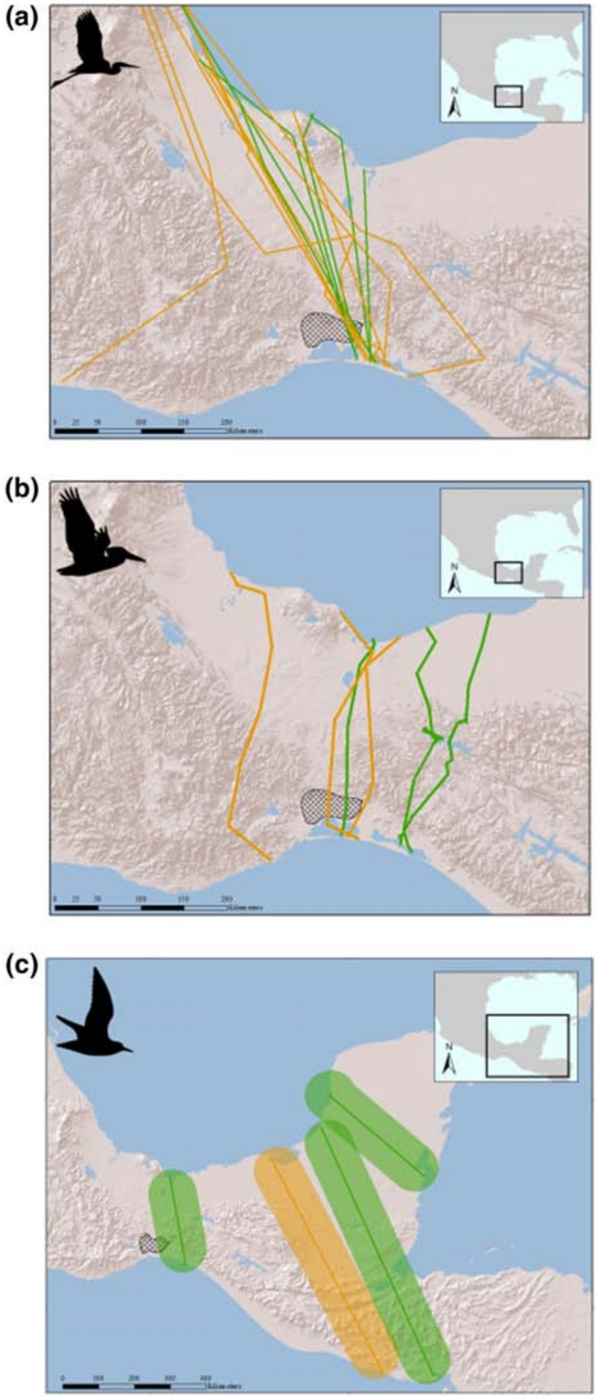

Figure 3. Migration routes of (a) reddish egrets (n = 5), (b) brown pelicans (n = 2), and (c) red knots (approximate; n = 4) in the Tehuantepec Isthmus, Mexico, 2010–2015. Orange routes are fall migrations; green routes are spring migrations; hatched area represents wind energy installations.

in detectability and sample sizes between the two techniques, further study is needed to determine which method best reflects population-level movement patterns.

Our data suggest that the proportion of individuals of the three target species involved in inter-oceanic migration is low relative to overall population size. However, anomalous migratory routes can serve important roles in population health and persistence by facilitating genetic mixing (Liedvogel et al. 2011). Dispersive migration may also help to distribute risk across the population (Johnson and Gaines 1990), and individuals in remote wintering areas may serve as a source of re-colonization following environmental catastrophe (King et al. 1985). A full understanding of complex migration pathways is also critical to estimating how risks such as disease transmission and spatially heterogeneous anthropogenic stressors are distributed across populations (Martin et al. 2007), as well as to develop conservation strategies for preserving species with complex migratory movements in the face of global change (Martin et al. 2007).

Our study also establishes that the migratory paths of at least three species of marine birds overlap spatially with terrestrial wind energy installations in the Tehuantepec Isthmus. Our analysis is focused on coastal marine bird species that breed or stage in the Gulf of Mexico; however, recent data from Arctic-breeding semipalmated sandpipers *Calidris pusilla* suggest that other species typically associated with coastal migration routes may be using the Tehuantepec Isthmus to move between Atlantic and Pacific coastal flyways (Brown et al. 2017). It is important to note that, while tracking data can suggest the potential for individuals to interact with terrestrial features along their movement paths, it does not prove that interaction is taking place (Drewitt and Langston 2006, Furness et al. 2013). Given that our data do not include flight altitudes, we are able to establish only macro-scale overlap between migrating birds and wind turbines. Establishing macro-scale interaction represents only an initial step in identifying locations and extent of potential conflict, with further targeted research needed to determine whether micro-scale interaction is likely. Furthermore, migratory birds in the Tehuantepec region may adjust their routes to avoid turbines (Villegas-Patraca et al. 2014, Cabrera-Cruz and Villegas-Patraca 2016), incurring energetic costs even in the absence of direct interaction (Masden et al. 2010).

While the phenology of marine bird migration through the Tehuantepec Isthmus was similar to that of raptors and other passage migrants previously observed in the region (Villegas-Patraca and Herrera-Alsina 2015, Cabrera-Cruz et al. 2017), movement patterns of the marine birds included in this study differ in several key respects from those of previously observed migrants. Two of the tracked species (reddish egrets and red knots) conducted all or part of their migrations at night, a strategy common to other herons and egrets (Contreras 2013), which may account for their low detectability in visual studies. Recent work using marine radar has improved understanding of nocturnal migration in the region (Villegas-Patraca et al. 2014); however, unlike diurnal observations, radar data cannot identify nocturnal migrants to species. In addition, coastal marine birds remained resident in the Tehuantepec Isthmus for long periods of time (up to six months), placing them at greater risk of collision-related mortality than passage migrants with shorter occupancy times (Krijgsveld et al. 2009, Villegas-Patraca et al. 2014).

Table 2. Timing and conditions of migration across Mexico of three marine-associated bird species from individual tracking data, 2010–2014.

Species	Season	$N_{individuals}$	$N_{migrations}$	Mean crossing date	Mean distance from turbines (km)	Absolute wind speed (km h^{-1})	Wind speed relative to monthly mean
Reddish egret	Fall	5	8	20 October	23.7	11.4	+39%
	Spring	2	6	6 April	1.9	7.3	+2%
Brown pelican	Fall	2	3	30 November	17.2	3.0	–58%
	Spring	2	3	19 March	20.6	7.0	+10%
Red knot	Fall	1	1	10 November	125	7.1	–3%
	Spring	3	3	3 April	388	5.9	–10%

Local observations and short-term tracking of overwintering waterbirds in the Lagunas del Istmo would help to clarify how resident habitat use affects collision risk in these species.

Mitigation strategies to reduce impacts of wind turbines on birds, including changing operations schedules, reducing rotor speeds, and improving turbine visibility (Drewitt and Langston 2006), require knowledge of both distribution and biology of at-risk species in the region of the installation. Wind turbine mitigation efforts in the Tehuantepec Isthmus have previously targeted Swainson's hawks *Buteo swainsoni* (Kochert et al. 2011) and Franklin's gulls *Larus pipixcan* (Villegas-Patraca and Herrera-Alsina 2015); however, the migratory waterbirds in our study differ from these target species in their migration patterns, flight behavior, and residence times. Moreover, risk factors of wind turbines are highly variable among avian taxa and depend on flight behavior, body size, and wing loading (Herrera-Alsina et al. 2013). In order to accurately evaluate collision risk for the species included in this study, further information is needed on micro-scale flight altitude and behavior throughout the residence period.

Conclusions and future directions

Our study uses individual movement data to identify a previously unknown waterbird migration route through the Tehuantepec Isthmus of Mexico, highlighting the importance of this region as a migration corridor between the Gulf of Mexico and the Pacific Ocean. In the Tehuantepec region, tensions between local communities and outside developers have inhibited implementation of on-the-ground monitoring and research that otherwise might inform local conservation planning (Juárez-Hernández and León 2014). Individual tracking, which does not require on-site observers, can be used to justify and refine targeted observation efforts.

Our study also provides initial evidence that migratory paths of marine-associated birds may place them at risk of encountering inland wind turbines. Mapping key migration routes for non-breeding marine birds in the Isthmus is a first step in evaluating micro-scale overlap of migration routes with turbine sites, and future capture and tracking of non-breeding individuals and observations of winter habitat use in the Tehuantepec Isthmus could clarify both winter home range characteristics and collision risk of non-breeding waterbirds using this region. This study contributes to an enhanced understanding of the means by which migratory populations may be affected by non-breeding stressors distant from their breeding locations.

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