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Continent-wide tracking to determine migratory connectivity and tropical habitat associations of a declining aerial insectivore

Kevin C. Fraser[1,*], **Bridget J. M. Stutchbury**[1], **Cassandra Silverio**[1],
Patrick M. Kramer[1], **John Barrow**[2], **David Newstead**[3],
Nanette Mickle[4], **Bruce F. Cousens**[5], **J. Charlene Lee**[5],
Danielle M. Morrison[5], **Tim Shaheen**[6], **Paul Mammenga**[7],
Kelly Applegate[8] and **John Tautin**[9]

[1]*Department of Biology, York University, 4700 Keele St., Toronto, ON, Canada M3J 1P3*
[2]*4146 Congressional Dr., Corpus Christi, TX 78413, USA*
[3]*Coastal Bend Audubon Society, 645 Sharon Drive, Corpus Christi, TX 78412, USA*
[4]*1501 Spoonbill Court, Woodbridge, VA 22191, USA*
[5]*Georgia Basin Ecological Assessment and Restoration Society, #4-1150 N. Terminal Ave,
Nanaimo, BC, Canada V9S 5L6*
[6]*15 Wigwam Road, Locust, NJ 07760, USA*
[7]*12345 396th Ave., Columbia, SD 57433, USA*
[8]*Mille Lacs Band of Ojibwe Department of Natural Resources, 43408 Oodena Drive, Onamia,
MN 56359, USA*
[9]*Purple Martin Conservation Association, Tom Ridge Environmental Center, 301 Peninsula Dr.,
Ste. 6, Erie, PA 16505, USA*

North American birds that feed on flying insects are experiencing steep population declines, particularly long-distance migratory populations in the northern breeding range. We determine, for the first time, the level of migratory connectivity across the range of a songbird using direct tracking of individuals, and test whether declining northern populations have higher exposure to agricultural landscapes at their non-breeding grounds in South America. We used light-level geolocators to track purple martins, *Progne subis*, originating from North American breeding populations, coast-to-coast ($n = 95$ individuals). We show that breeding populations of the eastern subspecies, *P. s. subis*, that are separated by *ca.* 2000 km, nevertheless have almost completely overlapping non-breeding ranges in Brazil. Most (76%) *P. s. subis* overwintered in northern Brazil near the Amazon River, not in the agricultural landscape of southern Brazil. Individual non-breeding sites had an average of 91 per cent forest and only 4 per cent agricultural ground cover within a 50 km radius, and birds originating from declining northern breeding populations were not more exposed to agricultural landscapes than stable southern breeding populations. Our results show that differences in wintering location and habitat do not explain recent trends in breeding population declines in this species, and instead northern populations may be constrained in their ability to respond to climate change.

Keywords: geolocator; songbird; South America

1. INTRODUCTION

Population dynamics of neotropical migratory songbirds are driven by the interaction of productivity on the breeding grounds and mortality, which occurs primarily during migration and the non-breeding season in the tropics [1–3]. Migratory birds are predicted to be more vulnerable to habitat disturbance and environmental change at their wintering grounds if they exhibit strong migratory connectivity, in which most members of a given breeding population migrate to the same region within the non-breeding range [4,5]. In contrast, species with weak migratory connectivity are buffered from habitat disturbance in specific non-breeding regions because reduced survival of individuals is spread diffusely across the breeding range [6]. However, understanding the population dynamics of long-distance migratory songbirds has been hampered by the difficulty in determining migratory connectivity [2,6] because until recently it was not possible to track migration of songbirds [7].

Connectivity patterns between breeding and wintering sites thousands of kilometres apart have been determined for migratory songbirds using large-scale band-recovery efforts [8–10], but for many species recovery records

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linking breeding and tropical 'wintering' sites are too infrequent. Stable isotope values of feathers, and to a lesser extent genetic markers, have been used to document migratory connectivity in several songbirds, but precision is generally restricted to large geographic regions [11–14]. Songbirds can exhibit coarse patterns of east–west parallel connectivity at a continental [10,12,14,15] or subcontinental [8,16] scale. Less common are patterns of leapfrog migration, where northern breeding populations have relatively southern non-breeding destinations [17], and crossover connectivity, in which western populations are connected to eastern non-breeding regions [18].

Many aerial insectivores in North America, particularly long-distance migrants, have experienced steep population declines since the mid-1980s [19,20]. There is a strong geographic pattern in declines, which are more prevalent towards the northeast of North America. One explanation for this pattern is that north-eastern regions receive relatively high levels of atmospheric pollutants, including acid precipitation, which in turn has negative effects on insect abundance and thus productivity of aerial insectivores [20]. Climate change is also expected to disproportionately affect populations in more seasonal habitats due to a phenological mismatch between food availability and timing of breeding in long-distance migrants [21]. Agricultural pesticide use may also influence aerial insectivore populations, through broad changes in their prey base [22]. Nebel *et al.* [20] suggested that northern populations may face higher mortality on the wintering grounds due to agricultural pesticides in South America, either through direct mortality or indirectly via reduction in food availability [23]. Associations with agricultural landscapes in the winter quarters could increase exposure to pesticides and their effects, potentially influencing year-round population dynamics of long-distance migratory birds. If this latter hypothesis is correct, then migratory connectivity should be strong in aerial insectivores and northern populations are predicted to have stronger associations with agricultural landscapes in the non-breeding season.

For the first time, using light-level geolocators, we tracked individual ($n = 95$) songbirds that originated from coast-to-coast breeding populations in North America and travelled to wintering sites in South America. Purple martins, *Progne subis*, are declining throughout much of their northern range [19,20] and their non-breeding range extends from the relatively undisturbed upper Amazon basin down to southern Brazil where the landscape has been converted almost entirely to agricultural use. Our primary objectives were to (i) measure the range-wide degree of migratory connectivity between breeding and non-breeding populations of purple martin and (ii) determine whether northern populations of this declining aerial insectivore may face distinct threats through greater association with agricultural habitat at their non-breeding grounds in South America.

2. METHODS

(a) Geolocator deployment
Purple martins were captured and fitted with geolocators during the breeding season by trapping birds in nest boxes at eight breeding locations across the range ($n = 421$, electronic supplementary material, table S1). Geolocators

(≤ 1.6 g; MK10s/12/12s/14s/20, British Antarctic Survey) were mounted using a leg-loop backpack harness [7,24] constructed with Teflon ribbon or, in some cases, polypropylene thread. Geolocators were retrieved ($n = 120$) at the same breeding sites in the year following deployment. Geolocator battery failure prior to arrival and residency at winter roosts reduced sample size to 95. At the Pennsylvania breeding site (2009–2011), the return rate of birds wearing geolocators was not lower than that of banded birds without geolocators (see the electronic supplementary material, table S2). Harness failure occurred for 10 per cent of birds when using a thread harness but only 3 per cent of birds using a Teflon harness.

(b) Analysis of light data from geolocators
Geolocators measured the intensity of visible light every 1 min and recorded the maximum reading within each 10 min interval (MK16, MK10) or each 2 min interval (MK12, MK20). Raw light data were corrected for clock drift (1–3 min lost during 10-month deployment) using BASTrak and analysed using TransEdit (British Antarctic Survey). We manually verified a sharp transition at each sunrise and sunset and ignored obvious shading events during the daytime. We used a light threshold level of 32 (MK16, MK10) or 5 (MK12, MK20) to define sunrise and sunset transitions, and used live calibration data (see below) from birds prior to migration to determine the average sun elevation that corresponded with this light threshold level at the breeding site. Transitions with light peaks or non-linear transitions before sunrise or after sunset were rejected from further analysis. Latitude was not determined for 15 days before and after the fall equinox when day length is similar everywhere.

Latitude and longitude coordinates were calculated with Locator software (British Antarctic Survey) using midnight locations because purple martins are diurnal migrants, and therefore midnight locations should be more accurate because birds are stationary during the night. No compensation for longitudinal movement was made when estimating latitude because birds were assumed to be stationary from sunset to sunrise. Locations that were clearly anomalous (i.e. >1000 km from previous location) were rejected as outliers.

All geolocators received a static pre-deployment and post-deployment calibration for 1 week in open habitat with a clear view of the horizon, to assess light sensitivity of units. Light sensitivity was virtually identical among units of similar model and was similar before and after deployment. Analysis of live locations for birds prior to migration was used to determine the average sun elevation (BASTrak, British Antarctic Survey) that corresponds to the light level (32 or 5, depending on geolocator model) that was used to define sunrise and sunset transitions. The sun elevation, in turn, is used in Locator (British Antarctic Survey) to determine location given the sun's position on a given date and time. Sun elevation was calculated separately for different geolocator models, after birds finished nesting but before migration, and averaged across individuals within each year to better represent average conditions for migrating birds at unknown locations.

(c) Estimating geolocator error
Geolocation accuracy was estimated for birds at each of the eastern breeding populations by averaging locations of individuals in late July and early August, prior to autumn migration. Average geolocator estimates closely matched breeding sites (see the electronic supplementary material,

table S3), and geolocator positions for individuals mismatched breeding sites by an average of 49–60 km in latitude (range: 0–210 km) and 38–48 km in longitude (0–196 km). Differences in geolocation accuracy among individuals reflect individual pre-migration habitat at dawn and dusk and differing weather conditions at the time of live calibration. During the pre-migration period, the standard error of latitude for an individual ranged from 0.15 to 1.0 (avg. 0.3) and for longitude ranged from 0.06 to 0.36 (avg. 0.2).

Arrival at the wintering ground was considered to have occurred when the latitude and longitude ceased to shift in a direction consistent with autumn migration, fluctuated around a narrow range of values (less than $2°$ longitude), consistent with a stationary bird, and fluctuated around a similar value for at least 10 days within the winter range. During stationary periods at the wintering grounds, location was determined by calculating average latitude and longitude during the period. Most (63 of 95) martins shifted roost locations while at the wintering grounds, averaging *ca.* 700 km between sites.

(d) Band recovery data for connectivity

Band recovery data can be used to independently assess migratory connectivity, and to supplement geolocator tracking data [8]. Analysis of North American band recovery data (1921–2010) for purple martins banded at breeding sites ($n = 2884$ recoveries) identified 12 birds that were recovered in South America after autumn migration and before spring migration (see the electronic supplementary material, figure S1). However, 11 of 12 birds were banded as a nestling and therefore their first breeding site was unknown. Band recovery data were therefore not included in our analyses.

(e) GIS data and analysis

Northern breeding populations of purple martins (*P. s. subis*) are declining more severely than central or southern populations (figure 2a). For all roost sites in South America occupied for ≥ 30 days, we used kernel density analysis to test whether the core wintering region of northern breeding populations was associated with more extensive agricultural land use than breeding populations from central and southern regions. We measured winter roost density of northern (SD, MN, PA, NJ, $n = 59$ individuals, 97 roosts) versus southern and central (VA, OK, TX, $n = 30$ individuals, 55 roosts) breeding populations based on points of 1–3 roosts per individual bird using fixed kernel densities in the program ArcGIS 10 [25]. We determined kernel densities at 20, 40, 60 and 80 per cent of the total density using a sample radius of 50 km (or 0.45 decimal degrees) and a cell size of 1 km². We derived land-cover data for the purple martin wintering range in South America from Eva *et al.* [26]. We calculated per cent of agricultural land-cover versus forest and other vegetated, non-agricultural cover (hereafter called forest) within a 50 km radius (which corresponds to longitudinal geolocator error) around each winter roost and compared roosts of northern versus south-central breeding birds using a *t*-test.

3. RESULTS

Migratory connectivity was very weak, and there was extensive overlap in non-breeding sites within South America for martins originating from across eastern North America (figure 1). Individuals from breeding sites up to 2000 km apart in both latitude and longitude were often mapped to within 100 km of each other in South America, the limit of geolocator accuracy. Birds from the western subspecies, *P. s. arboricola* ($n = 6$), appear to have a distinct wintering region in southeastern Brazil, whose core area is *ca.* 3000 km from the core wintering region of the eastern subspecies.

Most individuals (76%; 68 of 89) of the eastern subspecies roosted for the longest period in northern Brazil (*ca.* $6°$ S to $1°$ N) from the Rio Negro region eastward to the mouth of the Amazon River ($64°$ to $47°$ W). Many individuals had multiple roost sites that they occupied for at least 30 days (1 roost: 26%; 2 roosts: 61%; 3 roosts: 11%). Individuals moved an average of 700 km between roost sites (up to 1400 km in some cases), but all these additional roosts were within the same geographic region as defined by the longest occupied roosts. The average occupancy of the longest roost (124 days) was more than double that of other roost sites (2nd longest roost: 55 days, 3rd longest: 43 days). For the longest occupied roosts, there was no significant correlation between breeding and wintering latitude ($r_s = -0.12$, $p = 0.80$, $n = 89$), or between breeding and wintering longitude ($r_s = -0.04$, $p = 0.77$, $n = 89$) (see the electronic supplementary material, figure S2) and sex was not a significant factor in winter roost location ($t = -1.46$, df = 90, $p = 0.15$).

Individuals from a discrete breeding population had a broad distribution at the wintering grounds. For the Pennsylvania population, for instance, the average distance between individuals, for the longest occupied roost sites, was 903 km (± 23 km SE, $n = 34$ individuals, 561 comparisons) with an average nearest neighbour distance of 140 ± 20 km and average farthest neighbour distance of 1787 ± 336 km.

Birds originating from northern and south-central North American breeding populations shared a similar and mostly overlapping over-wintering area centred in northern Brazil near the Amazon River (figure 2b). The distance between the centre of northern (lat. $-2.51°$, long. $-62.19°$) and south-central (lat. $-1.34°$, long. $-61.6°$) wintering ranges was just 144 km, within a region dominated by relatively undisturbed evergreen tropical forest (figure 2b). Ground cover within 50 km of overwintering roosts was mostly forest (average for all birds $91\% \pm 1$ forest and $4\% \pm 0.8$ agriculture). Northern breeding birds did not have greater per cent agricultural ground cover at winter roosts than birds from southern and central breeding sites ($t = -0.59$, df = 109, $p = 0.55$).

4. DISCUSSION

For the first time, we determined the degree of range-wide migratory connectivity between northern breeding populations and corresponding non-breeding areas in the tropics using direct tracking of individual songbirds. We show that seven breeding populations of the eastern subspecies of purple martin (*Progne s. subis*) exhibit very weak connectivity, and share a broad, overlapping non-breeding region along the Amazon River in northern Brazil. This is remarkable, considering that breeding populations were separated by up to 2000 km, and other songbird species have exhibited sub-continental patterns of connectivity [8,16]. This shared core area
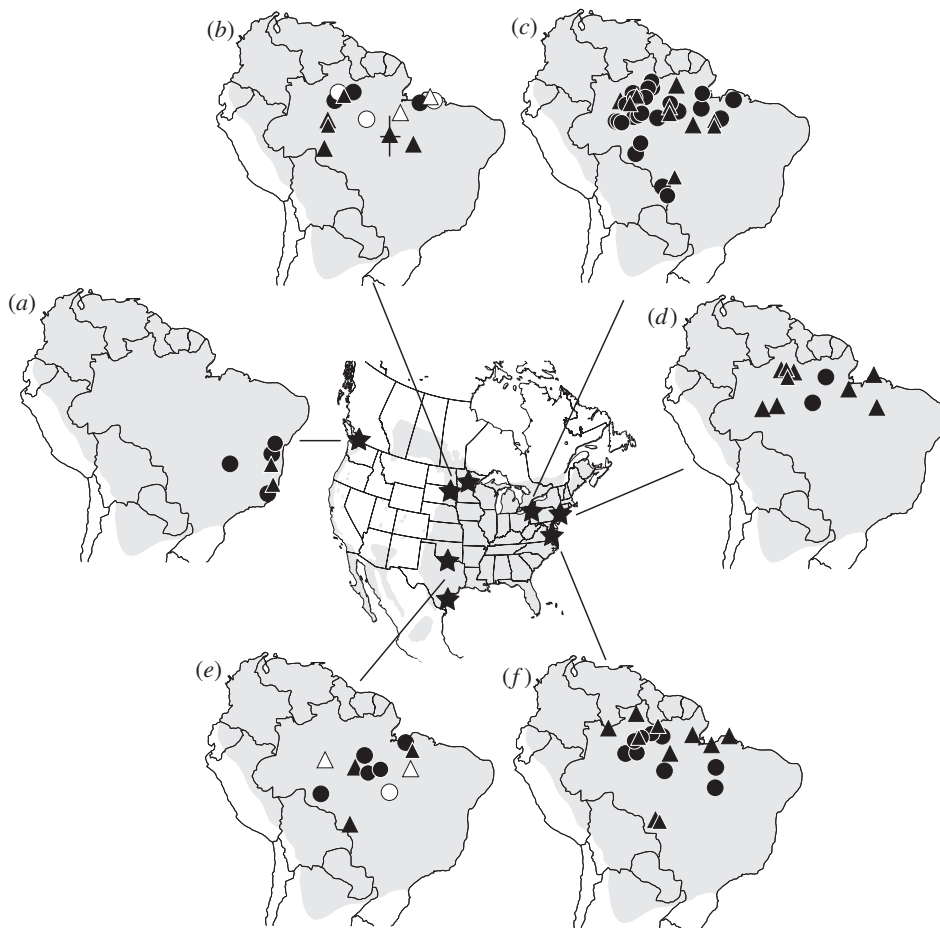
Figure 1. Migratory connectivity of purple martin breeding populations tracked with geolocators to South America; range shown with grey shading. The site with the longest winter residency (124 ± 5.4 days, $n = 95$) is shown for each individual (triangles are males, circles are females) from (*a*) British Columbia ($n = 6$), (*b*) Minnesota (white, $n = 5$) and South Dakota (black, $n = 9$), (*c*) Pennsylvania ($n = 34$), (*d*) New Jersey ($n = 11$), (*e*) Oklahoma (white, $n = 3$) and Texas (black, $n = 8$), and (*f*) Virginia ($n = 19$). British Columbia birds are *Progne subis arboricola* and all other populations are *P. s. subis*. Error bars for roost location in (*b*) shows typical standard deviation in latitude and longitude for estimated winter locations. Map of North America shows the breeding range in grey and stars indicate the location of geolocator deployments.

encompasses only about 20 per cent of the entire wintering distribution of the species, yet supports an estimated 80 per cent of the eastern subspecies. Threats to the core overwintering areas in the upper Amazon could therefore influence population dynamics across the eastern breeding range of purple martin.

Long-distance migratory songbirds that feed on aerial insects, as a group, show strong breeding population declines, with steeper declines in more northern populations of several species [20]. Direct tracking of individual Swainson's hawk (*Buteo swainsonii*) using satellite tags revealed that breeding population declines in North America were likely a result of intensive spraying of organophosphate insecticides and associated mortality (approx. 1% of global population) at wintering sites in South America [23,27]. Similarly, range-wide declines in dickcissel (*Spiza americana*) were attributed to associations with intensive agriculture and persecution at their South American wintering sites [28]. The use of agricultural habitats in the non-breeding season could expose purple martins to pesticides, causing either direct mortality or reduced food availability with subsequent fitness costs, potentially contributing to declines observed at breeding areas [20]. However, we found no significant difference between declining and stable

breeding populations in the use of agricultural non-breeding habitat. The core 'wintering' region for the eastern subspecies of purple martin, including declining northern breeding populations, is dominated by largely undisturbed tropical rainforest (figure 2*b*). Our kernel density analyses show that the centre of the core over-wintering area of northern and south-central birds was only 144 km apart. Owing to this overlap, eastern breeding populations likely experience similar conditions at their overwintering sites in South America, and wintering ground events are unlikely to be the cause of differential population declines in breeding populations. Thus we conclude that exposure to agricultural landscapes does not appear to be the cause of declines of northern breeding populations.

Proposed alternative explanations for population declines of purple martins (and other aerial insectivores) include the effects of acid rain on prey abundance at breeding sites, which is greatest in the northeast, and climate change [20]. For the latter, constrained migratory schedules can limit adaptive responses to climate change, and can result in severe population declines of long-distance migratory songbirds [21,29,30], and these patterns are expected to be stronger for birds in more seasonal habitats [21], such as more northern breeding sites of purple martin.
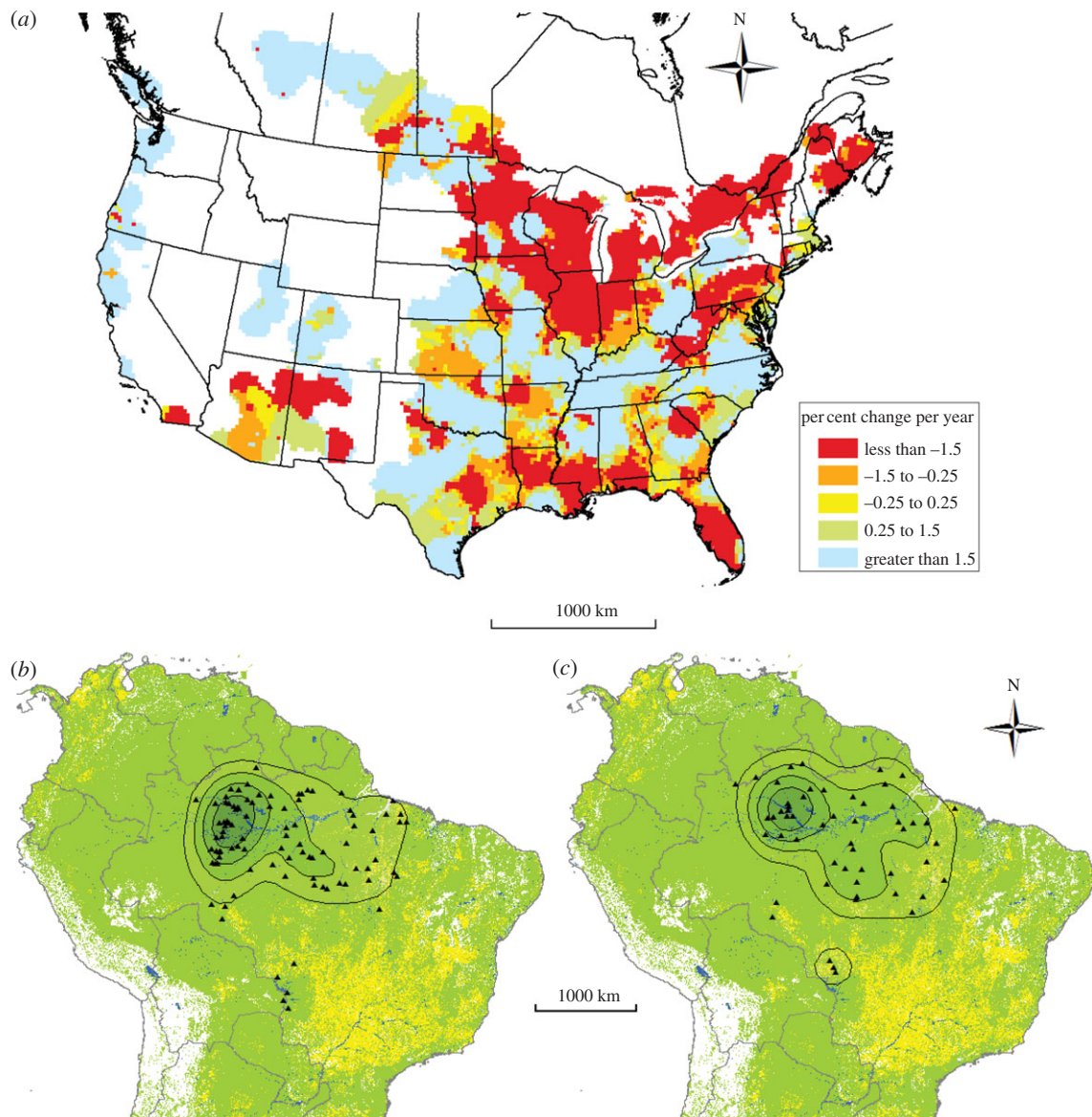
Figure 2. (*a*) Population trends based on the BBS data (1966–2010). Kernel density of all winter roost locations occupied for ≥30 days by martins (*P. s. subis*) from (*b*) northern breeding populations (Minnesota, South Dakota, Pennsylvania, New Jersey; *n* = 59 individuals, 97 roosts) and (*c*) central/southern breeding populations (Oklahoma, Texas, Virginia; *n* = 30 individuals, 55 roosts). Maps show kernels of 20, 40, 60 and 80% of the total density. Green shading represents forest and non-agricultural vegetated cover; yellow shading represents agricultural lands.

Populations of long-distance migratory birds may be most limited during the overwintering and migratory period, thus it is important to determine connections between different periods of the annual cycle in order to better understand, and mitigate, population declines [2]. Determining continent-wide connectivity using direct tracking provided the surprising result that breeding populations separated by up to 2000 km share a broad overwintering region in South America, suggesting that future habitat disturbance in this region would have a broad influence on population dynamics across the range. We also quantified habitat use thousands of kilometres away from breeding sites to show that the patterns of population decline in this long-distance migratory aerial insectivore are not associated with different threats on the wintering grounds. The dramatic increase in direct tracking of songbirds will soon establish the levels of migratory connectivity in a wide range of species, allowing for better conservation and management of declining songbirds.

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