

## Determining fine-scale migratory connectivity and habitat selection for a migratory songbird by using new GPS technology

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Migratory aerial insectivores are among the fastest declining avian groups, but our understanding of these trends has been limited by poor knowledge of migratory connectivity and the identification of critical habitat across the vast distances they travel annually. Using new, archival GPS loggers, we tracked individual purple martins *Progne subis* from breeding colonies across North America to determine precise (< 10 m) locations of migratory and overwintering roost locations in South America and to test hypotheses for fine-scale migratory connectivity and habitat use. We discovered weak migratory connectivity at the roost scale, and extensive, fine-scale mixing of birds in the Amazon from distant (> 2000 km) breeding sites, with some individuals sharing the same roosting trees. Despite vast tracts of contiguous forest in this region, birds occupied a much more limited habitat, with most (56%) roosts occurring on small habitat islands that were strongly associated with water. Only 17% of these roosts were in current protected areas. These data reflect a critical advance in our ability to remotely determine precise migratory connectivity and habitat selection across vast spatial scales, enhancing our understanding of population dynamics and enabling more effective conservation of species at risk.

In the current biodiversity crisis (Ceballos et al. 2015), migratory aerial insectivores are experiencing dramatic population declines (Nebel et al. 2010, Nocera et al. 2012, Michel et al. 2015, Smith et al. 2015). This diverse foraging guild includes swallows, swifts, nightjars, and flycatchers; many of which are long-distance migrants. Identifying specific, year-round critical habitat and determining migratory connectivity (a measure of the strength of connection between breeding and wintering populations) is important for identifying and mitigating the effects of threats to declining populations (Webster et al. 2002, Marra et al. 2006, Faaborg et al. 2010, Cresswell 2014). However, studying and conserving species that migrate long distances and cross political boundaries has been particularly challenging. New animal-borne tracking technology is rapidly allowing movement ecologists to track spatio-temporal patterns of habitat use for migratory animals with ever-greater precision (Trierweiler et al. 2014), even for small organisms such as migratory songbirds (Stutchbury et al. 2009, McKinnon et al. 2013). This 'golden age of bio-logging' (Wilmers et al. 2015) has the potential to contribute to major advances in the conservation of declining migratory species.

Pioneering geolocator tracking-technology identified the Amazon basin as the core overwintering region for a

widespread but declining North American breeding migratory aerial insectivore, the purple martin *Progne subis*, that overwinters in South America (Fraser et al. 2012). However, the spatial resolution of identified overwintering areas (~ 100–200 km), did not enable the determination of specific habitat selection within the broad matrix of the overwintering range, or the identification of exact roost sites and their conservation status. To determine precise (within 10 m) and accurate (using global positioning system) spatial connections across hemispheres, we used newly miniaturized GPS archival tags (1.1 g). We aimed to, 1) identify specific migratory and overwintering roost locations for individuals tracked from breeding colonies across North America (Fig. 1A), 2) test the hypothesis that at the finest spatial scale of the roost site, birds originating from different breeding colonies share habitat (i.e. 'weak' migratory connectivity), and thus, associated threats, 3) use remote-sensing data to identify specific habitat selection within the broadly identified overwintering range, and 4) determine the degree to which identified overwintering sites are encompassed by current protected areas. This study represents the first determination of range wide and fine-scale migratory connectivity for a Neotropical migratory species and reflects a critical step in identifying critical habitat for a declining aerial insectivore.

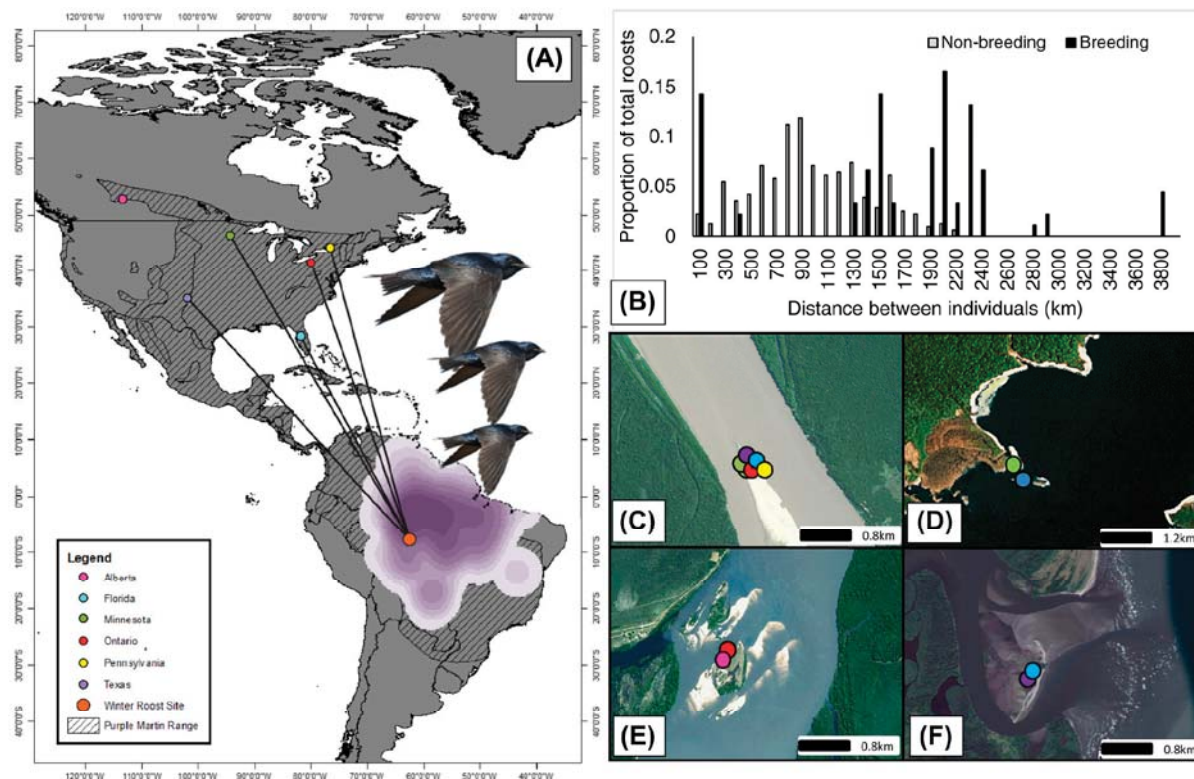


Figure 1. Spatial positions and associations of overnight roosting locations of a declining aerial insectivore (purple martin) determined using archival GPS tracking units. (A) Circles show GPS deployment locations at breeding colonies, lines show an example of a connection between individuals from different colonies and a shared roost in the Amazon; purple contours show the kernel density of overwintering locations ( $n = 402$ ) as previously determined with geolocator tracking units; black hatched lines show full breeding and nonbreeding range. (B) Distance (km) between all combinations of individuals (tracked with GPS units) when at breeding sites and at overwintering roosts. Values are displayed as the proportion of individual roosts at each distance. (C–F) Migratory and overwintering roost locations shared by two or more purple martins tracked from different breeding colonies using archival GPS units. (C) Shows a roost site on an island in the Madeira River, Amazonas that was shared by 6 individuals from breeding colonies > 2000 km apart. (D–E) shows two shared roost locations in Amazonas for birds originating from 4 different breeding colonies (Alberta and Ontario; Minnesota and Florida). (F) shows a shared (TX and FL) fall migratory stopover roosting location on a remote island off the Mosquito Coast of Nicaragua.



Figure 2. South American overwintering roost locations for purple martins identified using new archival GPS units. Colours correspond to breeding colony deployment locations (blue = FL; purple = TX; red = PA; yellow = ON; green = MN; pink = AB). Roost sites shared by multiple birds are denoted by a multi-coloured pinwheel, where each colour represents one bird from a different breeding colony. Shapes (circles, triangles, squares, diamonds) illustrate different individuals from each breeding colony and coloured lines show connections between roost sites for each bird.

## Methods

### GPS deployment and data analysis

We captured individual purple martins (weight  $51.8 \text{ g} \pm 4.6$ ) at their breeding nest boxes using drop-door traps and deployed 105 archival GPS tracking units (PinPoint 10, 1.1 g, Lotek Wireless) at 7 breeding sites during the 2014 breeding season (June–July). GPS tags were attached to birds using a leg-loop backpack harness made of Teflon ribbon (Stutchbury et al. 2009). During the 2015 breeding season we recaptured 14 birds returning with GPS tags to their colonies at 7 different sites; return rates varied by breeding location (Supplementary material, Appendix 1, Table A1). There was one case of harness failure (bird returned without GPS unit) and two cases where a bird with a GPS unit was spotted early in the season but did not remain at the breeding location to be captured. Using PinPoint Host software (Lotek, ver. 2.3.1.0), GPS units were pre-programmed to collect up to 10 roost locations during the non-breeding period before their internal batteries were depleted – 2 during the fall migration period and the remaining 8 during the nonbreeding period in South America. The timing of fall migration



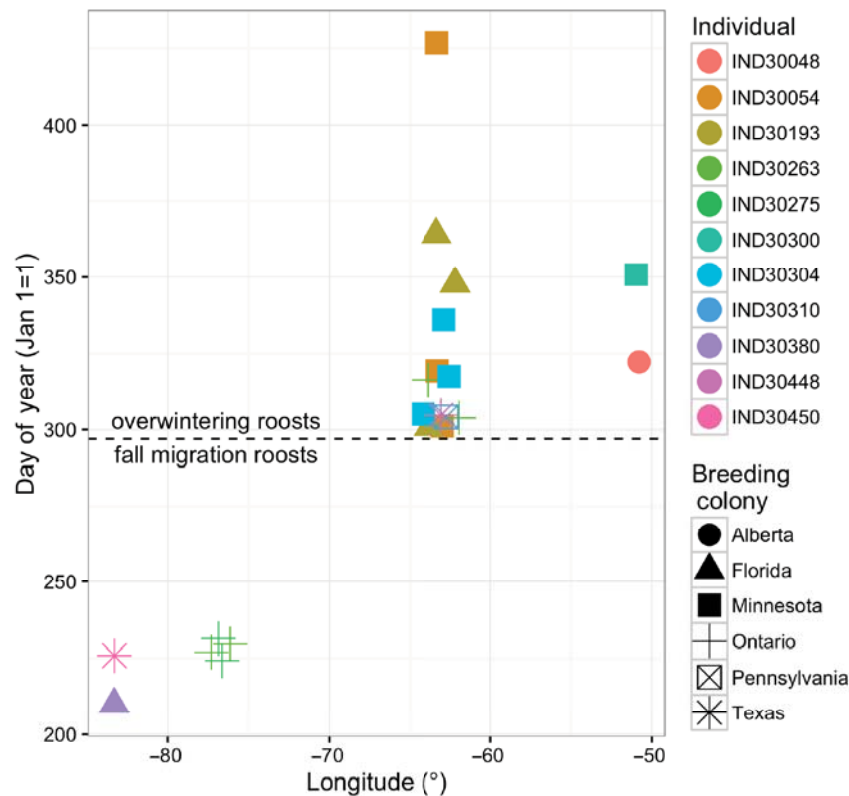


Figure 3. Spatio-temporal overlap between individual birds that shared roost locations in South America. Symbols reflect breeding colony of origin and colours denote individual IDs. Julian date is calculated from 1 January 2014, and continues into 2015 as '365 + new Julian date'. Dashed line represents the average wintering arrival date for the latest breeding population to complete fall migration (Alberta) and separates fall migration from overwintering roost sites.

and overwintering periods differ for each breeding population, and therefore data previously collected using light-level geolocators (Fraser et al. 2012, unpubl.) were used to determine population-specific GPS programs for each of the 7 breeding locations. Since purple martins move throughout the overwintering period (Oct–Feb, Fraser et al. 2012), we programmed the GPS units to record a location every 15 d at midnight, in order to capture multiple roost site locations for each individual. GPS tags were programmed to record locations from 15 July to 15 April, however only data from 30 Oct to 28 Feb were used in this analysis as this time period encapsulated the overlapping nonbreeding period for all breeding populations. Roost sites located using the GPS units were mapped using ArcMap10 (ESRI 2013).

### Spatial analyses

To determine migratory connectivity between breeding locations and overwintering roosts, data were analyzed in nine time intervals throughout the nonbreeding period (30 Oct–28 Feb; grouped at 15 d intervals), which allowed us to analyze spatial associations between individuals at different nonbreeding roost sites (with the assumption that 15-d intervals maintained independence of data in each analysis). The actual distances between each individual within sites at the breeding and wintering ranges were obtained using the Geographic Distance Matrix Generator ver. 1.2.3 (Ersts 2013). We determined the strength of connectivity between

breeding and nonbreeding sites by using Mantel correlation coefficients (Ambrosini et al. 2008), determined using the 'ade4' package (Dray and Dufour 2007) in R (R Development Core Team). This test calculates two distance matrices (one for breeding location and one for overwintering roosts) using the latitudes and longitudes recorded by the GPS tags. These two matrices were then compared to each other. The test also runs multiple random permutations ( $n = 9999$ ) to estimate the  $p$  value of the Mantel correlation coefficient. If birds that breed near to each other also winter near to each other then the Mantel coefficient should have a strong positive correlation between the two matrices (Ambrosini et al. 2008).

### Kernel density and habitat selection

We determined the size of the purple martin overwintering range by calculating a spatial kernel (ArcMap10, ESRI 2013) for all martin roost areas determined by using geolocators retrieved across the breeding range (Fraser et al. 2012, unpubl.). This included 402 roost areas, and by using an area function in ArcMap, we determined the resulting size of the kernel density was 8 046 621 km<sup>2</sup> (Fig. 1A). The contours of the kernel density are shown as quantiles, the cell size is 25 km<sup>2</sup> and the search radius is 500 km.

We characterized the habitat at overwintering roost sites in South America by quantifying several habitat features. Roost locations were characterized by 21 habitat types (adapted from

Eva et al. 2002) and then grouped into 8 more broad, similar categories (Supplementary material Appendix 1, Table A4). We determined whether roosts were in contiguous forest or on islands; either surrounded by water or by a habitat matrix that differed from the roost substrate, such as when a patch of roost trees were surrounded by scrub, agricultural fields or clearings (Eva et al. 2002). We measured the shortest Euclidian distance between each roost site and the nearest open water (river, lake) and anthropogenic disturbance (town). We also classified the roost substrate to category (trees, scrub, human structures, agricultural field). To determine whether purple martins were selecting these features within the habitat matrix of their overwintering ground, we compared roost site habitat to that at the same number of random points. We determined random latitudinal and longitudinal points using the program Geo Midpoint (GeoMidpoint 2015). These were located within a 2300 km radius centered on the mean location of all roost points ( $-4.67^{\circ}\text{N}$ ,  $-57.56^{\circ}\text{W}$ ). The search radius for the random points was restricted to within the area of the kernel density ( $8\,046\,621\text{ km}^2$ ). We used a mixed-effects logistic regression model (binomial distribution) to test the hypothesis that habitat features of roost sites identified using GPS units differed from (random) sites available to martins within their range but that were not selected as roost sites. Factors included in the model were, distance to town and distance to open water. The response variable was roost or control, where the control represents the expected habitat selection if purple martins chose habitat at random. Models were performed in R using the glm function and family = binomial, while nesting for individual. Because some values within the contingency table were below one, an additional analysis was performed where the difference between roost and control habitat classification, determined by Eva et al. 2002, was examined using a Fisher's exact test, while blocking for individual. As this method required multiple comparisons, we used Bonferroni's adjusted alpha value method where,  $\alpha_1 = \alpha/k$ ,  $\alpha_2 = \alpha/k - 1$ , etc., for each significant p-value, in increasing order.

To determine which roost locations were currently in protected areas in South America, we used data from a world database of protected areas provided by a joint project of the IUCN and UNEP-WCMC (2015). We plotted protected areas and GPS points (ArcMap 10, ESRI 2013), and counted the number of roost locations where they overlapped with protected sites.

Data available from Movebank Data Repository: <doi:10.5441/001/1.5q5gn84d> (Fraser et al. 2016).

## Results

We found that each bird used multiple roost locations (6–10 per bird, Supplementary material Appendix 1, Table A2), allowing us to identify a total of 128 nonbreeding migratory and overwintering roost sites. Most (93%) birds had overwintering roost locations in the Amazon Basin of Brazil (Fig. 2;  $-1.34^{\circ}$  to  $-17.18^{\circ}$  latitude;  $-65.29^{\circ}$  to  $-47.54^{\circ}$  longitude). Spatial analyses revealed extensive mixing at the nonbreeding grounds of birds originating from the 7 widely separated breeding sites (Mantel test coefficients for winter time series: range of coefficients from  $-0.11$  to  $0.22$ ; Supplementary

material Appendix 1, Table A3). The spatial proximity of birds breeding great distances apart in North America, sharply decreased at South American roosts (Fig. 1B; Supplementary material Appendix 1, Fig. A1), with some birds sharing the same roost site. Remarkably, five birds originating from breeding colonies 400–2300 km apart in North America roosted within 30 m from each other on the tip of the same, small vegetated island in the Madeira River in the Amazonas State of Brazil (Fig. 1C). We identified 4 other instances where two birds originating from breeding sites  $> 2000$  km apart shared roosts in the Amazon, and 1 instance where distant breeders roosted together during fall migration on the same, small coastal island in a very remote location off the Mosquito Coast of Nicaragua (Supplementary material Appendix 1, Fig. A2). We also found strong temporal overlap in shared roost locations, even with the inherent, short duration of GPS fixes (Fig. 3).

Despite vast tracts of contiguous forested habitat within the overwintering region, 56% of roost sites were on small habitat islands (defined as islands 190–900 m<sup>2</sup>, and surrounded (on all sides) by open water or islands of roost habitat surrounded by a different habitat matrix, as when a patch of roost trees is surrounded by scrub or wetland habitat). About one third (30%) of roost sites were surrounded by open water, on vegetated islands in the Amazon River and its tributaries (Fig. 1C–F). Few roosts (9%) were associated directly with human habitation and towns (by location within town limits). Purple martin roosts were significantly closer to water ( $z\text{-value} = -4.39$ ,  $p < 0.0001$ ) but were not significantly closer to disturbance (towns) relative to random sites ( $z\text{-value} = -1.083$ ,  $p = 0.279$ ) (Supplementary material Appendix 1, Table A5). As compared to random sites, roosts were significantly associated with island/shore, grass and shrubland, evergreen broadleaf, and urban habitats (Supplementary material Appendix 1, Table A6; Fig. A3). We found that only 16.7% (16 of 96) of the roost sites we identified in South America were in protected areas (Fig. 4).

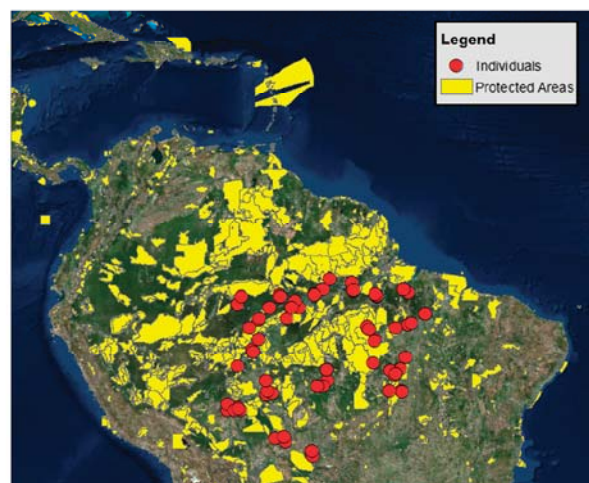


Figure 4. Map of currently protected areas versus roosting locations for purple martin identified with GPS units. Areas in yellow show spatial extent of habitat that currently has some level of protection (IUCN and UNEP-WCMC 2015). Red circles show roost locations of individuals.



## Discussion

Given that we tracked only a fraction (0.0001%) of the estimated global breeding population of purple martins (estimated at ~ 7 million individuals, Partners in Flight Science Committee 2012), it is remarkable that we found shared roosts at such small spatial scales. These results suggest that the birds we tracked joined large aggregations of conspecifics for roosting during migration and the overwintering period. Considering the close spatial proximity of overwintering roost sites for birds originating from widely dispersed North American sites, localized effects of habitat loss in Brazil could impact overwintering habitat for birds from across their entire breeding range; however their broad overwintering distribution and use of multiple roost sites could provide some buffer to localized effects of habitat loss.

The application of light-level geolocators has been very useful for delineating spatial connections between breeding and overwintering sites for Palearctic (Ouwehand et al. 2015) and Nearctic-Neotropical migrants (McKinnon et al. 2013), including purple martins (Fraser et al. 2012), and have been recently shown to provide overlapping spatial results (within ~ 43–495 km) with more precise archival GPS tags (Rakhimberdiev et al. 2016). However, the accuracy of these spatial connections (e.g. ~ 50–200 km for geolocators), while valuable for many applications and studies, is not at the scale needed for studying site-specific impacts nor the conservation and management of specific habitat. Within the 8 046 621 km<sup>2</sup> of potential overwintering habitat determined by using geolocators (Fig. 1A), archival GPS units allowed us to determine exact roost site locations within this broad region that could not have been identified using other tracking methods. Using geocator data, we previously determined that martins had roosting areas that were 91% forested (Fraser et al. 2012). We have now determined precise habitat selection for martins, and found that they are not choosing contiguous forest, but rather are selecting very specific habitat features within their range; their roost sites were on relatively rare habitat islands, that were close or adjacent to open water, and were not more likely to be closer to human disturbance than randomly selected non-roost sites. Indeed, island habitats, where we may expect fewer land-based or arboreal predators, may be an important feature of non-breeding habitat selection for martins and possibly other species.

For purple martins, most roost locations previously identified by on-the-ground observations were in very close proximity to human habitations, within towns, and often using human-made structures, such as oil refineries, as a roost substrate (Hill 1993, Ottema and Chin-Joe 2012), leading to the conclusion that preferred overwintering roost sites are most common very near or upon human structures. However, while we identified some proximity of martin roosts to human disturbance, only a small percentage (9%) of the roosts we identified were associated directly with human habitation. The median distance between roosts and human disturbance (towns, roads, agricultural fields and forest clearing) was 7.8 km (range 0–96 km), with many roosts in very remote parts of the Amazon basin. Thus, determining habitat use through direct tracking provides a method that is not

biased by proximity and accessibility of overwintering habitat to human observers.

Our data show that five of the fourteen individuals tracked shared a single roost site location. Given random mixing of individuals at the overwintering range (supported by data presented here as well as Fraser et al. 2012), this roost site may have been visited by 36% of the global population of purple martins, which would correspond to > 2.5 million adult individuals visiting this location throughout the overwintering period. This estimate may also be conservative, as our capture probability for shared roost sites was low, based upon the discrete number (1–9) of GPS-derived locations we obtained for each bird. On-the-ground observations of overwintering roosts sites in this region are extremely rare, but one estimate suggests that roosts may contain 25 000 to 80 000 individuals at a given time, comprised of mostly (55%) purple martins *Progne subis*, but also included brown-chested martins *Progne tapera* (40%), and gray-breasted martin *Progne chalybea* (5%) (Hill 1993). Considering that martins move widely between roosting areas throughout the overwintering period (Stutchbury et al. 2016), it is conceivable that there is great turn-over at individual roost sites. Further data on roost dynamics, including the size of roosts, itineracy, and the degree to which roost sites are maintained across years would be extremely valuable, and could be based upon the locations identified in this study.

Determining the degree to which migratory birds from the same breeding sites share overwintering habitat (Webster et al. 2002, Marra et al. 2006, Ambrosini et al. 2008), as well as the interactions between these lifecycle stages, is important for understanding the impacts of global change on populations, and to mitigate these effects (Faaborg et al. 2010). Nonbreeding habitat associations for species overwintering in South America remain largely unknown (Stotz et al. 1992, Stouffer 2001, Diniz et al. 2014), in part due to the remoteness of many areas in the Amazon basin as well as limits to research capacity (Malhado et al. 2014). Tracking using new animal-borne devices such as archival GPS units, coupled with remote sensing data, provides a tremendous new opportunity to study year-round habitat use and environmental impacts on individuals and populations (Hallworth and Marra 2015). Identifying critical non-breeding areas allows targeted on-the-ground conservation work in wintering areas of these species, and should encourage more cross-border collaboration between Brazilian and North American conservation groups. Several migratory aerial insectivore species showing steep population declines (Nebel et al. 2010, Michel et al. 2015, Smith et al. 2015), such as cliff and bank swallows, also overwinter in the Amazon region.

## Conclusion

For the first time, we quantified range-wide and fine-scale (< 10 m) migratory connectivity and remotely identify precise habitat selection for a declining migratory songbird. We show that individual aerial insectivores breeding across North America share roosting locations in the Brazilian Amazon, whereby relatively small, and localized habitat loss could impact important roost sites shared by birds from across the breeding range of the species. We show that few (17%) of the roost locations we identified are currently in protected



areas, and habitats in this region are under threat from multiple factors. Nearly half (47.8%) of the humid tropical forest world biome has already been lost (Hansen et al. 2008), with deforestation having accelerated by 62% between 1990 and 2000 (Do-Hyung et al. 2015). In Brazil, which hosts the majority of identified martin roosts, forest has been lost at a rate of 1381 km<sup>2</sup> yr<sup>-1</sup> (Hansen et al. 2013). In addition to forest clearing in the Amazon, land flooding for hydroelectric projects is expected to cause permanent habitat losses of 10 million ha, or 2% of the Amazon region (Fearnside 2006). We identified that river island roost sites are important habitat for purple martins, but these very habitats are under direct threat of planned hydroelectric development, where already flooded locations have led to local extinctions of both terrestrial and arboreal fauna (Benchimol and Peres 2015). There is growing evidence that the Amazon Basin provides important overwintering habitat for other Nearctic–Neotropical migrants (Heckscher et al. 2011), including species that use vegetated islands (Diniz et al. 2014). The ability to discover such precise habitat use information from thousands of kilometers away offers important new opportunities to study behaviour and population dynamics, to identify critical areas to conserve for species at risk, and is expected to yield many new discoveries in the coming years.

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Supplementary material (Appendix JAV-01091 at <[www.avianbiology.org/appendix/jav-01091](http://www.avianbiology.org/appendix/jav-01091)>). Appendix 1.