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Precise direct tracking and remote sensing reveal the use of forest islands as roost sites by Purple Martins during migration

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ABSTRACT. Direct tracking methods in combination with remote sensing data allow examination of habitat use by birds during migration. Species that roost communally during migration, such as some swallows, form large aggregations that can attract both avian and terrestrial predators. However, the extent to which they might use patchy habitats that could reduce predation risk during migration is unknown. We tested the hypothesis that Purple Martins (*Progne subis*) use forest islands (patches of suitable forest habitat surrounded by unsuitable habitat) as roost sites during migration between breeding sites in North America and overwintering sites in South America. We used high-precision (< 10 m), archival GPS units deployed and retrieved during the 2015 and 2016 breeding seasons, respectively, at 12 colonies located across eastern North America. We found that Purple Martins roosted in forest islands more often than expected based on availability during both spring and fall migration. Despite an apparent association with urban habitats by Purple Martins based on observational and radar data in North America during the fall, the roost locations we identified during spring and fall migration were not more closely associated with urban areas than random locations. The use of forest islands during both spring and fall migration suggest that Purple Martins may use these habitats to reduce predation risk during migration. Our results suggest that some species of birds may use similar habitats as stopover sites during migration and that patches of forest habitat may be important conservation targets for Purple Martins and other species. Identifying habitat use during migration represents an important advance in support of full annual-cycle conservation of Purple Martins and other migratory species with declining populations.

RESUMEN. **Rastreo directo preciso y sensores remotos revelan el uso de islas de bosques a través de las migraciones de primavera y otoño por parte de *Progne subis***

Métodos de rastreo directo en combinación con información de sensores remotos permiten examinar el uso de hábitat por las aves durante la migración. Especies que usan dormideros comunales durante la migración, como es el caso de algunas golondrinas, forman congregaciones grandes que pueden atraer aves depredadoras así como depredadores terrestres. Sin embargo, el grado en el cual pueden usar los hábitats fragmentados que pueden reducir el riesgo de depredación durante la migración hasta el momento es desconocido. Pusimos a prueba la hipótesis que *Progne subis* usa islas de bosques (parches adecuados de hábitat boscoso rodeado por hábitat inadecuado) como dormideros durante la migración entre los sitios de reproducción en Norte América y los sitios de invierno en Sur América. Usamos unidades de GPS de alta precisión (< 10 m) los cuales fueron instalados y recuperados durante las temporadas reproductivas del 2015 y 2016, respectivamente, en 12 colonias ubicadas a través del este de Norte América. Encontramos que *Progne subis* duerme en islas de bosques con mayor frecuencia que lo esperado basado en la disponibilidad durante las migraciones de primavera y otoño. A pesar que existe una asociación aparente con hábitats urbanos por parte de *Progne subis* basado en datos de observaciones y de radar en Norte América durante el otoño, las localizaciones de los dormideros que identificamos durante las migraciones de primavera y otoño no estuvieron mas estrechamente asociadas con áreas urbanas que localidades seleccionadas por azar. El uso de las islas boscosas durante las migraciones de otoño y primavera, sugiere que *Progne subis* puede usar estos hábitats para reducir el riesgo de depredación durante la migración. Nuestros resultados sugieren que algunas especies de aves pueden usar hábitats similares como sitios de parada durante la migración y que los fragmentos de bosque pueden ser objetivos importantes para la conservación de *Progne subis* y otras especies. La identificación del uso del hábitat durante la migración representa un avance importante en el apoyo para

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la conservación del ciclo anual completo de *Progne subis* y otras especies migratorias con poblaciones en disminución.

Key words: archival GPS, biologging, direct tracking, *Progne subis*, stopover ecology

Many species of migratory songbirds are experiencing steep population declines, but our understanding of contributing factors remains poor (Sillett et al. 2000, Sillett and Holmes 2002, Hostetler et al. 2015, Marra et al. 2015). A primary limitation in the conservation of migratory species throughout the annual cycle has been the difficulty in identifying habitats used during migration (Buler et al. 2010, Thorup et al. 2017). Our understanding of migratory stopover habitat has generally been limited to regional snapshots along migratory routes (Paton and Matthiopoulos 2016). With the onset of the "golden-age of biologging" (Wilmers et al. 2015), lightweight tracking devices that provide precise locations (< 10 m) are now available for small songbirds. In combination with detailed habitat data derived through remote sensing, investigating the habitats used by long-distance migrants across the annual cycle is now possible (Hallworth and Marra 2015, Siegel et al. 2016, Fraser et al. 2017, 2018a, 2018b).

For colonial-breeding species, large aggregations provide safety in numbers, but are also more conspicuous to predators, and thus, breeding colonies may favor isolated or patchy habitats that provide some protection by reducing access for arboreal or ground-based predators (Ocampo and Londoño 2015, Natusch et al. 2017). However, migration may pose the greatest survival risk for songbirds (Sillett and Holmes 2002) so the use of stopover habitat during migration should also favor safe havens while maximizing refueling potential (Alerstam 2011). For colonial-roosting birds, the use of forest islands (a patch of appropriate forest habitat surrounded by non-forest habitat) for stopover or roost sites could provide protection from predators, especially during migration when individuals may be exposed to hazards in unfamiliar terrain (Alerstam and Lindström 1990, Sillett and Holmes 2002, Berthold et al. 2003). However, the possible use of forest island sites by communally roosting species during migration has not been investigated.

Purple Martins (*Progne subis*) are long-distance migratory songbirds that migrate between North and South America annually (Fraser et al. 2012, Brown and Tarof 2013). During the winter, Purple Martins gather in large roosts of thousands of individuals that most frequently occur on islands (land surrounded by water, Fraser et al. 2017). Most of what is known about habitats used for roosting by Purple Martins during migration is anecdotal, and they have often been observed roosting in urban areas and towns (Brown and Tarof 2013). Direct tracking data show that they also use more remote areas far from human observers during migration (Fraser et al. 2013a,b, 2017). Using weather surveillance radar data, a recent study of roost sites used by Purple Martins after breeding in North America revealed that most were associated with croplands and urban areas, but some were also in forests and habitats associated with water (Bridge et al. 2016). There has been no quantification either of roost habitats used by Purple Martins during spring migration or of habitats used for roosting outside of eastern North America. Additional study is therefore needed to quantify and integrate patterns of habitat use during the spring and fall migration of Purple Martins.

We used GPS units that provided locations at a fine-scale (< 10 m) in combination with land-cover data derived through remote sensing to examine habitat use by roosting Purple Martins during migration. Our objectives were to examine habitat use during both spring and fall migration to test the hypothesis that Purple Martins more frequently use forest island habitats as roost sites, and determine whether roosts were located in areas of urban development and water as suggested by observational data and radar data during fall migration in North America (Brown and Tarof 2013, Bridge et al. 2016).

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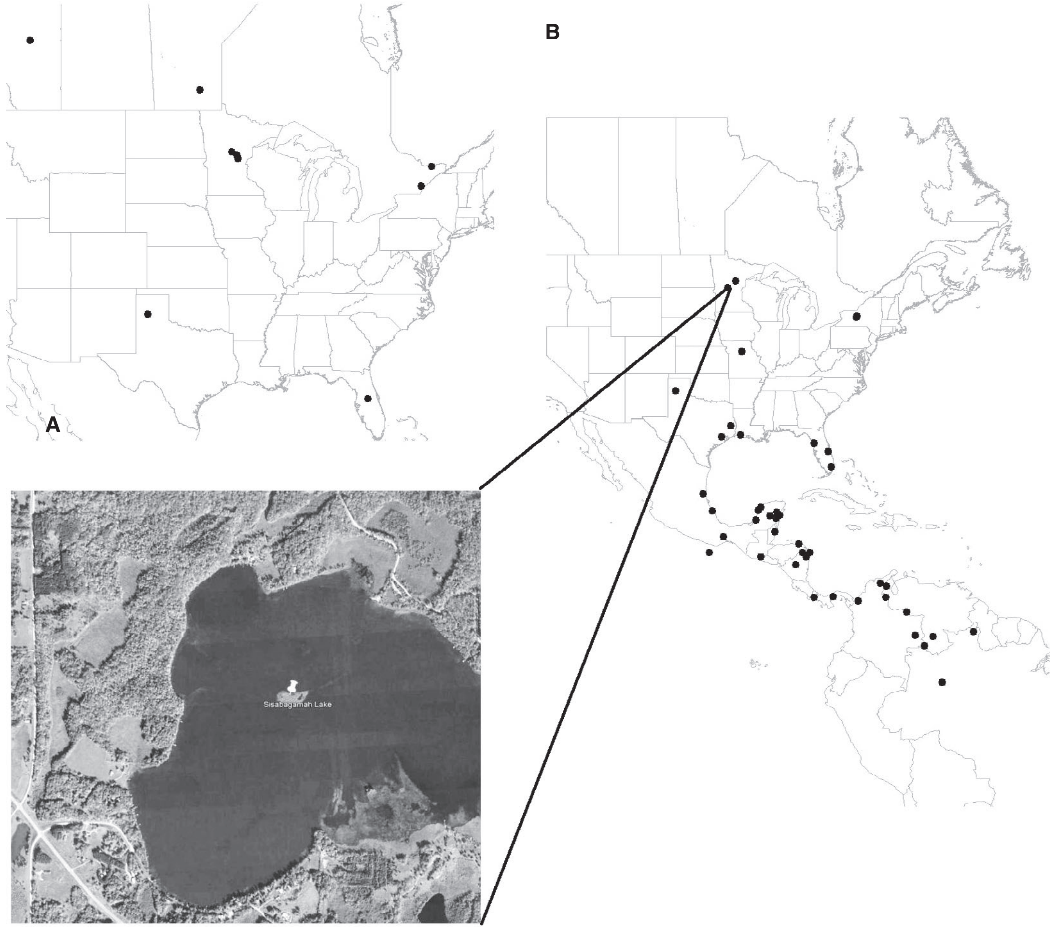

Fig. 1. Location of (A) nine breeding colonies and (B) 49 migratory roost locations of Purple Martins. The inset map shows the location of a migratory roost site on an island in Minnesota.

METHODS

Purple Martins (mean mass = 51.8 ± 4.6 g) were captured using drop-door traps at 12 breeding colonies (Fig. 1). We deployed 271 archival GPS tracking units (PinPoint 10, 1.1 g, Lotek Wireless, Fig. 1) on martins using a back-pack style harness made with Teflon ribbon (Stutchbury et al. 2009). Units were preprogrammed (PinPoint host software, Lotek ver. 2.11.2.9) to either collect locations at midnight every 15 days during the non-breeding period (postfall departure date and prespring arrival date; Fraser et al. 2017) or a location weekly at midnight (2015–2016). In 2016, 52 units were programmed to take up to 10 points every 15 days at midnight during spring migration (February–May).

Birds were considered migrating (fall or spring) if outside of their breeding colonies or overwintering roosts and using breeding-population-specific movement patterns determined with geolocators (Fraser et al. 2017). The timing of fall and spring migration, and the amount of time spent in non-breeding areas, varies with breeding location and was previously determined using light-level geolocation data (Fraser et al. 2013a, 2013b [departure dates vary between ordinal dates 13–134 in spring and between ordinal dates 181–272 in fall]). These known timing patterns for each breeding area were used to determine the timing of GPS schedules most suited to each colony. For analysis, migration points were divided into three regions, North, Central, and South America, because land cover changes across these three regions.

To address our main objective of habitat use by Purple Martins during migration, we applied a used versus available framework (Arthur et al. 1996), comparing locations used by Purple Martins to those available for use. For each migration point used, five random available points were generated within a 325-km radius half circle of the point, where the half circle was oriented such that a bird migrating north would have the half circle pointed to the south. Random points could occur anywhere within the half circle. We chose 325 km because it is half of the average daily movement (650 km) of Purple Martins tracked with geolocators during migration (Fraser et al. 2013a,b). Thus, 325 km conservatively included the range of available habitats that could have been selected as roost locations.

We considered a 5:1 ratio of available to used points adequate to reduce bias and ensure convergence of parameter estimates (Northrup et al. 2013). We recorded the distances to open water and the nearest urban development (including road intersections and small towns with a population size < 100) and whether the point (20-m diameter patch around the point) was a forest island based on Google Earth Pro imagery. We defined a forest island as a patch of forest habitat at least 1000 m from other forest habitat and < 11,000 m^2 in size. We used 1000 m as a conservative estimate of a distance that would limit arboreal predators from easily accessing roost locations (particularly when water/wetland was present). We used < 11,000 m^2 as a cut-off to encapsulate the lower end of the distribution of patch sizes in our used vs. unused data set, thus reflecting the smallest patches.

We compared used versus available points using a mixed effect model. We included individual, nested within region (North, South, or Central America), as a random effect and included habitat indices as fixed effects in our analyses. These habitat indices were distance to urban development, distance to open water (nearest body of water or river of any size visible on Google Earth imagery), and whether a point was on a forest island. We ran the binomial mixed effect models (family = binomial) using the “lme4” package in R (Bates et al. 2015, R Core Team 2017; “lme4” version 1.1-13, R version 3.4.0). We used Nakagawa et al.’s (2012) method for obtaining an *r*-squared from a generalized linear mixed effects model on our model using the “MuMIn” package in R (R Core Team 2017, Barton 2018).

RESULTS

In the year following deployment, we resighted 49 birds with GPS units at 12 breeding sites (mean = 3.3 tags per site, range = 1–6). Of those 49, 28 (19 male and nine female) GPS units were retrieved with data for both spring and fall migration, four were retrieved, but contained only data for the overwintering period (not migration), 12 retrieved tags had failed, four tags were spotted, but not retrieved, and one harness failed and the individual returned without its tag. Return rates of birds with GPS units varied by year and breeding colony location, but were similar to return rates in the same years and colonies of Purple Martins with geolocators (Fraser et al. 2017, Table S1) that have been found to be similar to those of birds that were only banded (Fraser et al. 2012). As such, we infer that the relatively low return rate of GPS units reflected low survival overall in 2015–2016 at these colonies.

We identified 48 roost locations from the 28 tags with migration data (Table S1). Forest patches at the used and available locations were between 50 and 60,000 m^2 in size (mean = 4998 m^2, median = 1000 m^2). Our model showed that Purple Martins used forest islands more frequently than they occurred on

Table 1. Binomial mixed model results comparing used and available Purple Martin migration habitat. Positive beta values represent positive use, where a resource is used disproportionately more than it is available. Negative beta values represent negative use, where a resource is used disproportionately less than it is available.

Fixed effect	β	Standard error	*P* value
Habitat island	3.40	0.66	< 0.001
Distance to water	−0.87	0.37	0.02
Distance to town	−0.10	0.20	0.62

Table 2. Characteristics of random points versus points used by Purple Martins during spring and fall migration. Used points were identified using GPS tracking units. Summary statistics are provided for continuous variables, and counts per category for categorical variables.

	Patch area (m^2)	Distance to water (m)	Distance to town (m)	Habitat island	
Random					
Minimum	3000	0	0	No	203
Quartile 1	4950	955	4900	Yes	3
Median	844.5	6460	7900		
Mean	1532.2	13,287	14,596		
Quartile 3	1792.5	22,135	13,000		
Maximum	3900	97,000	150,000		
Points not on a patch	202				
Used					
Minimum	50	3	0	No	29
Quartile 1	450	27	1700	Yes	19
Median	550	574	3750		
Mean	1082	3779	12,093		
Quartile 3	1300	2225	10,250		
Maximum	6000	37,000	100,000		
Points not on a patch	19				

the landscape ($\beta = 3.40$, SE = 0.66, $P < 0.001$, Table 1) and that they roosted in areas farther from water ($\beta = -0.87$, SE = 0.37, $P = 0.02$). The model had a marginal r-squared of 0.38 (variation explained by fixed variables), and a conditional r-squared of 0.38 (variation explained by the fixed and random variables). Although we did not detect birds using roost sites over multiple nights, we were limited in our ability to detect repeated use of roost sites because we only sampled locations every 15 days. We found that most of the 48 roost sites were in forest habitat (75%), but Purple Martins also roosted in agricultural areas (13%), urban areas (8%), wetlands (2%), and cut forests (2%) (Table 2).

DISCUSSION

We found that Purple Martins disproportionately used forest islands at roost sites during migration. Combined with recent data about habitat use in overwintering areas that also demonstrated selection for isolated patches (Fraser et al. 2017), our results suggest that the use of remote forest habitats may reflect a year-round pattern of habitat use by Purple Martins. Forest islands may sometimes be used because they are the only habitat available, such as in urban landscapes. However, we found that Purple Martins often used isolated forest patches along their migratory routes, both when traveling through more developed regions as well as in more isolated, undeveloped locations. These results suggest that the use of forest patches may reflect a more general habitat preference and is not due to the general availability of these habitats. This conclusion is also supported by our results showing that Purple Martins disproportionately used isolated forest islands relative to the frequency at which they occurred in the landscape. The use of island-like habitats may afford enhanced protection from predators, while nearby open spaces may provide suitable foraging areas for these aerial foragers.

Observational data and anecdotal accounts suggest that Purple Martins commonly roost or stopover in areas near human development (Brown and Tarof 2013). However, we found no association with developed areas by Purple Martins during spring and fall migration. Roost locations we identified were commonly in more remote locations (e.g., small island in a lake in Minnesota; inset Fig. 1), far from human settlements where observations would be less likely. Similarly, direct tracking using GPS tags revealed that roost sites in overwintering areas were most often associated with island-like habitats near water, with few (< 9%) roost sites in human-developed areas (Fraser et al. 2017).

Purple Martins, unlike many migratory songbirds, are colonial. Coloniality in birds may have evolved as an antipredator strategy, whereby birds roost in large numbers to reduce individual predation risk (Robinson 1985, Rolland et al. 1998, Natusch et al. 2017), even though coloniality also increases the detectability of roosts by predators. As such, habitat use by colonial birds may favor more passive antipredator defenses (Danchin and Wagner 1997, Lima 2009, Natusch et al. 2017). Some colonial birds use isolated patches of nest-site habitat such as small river islands or forest patches to reduce predator access (Natusch et al. 2017). Such habitat use during breeding may be similar to what we found during migration, with Purple Martins more common in patchy habitats isolated from more contiguous forest by more open habitat. Thus, we have expanded the investigation of the use of these isolated patchy and forest islands to the migration season and show that martins may be cueing into habitat with these shared qualities across multiple seasons.

Recent studies of fall roosting sites at a broad spatial scale using weather surveillance radars suggest that Purple Martins and, possibly, co-roosting Tree (*Tachycineta bicolor*) and Bank (*Hirundo rustica*) swallows, use habitats that span forested to urban areas during fall migration through Ontario, Canada, and the United States (Bridge et al. 2016, Kelly and Pletschet 2018). In North America, Purple Martins have commonly been found to roost in habitats associated with urban areas and cropland during fall migration (Kelly and Pletschet 2018). Expanding this investigation to all of spring and fall migration, we found that most roost sites (75%) were in forested habitats. The second most common roost substrates were in agricultural lands (13%). Agricultural lands may provide the combination of forested patches of habitat adjacent to open areas that Purple Martins seem to select during migration. We found that few roost sites (8%) were located in urban areas during fall migration in North America, suggesting that conservation efforts aimed at stopover habitat for this species should target forested islands and forested areas in general.

Populations of Purple Martins, like those of other aerial insectivores, are declining across much of their range (Nebel et al. 2010, Smith et al. 2015, Michel et al. 2016, Sauer et al. 2017). Identifying habitats used during migration is an important step in identifying areas and habitats that may be important for conservation planning (Hostetler et al. 2015, Marra et al. 2015). More work is also needed to understand how the use of forest islands by Purple Martins might impact their survival because what may have been advantageous in the past may no longer be so in anthropogenically altered landscapes. The continued application of new direct tracking technology to determine the location of major stopover locations, including areas that may be inaccessible to researchers (Hallworth and Marra 2015, Fraser et al. 2017), could further inform the protection of these habitats. We also hope that our results will stimulate further research on the use of forest islands in other systems and, particularly, studies of habitat use by migrants in isolated or patchy habitats that may become increasingly common in anthropogenically disturbed and urban areas in the future.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website.

Table S1. Locations for GPS units deployed on Purple Martins at breeding colonies from 2014 to 2016. Return rates varied by year and colony site and were comparable to geolocator return rates (11) and birds banded, but with no migration tracking device (17).