Ecological Causes and Consequences of Intratropical Migration in Temperate-breeding Migratory Birds

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ABSTRACT. New discoveries from direct tracking of temperate-breeding passerines show that intra-tropical migration (ITM) is common in a growing number of species which has important implications for understanding their evolution of migration, population dynamics, and conservation needs. Our large sample size (*N* = 191) for Purple Martins *Progne subis subis* tracked with geolocators to winter sites in Brazil, combined with geolocator deployments at breeding colonies across North America, allowed us to test hypotheses for ITM which has not yet been possible to do for other species. ITM in Purple Martins was not obligate; only 44% of individuals exhibited ITM and movements were not coordinated in time or space. We found no evidence to support the resource hypothesis; rainfall, and temperature experienced by individual birds during their last 2 weeks at their first roost site were similar to conditions at their second roost site after ITM. Birds generally migrated away from the heavily forested northwestern Amazon to less forested regions to the south and east. ITM in this aerial insectivore appears to support the competition avoidance hypothesis and may be triggered by increasing local density in the core wintering region. Full-life cycle models and migratory networks will have to incorporate ITM to properly address seasonal carry over effects and to identify which wintering regions are most important for conservation.

Introduction

Long-distance migration occurs in many animals including birds, bats, ungulates, turtles, fishes and insects and may be obligate (all individuals migrate) or partial (a portion of the population is sedentary; Chapman et al. 2011). Migration often involves individual round-trip journeys between widely separated breeding and non-breeding regions and is strongly associated with seasonal changes in food resources due to large-scale and predictable changes in temperature or rainfall patterns (Newton 2008). Birds are well known for their seasonal migrations between temperate and tropical regions. In Canada, for instance, over 80% of birds that breed in the boreal forest are obligate migrants leading to spectacular seasonal movements of 2-3 billion birds each autumn and spring (Wells 2011). Recent advances in technology have made it possible to track the timing and routes of small birds, including passerines, for the first time (Stutchbury et al. 2009). Extreme examples of migration performance include the Blackpoll Warbler (*Setophaga striata*), a 12 g boreal forest songbird, that completes a 2500 km ocean-crossing in autumn requiring up to 3 days of non-stop flight (DeLuca et al. 2015). Northern Wheatears (*Oenanthe oenanthe*) breeding in the eastern Canadian arctic travel over 14,000 km to their non-breeding (‘wintering’) grounds in western Africa (Barlein et al. 2012). Much of the emphasis of these tracking studies has been on revealing migration pace and routes, but also determining the extent to which different breeding populations mix at wintering sites to better inform conservation (Fraser et al. 2012, Hallworth et al. 2015, Stanley et al. 2015).

A less charismatic but nevertheless intriguing discovery for many long distance migratory passerines has been that individuals may exhibit additional long-distance movements within the tropics after they arrive at their wintering grounds (Heckscher et al. 2011, Fraser et al. 2012). This is a form of intra-tropical migration (ITM) which until recently has been a term used to describe the seasonal migration of tropical species within the boundaries of the tropics (Morton 1977). ITM in tropical species likely evolved to allow birds to track large-scale seasonal shifts in tropical food resources and is most common in frugivores and nectarivores (Levey and Stiles 1992). ITM for temperate-breeding species can be defined as the prolonged occupation of two or more widely separated sites within their tropical wintering grounds and is distinct in timing and/or direction from fall or spring latitudinal migration movements (Heckscher et al. 2015). These are not simply short-distance movements in search of improved environmental conditions and food resources (e.g. altitudinal migration; Boyle et al. 2010) but rather rapid movements over long distances, hundreds or even thousands of kilometers, after birds first occupy a wintering site for a prolonged period.

ITM in temperate-breeding birds is emerging to be an important feature of the migration ecology of passerines (table 1). In only a few years ITM has been documented in a wide range of temperate-breeding passerines that are dispersed throughout the phylogeny (flycatchers, thrushes, blackbirds, swallows, pipets, Old World warblers). These species represent a wide variety of diet (fruit, soil arthropods, seeds, aerial insects), winter social organization (solitary, flocking, large nocturnal roosts) and winter habitat (forest, grasslands, desert). ITM is likely to be discovered in many more long-distance migratory birds in the coming years and has important implications for the evolution of migration, modelling population dynamics, and for identifying a species' conservation needs in the face of habitat loss and climate change. Another important implication is the potential ecological role of ITM birds as they move within and among tropical ecosystems (Loiselle and Blake 1991).

ITM in temperate-breeding passerines has come as a surprise and is barely mentioned in recent reviews (Faaborg et al. 2010) in part because advances in tracking technology are so recent. With few exceptions, it has generally been assumed that obligate long-distance migrants are relatively stationary once fall migration has ceased and birds switch physiologically from hyperphagia and migratory restlessness to a sedentary non-breeding lifestyle (Newton 2008). Indeed, the 'wintering' period of temperate-tropical migrants has been referred to as the 'stationary' period (Sillett and Holmes 2002) to avoid the inaccuracy of labelling a period in the tropics using a temperate zone term. Demographic studies of wintering passerines have focused on sedentary and territorial species because that is the only way the fate of individuals can be determined in the non-breeding season, through band re-sighting (Sillettt and Holmes 2002) or short distance radio-tracking (Kresnik and Stutchbury 2014). Many species that do exhibit ITM (table 1) are gregarious and non-territorial at wintering sites and so their winter ecology has not been well studied. Several temperate-breeding passerines have been described as nomadic on their tropical wintering grounds based on seasonal changes in abundance (Greenberg 1984). However, without tracking technology it is not possible to document whether disappearance of marked individuals from study sites, or temporal shifts in species occupancy patterns, represent short-distance habitat shifts or sudden long-distance ITM.

Hypotheses to explain ITM in temperate-breeding passerines can be drawn from the literature for tropical species. Migration within the tropics may have evolved in response to broad and fairly predictable geographic differences in habitat quality and resource availability (Levey and Stiles 1992). In Bobolink (*Dolichonyx oryzivorous*) ITM is obligate and occurs southward between three distinct and distant regions of South America and is remarkably synchronized spatially and temporally among widely separated breeding populations from across North America (Renfrew et al. 2013). ITM in Bobolink is likely driven by predictable seasonal changes in grassland productivity over large spatial scales and appears to be part of an endogenous migration program that is shared both within and between populations. Upon arrival at their wintering grounds, Veery (*Catharus fuscescens)* first occupy lowland forest in southern Amazonia and the generally northward ITM that occurs from Dec-Mar in this ground-foraging bird may be prompted by the seasonalflood pulse of Amazonian rivers (Heckscher et al. 2015). Eastern Kingbirds (*Tyrannus tyrannus*) also migrate to the Amazon Basin (Bolivia and Brazil) and then move to a second wintering site in northwesternSouth America (Colombia, Ecuador, and Peru; Jahn et al. 2013). Movements are not highly synchronized among individuals in these two species and individual variation in timing may be triggered by local resource availability (Heckscher et al. 2011) or individual timing of feather molt (Jahn et al. 2013). The resource availability hypothesis predicts that habitat, temperature and/or rainfall differ favorably between first and second wintering sites of individuals.

In some temperate-breeding species ITM is not obligate and is highly variable within a population (table 1) which raises the question of why some individuals are sedentary and others are not. Partial migration is common in animals and may occur if individuals face different trade-offs (Chapman et al. 2011). Migration between different habitat types can result in access to higher quality food, or lower predation risk, but these benefits may be offset by costs that are experienced during, or after, migration. This can result in equal pay-offs for migrants and residents. In a tropical lekking bird, the White-ruffed Manakin (*Corapipo altera*) males who migrate altitudinally during the non-breeding season benefit via increased survival but then pay a reproductive cost the next year due to decreased social status and mating success (Boyle et al. 2011). Long distance ITM is expected to incur energetic costs and risk. During temperate-tropical migration daily mortality rates of birds may be 6–15 times higher compared with their sedentary period on the breeding or wintering grounds (Sillett and Holmes 2002, Klassen et al. 2013). Even if ITM results in better habitat, food resources or environmental conditions these benefits may not outweigh the costs of migration for some individuals.

Migratory strategies in partial migrants can also be condition or density dependent in a wide variety of vertebrates (Chapman et al. 2011). Numerous studies have found that larger individuals (usually males) are more likely to remain sedentary due to the energetic advantages of a lower surface area to volume ratio which allows them to better withstand food shortages (Chapman et al. 2011). The competition avoidance hypothesis suggests that migrants are poor competitors who cannot gain access to sufficient resources when density is high, and results in lower fitness for migrants than residents. Altitudinal migration in American Dippers does not increase individual survival or reproductive success relative to sedentary birds (Green et al. 2015). Partial migration in this species is likely caused by density-dependent competition, with less competitive individuals being forced to migrate to higher elevations in order to obtain a breeding territory. If poor competitive ability triggers migration, then one would expect young birds to be more likely to migrate to lower density sites. For temperate-tropical migrants, negative density-dependent effects can be high for territorial species that occupy good quality wintering habitat (Marra et al. 2015). However, few studies have quantified density-dependence on the wintering grounds and it is not known to what extent could trigger ITM in some species.

Purple Martins: Testing Hypotheses for ITM

Our direct tracking has shown that 44% Purple Martins (*Progne subis subis*) exhibit ITM within the

Amazonian region of Brazil, with first and second winter sites averaging 700 km apart (Stutchbury et al. 2009; Fraser et al. 2012, this study). Our unusually large sample size (*N* = 191) combined with geolocator deployments at breeding colonies across North America allows us to test alternative hypotheses for ecological drivers of ITM, which has not yet been possible to do for other species (table 1). Martins originating from across the breeding range mix extensively in northern Brazil and the core wintering region is in the northwestern Amazon, where regional forest cover is over 90% (Fraser et al. 2012). Purple Martins are aerial insectivores and on the wintering grounds they gather at night in large mixed species *Progne* roosts which can comprise tens of thousands of birds (Hill 1993, Davidar and Morton 1993).

First, we test if variation in ITM between individuals is predicted by age, sex, migration distance, or year. ITM may be condition-dependent and therefore more common in older, experienced birds compared with females or younger birds who are smaller in size, and thus have less capacity to withstand food shortages (Ketterson and Nolan 1982). Aerial insectivores are susceptible to starvation if food resources collapse for a week (Brown and Brown 2000, Tarof and Brown 2013). ITM may also depend on the energetic costs of temperate-tropical migration. Individuals with relatively low energetic costs of migration from their breeding site (i.e. from southern populations) be more likely to exhibit ITM than northern populations that have migrated 2,000 km farther, or more, to get to Brazil. Second, we test the resource hypothesis by comparing the environmental conditions that individuals experienced during the last 2 weeks at their first roost site with conditions after ITM during the first 2 weeks at their second roost site. Second roost sites were predicted to have higher forest cover, higher temperature or higher rainfall than first roost sites. Little is known about the habitat preferences of Purple Martins on their wintering grounds because it is only since tracking became possible that it was discovered that the core wintering region of the eastern subspecies *Progne subis subis* is the heavily forested Amazon basin (Fraser et al. 2012) and not urban and agricultural areas in southern Brazil (Tarof and Brown 2013). Aerial insects are likely more abundant in warmer and wetter regions but little is known about how prey availability varies geographically or seasonally within the Amazon.

Third, we test the competition avoidance hypothesis by examining arrival patterns in Brazil for individuals originating from different breeding populations. High density winter roosts (Hill 1993, Davidar and Morton 1993) may be costly via increased disease transmission, increased competition for optimal sites within roosts, or increased competition for food. It is not known to what extent tens of thousands of martins concentrated into one roost site leads to local depletion of aerial insect food resources. Kelly et al. (2013) estimated that 20 million Purple Martins arrive on the wintering grounds each fall. Roost density is presumably lower early in the wintering season when southern breeding populations of Purple Martins first arrive and may increase rapidly as more northern birds pour into the core wintering region. If so, we predict that the earliest arriving birds will occupy the core winter region of northwestern Brazil and that later arriving birds will continue past this region and occupy peripheral wintering sites.

Methods: Purple martins were captured at their nesting boxes and fitted with geolocators (British Antarctic Survey, models MK10, MK12, MK14, MK20 and Biotracker equivalent models) during the nesting period (2007-2014, *N* = 987 geolocators) at multiple breeding sites in Canada (Alberta) and the U.S. (Florida, Minnesota, New Jersey, Pennsylvania, South Carolina, South Dakota, Texas, Virginia; fig. 1). For more details on methods see Fraser et al. (2012). Geolocators were retrieved in the year following deployment and we obtained year-round migration data for 191 different individuals. The return rate of individuals fitted with geolocators varied across years

(25-48%) and did not differ from birds that were banded but not fitted with a geolocator; Fraser et al. 2012, 2013). Most (80%) geolocators were deployed on birds in at least their second year of breeding, as identified by their distinct adult plumage characteristics that differ from one year-old birds (Tarof and Brown 2013). Exact age of adults $\geq$ 2 years old was determined if they were first banded as nestlings or 1-year olds and minimum age based on birds first banded in adult plumage. The final sample size of tracked birds consisted of 88 males [1 year old (9), minimum age 2 years (62), minimum age 3 years (17)] and 103 females [1 year old (28), minimum age 2 years (63), minimum age 3 years (12)].

Geolocators measured the intensity of visible light every 2-10 min, depending on the model, and after retrieval the raw light data were analyzed using TransEdit (British Antarctic Survey). In brief, 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 to define sunrise and sunset transitions, and used live calibration data from birds prior to migration to determine the average sun elevation that corresponded with this light threshold level at the breeding site. Latitude and longitude coordinates were calculated with Locator software (British Antarctic Survey) using midnight locations because purple martins are primarily diurnal migrants (for details see Fraser et al. 2012). Latitude was not determined for 15 days before and after the fall and spring equinoxes when day length is similar everywhere. Geolocator accuracy at breeding sites prior to migration, averaged across individuals, was 20-60 km for latitude and 20-75 km for longitude (Fraser et al. 2012). To facilitate data analyses for this study we defined ITM as a movement > 500 km that occurred after a bird had spent 30 d on its wintering site, and if the bird occupied the new winter roost for at least 30 d. This definition of ITM ensures the movements fall far outside geolocator measurement error for individuals.

To map roost sites of ITM and non-ITM birds 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 km^2. We derived land-cover data for the purple martin wintering range in South America (Eva et al. 2002; Fraser et al. 2012). We calculated percent of agricultural land-cover versus forest and other vegetated, non-agricultural cover (hereafter called forest) within a 50 km radius (which corresponds to average longitudinal geolocator error) around each winter roost. We also obtained weather data using the ECMWF Global Atmospheric Reanalysis through Movebank (www.movebank.org) for average daily temperature and rainfall for each individual two weeks prior to ITM and at the second site for two weeks after ITM.

Results: Out of 191 individual birds tracked, 85 (44%) underwent at least one ITM (defined here as ≥ 500 km movement) during the winter season, after arriving at their first prolonged (>30d) roost site (fig. 2). The first ITM was a mean distance of 776 km ± 43 (SE) from the first roost site. Average duration of roost occupancy was 66 ±3 d at the first wintering site and 77.6 ± 3.4 d at the second site (paired *t*-test, $t = -2.06$, $N = 85$, $P = 0.042$). Only 18 of these 85 ITM martins underwent a second ITM. Average distance from second to third site was 763 ± 47.5 km (max 1100 km) and occupancy duration of the third site was 58.1 ± 4.6 d.

Birds that underwent ITM ($N = 85$) were compared with individuals who were stationary (i.e., did not shift more than 500 km within a season, $N = 106$) to test for possible effects of year, breeding latitude (as a proxy for distance to wintering range), minimum age, and sex using logistic regression analysis. However, none of these variables were significant predictors of which individuals exhibited ITM (year: Wald's X^2=0.37, P = 0.54; latitude: X^2=0.36, P = 0.54; age: X^2=0.08, P = 0.77; sex: X^2=0.06, P = 0.80).

If the cause of ITM is geographic variation in food resources then the movements should be coordinated as they track those resources. Birds that underwent ITM had similar first roost sites as birds that did not undergo ITM (fig. 2). First roost sites were primarily concentrated in the northwestern Amazon and second sites were primarily in the eastern Amazon. However, at a population level there was much geographic overlap in regions occupied by first versus second roost (fig. 2). Only rarely (7%; 6 of 85) was ITM in a westerly or northwesterly direction (i.e., in a direction consistent with spring migration toward Central America). Unlike Bobolink (Renfrew et al. 2013) ITM timing was not synchronized within or between birds from different breeding regions (fig. 3). Within birds from the same breeding region, ITM occurred throughout the wintering season (fig. 3).

If forest cover is related to habitat quality, and birds undergo ITM to improve habitat quality, then ITM birds should initially have lower forest cover than non-ITM birds. But average forest cover within 50 km of roosts for non-ITM birds was 82.1% ± 2.1 (*N* = 106) and did not differ significantly from first roosts of ITM birds (85.2% ± 2.2, *N* = 85; t-test: t = -1.0, df = 189, P= 0.32). For ITM birds, second roosts had significantly less forest cover (70.4% ± 2.9%) than first roosts (fig. 4A; paired t-test: t = 3.98, df = 84,P < 0.001). After ITM birds occupied regions with a more agricultural land use (fig. 4A; first site: 5.1% ± 1.3 versus second site: 19.1% ± 2.5). The extent of natural savannah and grassland habitat near roost sites was < 10% for the majority of birds regardless of migration strategy. There was no significant difference in average daily temperature or rainfall (fig. 4 B,C) between first and second roost sites (paired t-test: temperature: t = -1.6, df = 84, P =0.10; rainfall: t = 1.54, P = 0.13).

We indirectly tested for evidence of density-dependence by examining how arrival date affects the location of a bird's first winter roost site. Birds from northern latitudes arrived at wintering sites several months after the first arrival of birds from southern latitudes (fig. 3). The entire arrival period in Brazil spanned 4 months across the breeding populations from Florida to Alberta. Birds arriving in the first 30d of this winter season settled almost exclusively (90%) in the core winter range of the northwestern Amazon (fig. 4*A*) while later arriving birds were increasingly more likely to settle far outside the core. Only 29% of birds that arrived during the last month of the four-month species-wide arrival window settled in the core (fig. 4*D*).

Discussion: Unlike some species (Heckscher et al. 2015; table 1), ITM in Purple Martins is an example of partial rather than obligate migration and ITM in martins is not coordinated temporally or spatially (fig 2, 3). ITM does not appear to be condition-dependent because it is not predicted by age, sex, or breeding latitude. Purple Martin ITM also does not appear to track large scale changes in resources. Forest cover was lower, not higher, after ITM but this does not necessarily reflect active habitat preference. Extensive forest loss in the eastern Amazon has occurred in the past few decades (Morton et al. 2006) and individuals that move away from the corewintering region in the western Amazon may have little choice but to occupy less forested landscapes. The core wintering region occupied by Purple Martins in northwestern Brazil has higher annual rainfall, and a far shorter and less pronounced dry season, than other parts of Brazil (Villar et al. 2009). Purple Martin ITM showed a south and eastward shift toward drier regions but movements occurred over a broad time period (Oct-Mar) and second sites did not have more rainfall that first sites. To test the extent to which ITM is facultative in martins, and thus varies from year to year depending on the conditions an individual encounters (Newton 2012) would require repeat-tracking of individuals in multiple years.

Instead, we suggest that ITM away from the core wintering region in the northwestern Amazon could be triggered by increasing roost density. Although Purple Martins occupy a large geographical area in Amazonia, roost sites may be limited in number due to the use of traditional roost sites and social attraction. For migratory roosts in North America, roost sites are often small islands or bridges, are re-occupied annually for decades, contain tens of thousands of birds, and are associated with lakes or rivers (Russell et al. 1998). Rather than viewing the upper Amazon as limitless in terms of available habitat for Purple Martins, roost sites could be finite in number and have their own carrying capacity. Interspecific competition may play a role also, because *Progne* roosts in Brazil are described as being comprised mostly of Gray-breasted Martins (*P. chalybea;* Davidar and Morton 1993). Aerial insectivores are non-territorial and so one might assume density-dependent regulation is unimportant on the wintering grounds, at least compared with territorial species (e.g. Marra et al. 2015). However, it is not known how roost size affects individual fitness or whether high density at a given roost triggers ITM. For this, and other species with ITM, understanding the evolution of ITM will require field studies on the wintering grounds which, in most cases, are logistically very difficult to undertake.

ITM and Evolution of Migration

Intra-tropical migration as a second migration system in long-distance latitudinal migrants should not be surprising to temperate zone biologists. Individuals of these species have already flown some thousands of kilometers on fall migration and ITM movements are short distance by comparison (table 1) and ITM in tropical species is well known (Morton 1977). However, most winter ecology studies of migratory passerines have been on territorial insectivorous species because these are easier to study. One can band individuals, map territories, monitor body condition and survival over time, and even do removal experiments to test how territory quality affects fitness (Studds and Marra 2005, McKinnon and Stutchbury 2015). Species that inconveniently move outside the study site on a regular basis would be avoided and hence are understudied and unappreciated. Since ITM has just recently been discovered in temperate-breeding passerines, it remains unknown how or if individuals prepare physiologically for ITM. Migratory birds enter a distinct physiological state to prepare for, and execute, fall and spring migration which involves 'migratory restlessness' (which is nocturnal for many passerines) and rapid accumulation of fat stores to fuel migration (Newton 2008). Obligate migration is under genetic control, mediated by day length and other environmental factors, and is highly predictable from year to year. With this strong endogenous control of long distance migration, it is reasonable to have assumed that migration behavior is physiologically turned off once birds arrive at their destination. Another reason that ITM is surprising is that the stationary period is one of relative safety for migratory birds (Sillett and Holmes 2002, Klassen et al. 2013) so the benefits of ITM must be high enough to offset energetic and mortality costs. These benefits are most obvious in the temperate zone where seasonal shifts in resources are extreme. In comparison we know little about how habitat quality varies geographically within the winter range of long-distance migrants.

Heckscher et al. (2015) suggested that distinct ITM movements in *Catharus* thrushes supports the hypothesis that within-tropics movements of resident birds preceded and perhaps facilitated the evolution of Nearctic–Neotropical migration (Levey and Stiles 1992). ITM may therefore be an ancestral state that persisted in some species after migration to temperate regions evolved. The ecology and behavior of migrants while they are in the tropics should therefore be similar to that of tropical species (Chesser and Levey 1998). The Purple Martin is the only Nearctic-breeding species of New World martin (*Progne*) and apparently diverged relatively long ago from its tropical congeners (Moyle et al. 2008). Thus ITM in Purple Martins may be an ancestral trait that evolved due to historical differences in habitat quality that do not necessarily persist today.

Studies of partial migration in many animals has laid the theoretical and empirical foundation for understanding the evolution of migration because it is possible to quantify how the costs and benefits of migration vary among individuals in a population (Boyle et al. 2011, Chapman et al. 2011, Green et al. 2015). However, it will be some time before it is possible to use ITM to similarly advance our understanding of long-distance migration. At present, the only tracking technologies available for small birds are archival devices which means that migration data can only be collected for individuals that survive both of their temperate-tropical journeys and any ITM movements that occur. We cannot yet test if ITM has a positive or negative effect on winter survival or spring migration survival or how this compares with individuals that remain sedentary on their wintering grounds. As new live-tracking technology becomes available in the future, ITM species will be important for testing hypotheses for how long distance movements out of the tropics evolved.

Intra-tropical Migration and Population Dynamics

Many migratory species are in decline but understanding and predicting their population dynamics is challenging because individuals occupy widely divergent and geographically distant habitats during a single year. There is currently a large effort underway to gather sufficient demographic data on reproduction and survival, and to measure seasonal carry-over effects, to create ‘full-life cycle’ models to better predict population dynamics of migratory birds (Harrison et al. 2011). For most species we do not yet know the geographical patterns of migratory connectivity between breeding and wintering sites, which is a prerequisite for predicting how habitat loss in one region will affect overall population dynamics. Network modeling has been used to show, theoretically, that shifts in migratory connectivity patterns can occur in response to habitat or climate changes and that habitat loss in one region can affect sub-populations even in regions that are not directly connected. For instance, Taylor and Stutchbury (2015) developed a network model, parameterized by integrating long-term monitoring data with direct tracking (Stanley et al. 2015) to explain population trends in the rapidly declining Wood Thrush (*Hylocichla mustelina*). Migratory connectivity in this species is moderately strong with an overall pattern of parallel, leapfrog migration (fig. 6*A*) and this species does not undergo intra-tropical migration. This network model suggests that species-level declines in Wood Thrush are driven primarily by tropical deforestation in Central America and that future shifts in migratory connectivity could lead to unexpected population declines in key breeding regions. Even species that are sedentary on the wintering grounds, like the Wood Thrush, quantifying the migratory network and then developing a network model to predict population dynamics is difficult (Taylor and Stutchbury 2015).

The reality is that many migratory passerines undergo further movements on their tropical wintering grounds which greatly complicates the concept of migratory connectivity. Most studies simply describe migratory connectivity qualitatively (and subjectively) as ‘weak’ versus ‘strong’ to describe the extent to which breeding populations mix on the wintering grounds. For Bobolink, all breeding populations apparently converge in northern Venezuela and also share the same subsequent ITM movements, so migratory connectivity is essentially 100% (fig. 6*B*). This does not overly complicate population dynamic modelling because the migratory network is relatively simple. But for other species, like Purple Martins, where ITM is partial migration and movements are not as predictable spatially or temporally, the migratory network becomes more complex (fig. 6*C*). Nevertheless, tracking many birds from across the breeding range combined with Breeding Bird Survey estimates of population size in each breeding region allows us to quantify the percentage of the eastern Purple Martin subspecies (*P. subis subis*) population that occupies each of three Amazonian wintering regions for at least 30 d. The northwestern Amazon is an important wintering region for 70% of Purple Martins. Full-life cycle models and migratory networks are essential for predicting population dynamics of declining temperate-breeding species and will have to incorporate ITM to properly address seasonal carry over effects and to identify which wintering regions are most important for conservation.

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Table 1. Passerine species in which long-distance intra-tropical migration (ITM) has been documented on the wintering grounds using direct tracking. Table shows non-breeding diet and social system, number of birds tracked (*n*), location of wintering grounds, timing of ITM and percentage of birds tracked that underwent ITM.

Species	Non-breeding Diet	Non-breeding Social System	*n*	Fall Migration Distance (km)	Winter Grounds	Timing of ITM	ITM Distance (km)	% ITM
E. Kingbird[1]	Frugivore	Small flock	7	7000	South America	Dec-Mar	1200	86%
W. Kingbird[1]	Frugivore	Small flock	5	1500	Central America	Oct	2500	100%
Fork-tailed Flycatcher[2]	Frugivore	Small flock	6	3500	South America	Apr-May*	800	83%
Purple Martin[3]	Aerial insectivore	Roost	191	6000	South America	Sept-Mar	800	44%
Tree Swallow[4]	Aerial insectivore	Roost	11	>2700 km	Southern Mexico	?	~500	9%
Barn Swallow[5]	Aerial insectivore	Roost	66	4000	Central Africa	?	~750	15%
Veery (eastern)[6]	Omnivore	Solitary	25	6400	South America	Jan-Mar	1400	100%
Veery (western)[7]	Omnivore	Solitary	9	9000	South America	Mar-Apr	1400	89%
Swainson's Thrush[8]	Omnivore	Solitary	9	4000	South America	Dec-Jan	420	30%
Swainson's Thrush[9]	Omnivore	Solitary	12	2500	South America	Nov-Dec	900	18%
Bobolink[10]	Granivore	Roost	15	6000	South America	Nov	4000	100%
Tawny Pipit[11]	Insectivore	Solitary	6	4230	Western Africa	Nov-Jan	472	83%
Great Reed Warbler[12]	Insectivore	Solitary	7	6300	Central Africa	Dec-Jan	700	100%

[1] Jahn et al. 2013a; [2] Jahn et al. 2013b; [3] this study; [4] Laughlin et al. 2013; [5] Liechti et al. 2015; [6] Heckscher et al. 2011, 2015; [7] Hobson and Kardynal 2015; [8] Delmore et al. 2012; [9] Cormier et al. 2013; [10] Renfrew et al. 2013; [11] Briedis et al. 2016; [12] Lemke et al. 2013

*austral migrant

Figure 1. A) Breeding and wintering range of the Purple Martin (*Progne subis subis*) showing breeding ground sites where geolocators were deployed. Southern populations (< 30° N, black): southern Texas, Florida; central populations (30-40° N, dark grey): northern Texas, South Carolina, Virginia; northern populations (white, > 40° N): Alberta, South Dakota, Minnesota, Pennsylvania, New Jersey. Winter range determined from wintering sites occupied for at least 30 d (*N*= 191 unique individuals, 332 roost sites).

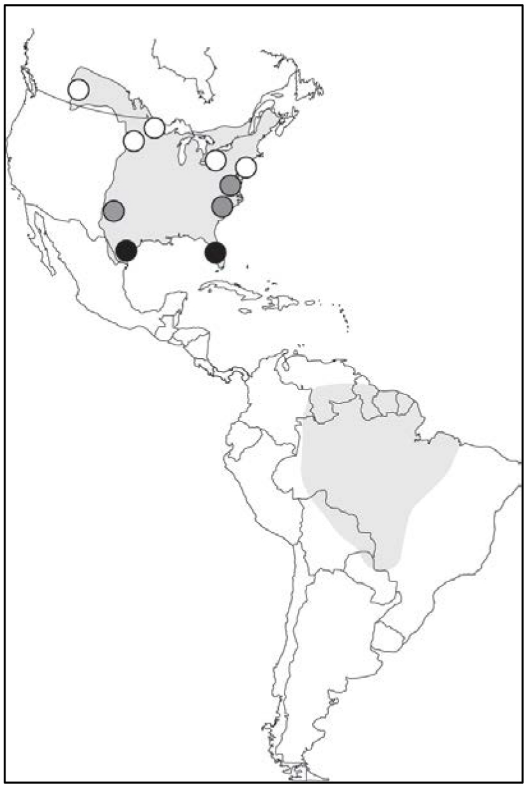
Figure 2. *A*) Average position of winter roost site (estimated from geolocator tracking) of Purple Martins (*N* = 106) that did not undergo intra-tropical migration (ITM), *B*) First winter roost sites of ITM birds (*N* = 85 individuals), *C*) second roost sites of ITM birds. ITM was defined as moving at least 500 km between roost sites that were occupied for 30 d or more. Maps show kernels of 20, 40, 60 and 80% of the total density. Background shows forest cover (green) and agricultural landscapes (yellow).

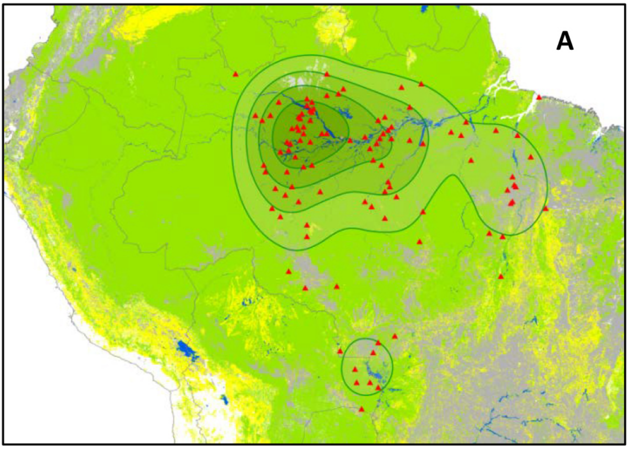
Figure 3. Variation in timing of arrival on the wintering grounds (black bars), intra-tropical migration (ITM: white bars), and departure on spring migration within and between breeding regions (black bars). *A*) Northern populations (> 40° N; *N* =103, *N* = 41); *B*) Central populations (30-40° N, *N* = 44, *N* = 17); *C*) Southern populations (< 30° N; *N* = 44 for arrival/departure, *N* = 23 ITM).

Figure 4. Boxplots showing (*A*) difference in landscape cover between first and second winter site (*N* = 85), and difference in *B*) average daily temperature and *C*) average daily precipitation for individuals before and after their first (*N* = 85) and second (*N* = 18) ITM movements.

Figure 5. Relationship between arrival date on the wintering grounds and location of first prolonged (≥ 30d) winter site (*N* = 191) for all birds tracked with geolocators. Panels A-D show arrival date in 30d intervals from first observed arrival (7 July = day 1). Dashed rectangle shows core winter range based on kernel density (-7° to 0° latitude, -57° to -65° longitude). Circles: no subsequent intra-tropical migration (ITM); Triangles: subsequent ITM (2nd location not shown).

Figure 6. Migratory connectivity networks for species where *A*) individuals are sedentary on their wintering grounds (Wood Thrush; from Stanley et al. 2015), *B*) all individuals undergo ITM to distinct regions (Bobolink), and C) ITM is variable within populations and sites are overlapping (Purple Martin). Circles are breeding regions and squares are wintering regions. Width of lines approximate the frequency of birds moving between sites.

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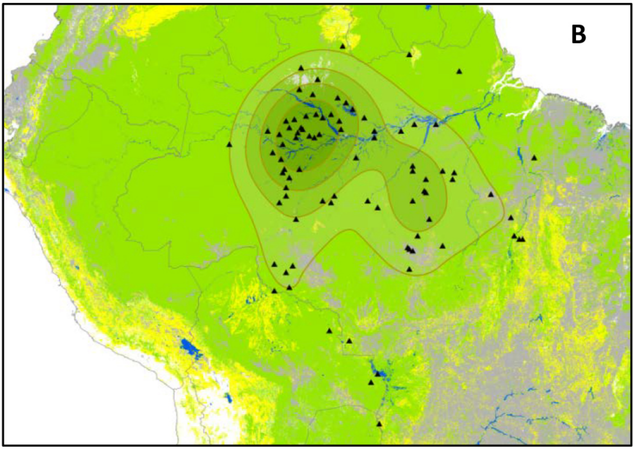
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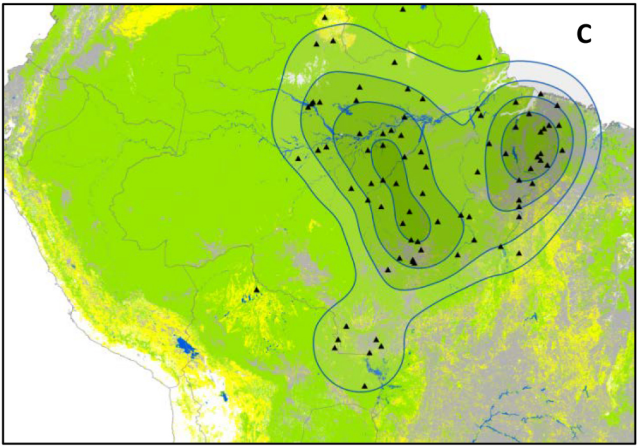
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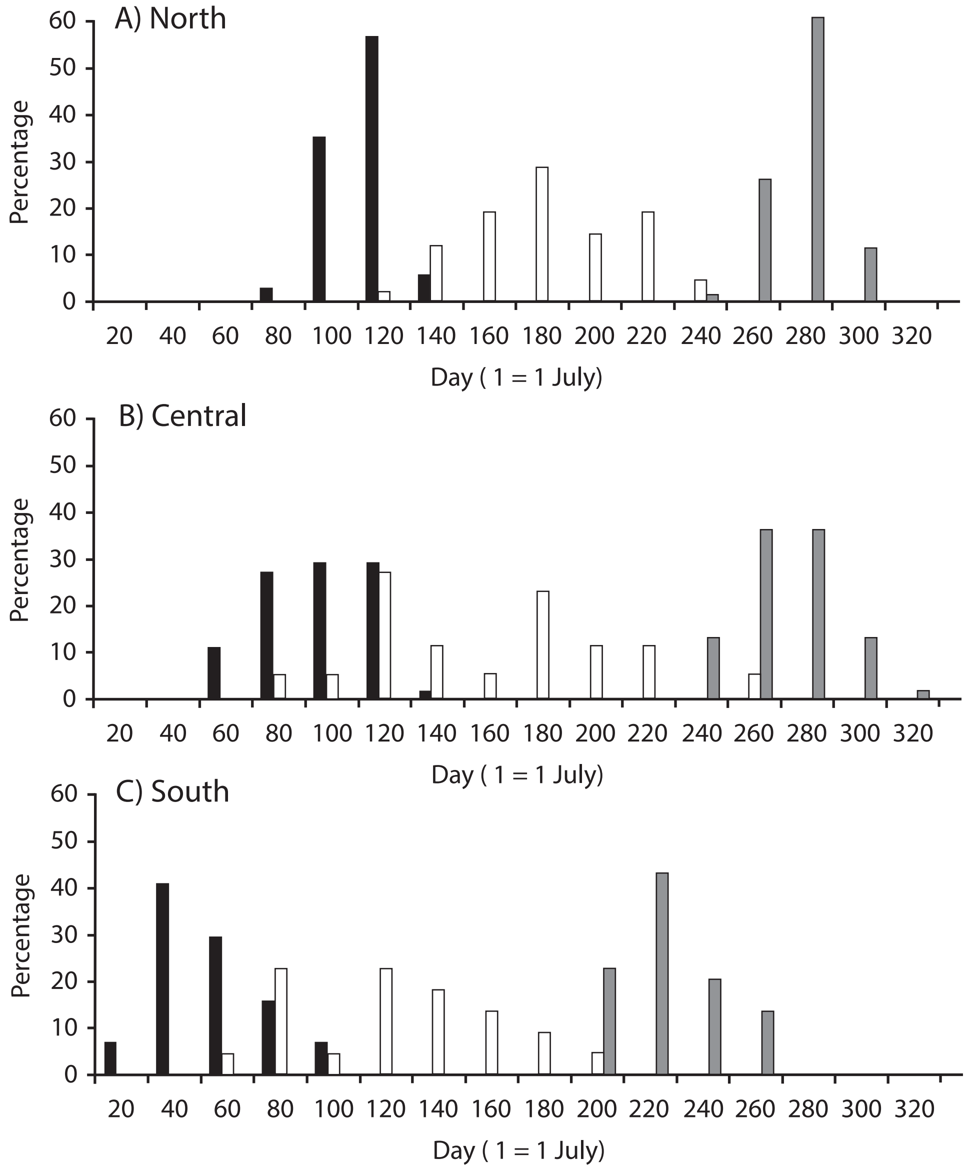
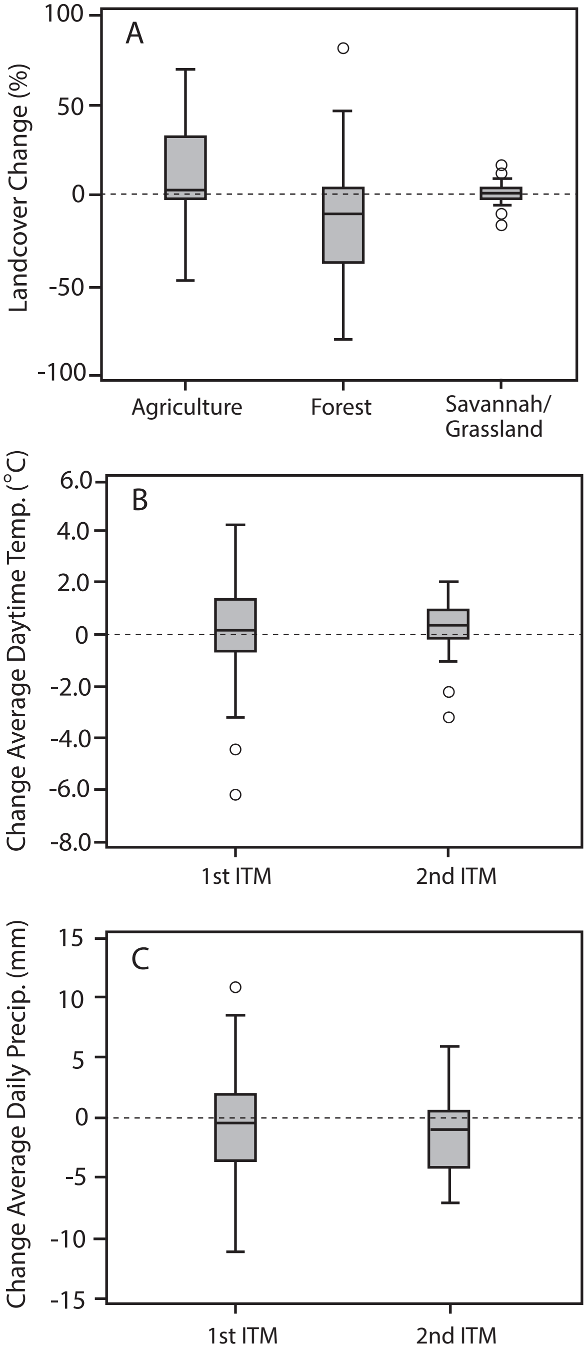
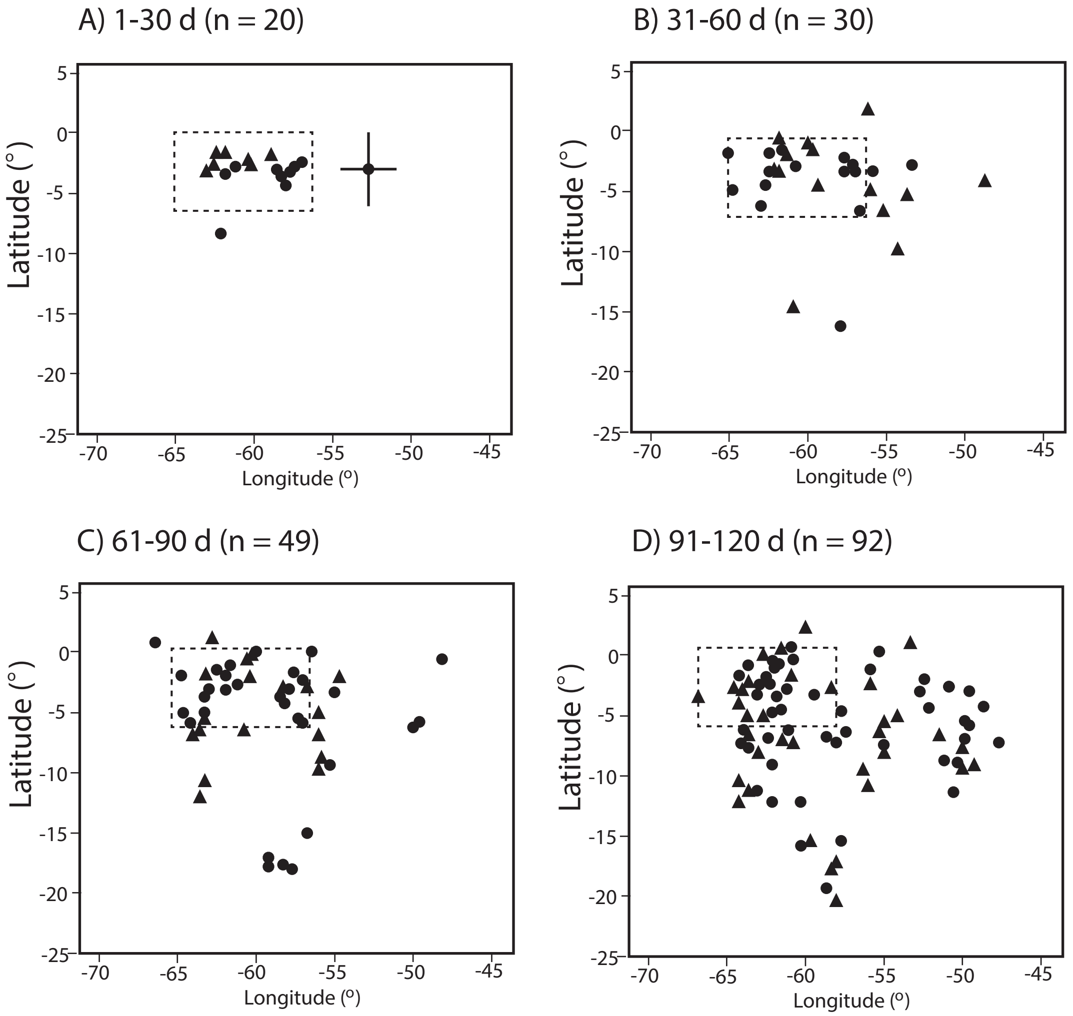
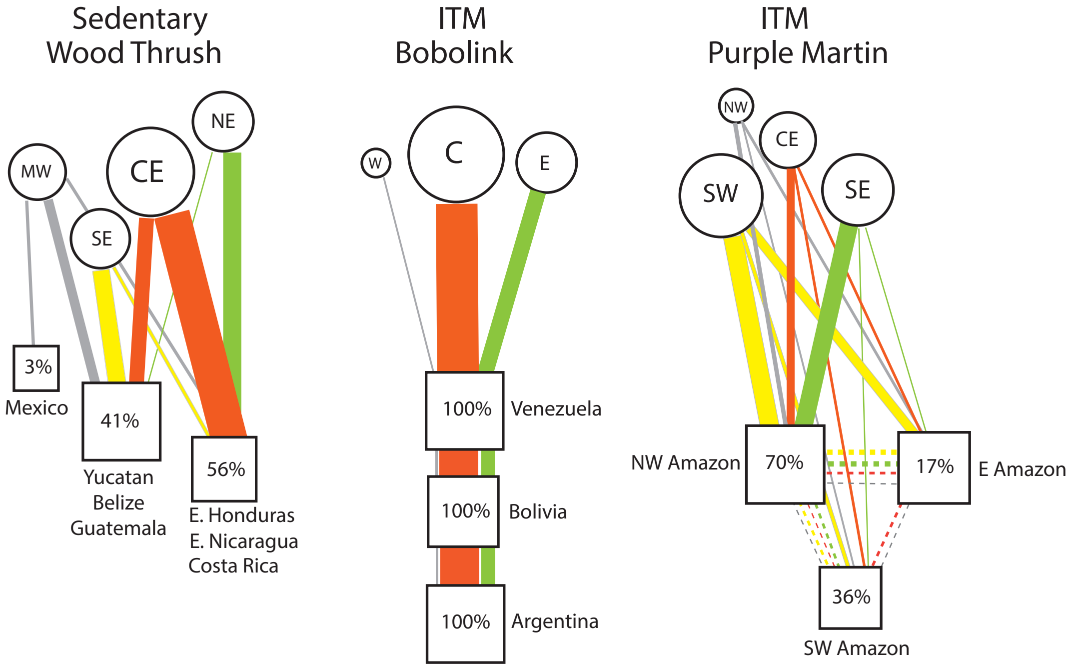

A) North
Percentage
0
10
20
30
40
50
60
20
40
60
80
100
120
140
160
180
200
220
240
260
280
300
320
Day (1 = 1 July)
B) Central
Percentage
0
10
20
30
40
50
60
20
40
60
80
100
120
140
160
180
200
220
240
260
280
300
320
Day (1 = 1 July)
C) South
Percentage
0
10
20
30
40
50
60
20
40
60
80
100
120
140
160
180
200
220
240
260
280
300
320
Day (1 = 1 July)


A
Landcover Change (%)
100
50
0
-50
-100
Agriculture
Forest
Savannah/
Grassland
B
Change Average Daytime Temp. (°C)
6.0
4.0
2.0
0
-2.0
-4.0
-6.0
-8.0
1st ITM
2nd ITM
C
Change Average Daily Precip. (mm)
15
10
5
0
-5
-10
-15
1st ITM
2nd ITM


A) 1-30 d (n = 20)
B) 31-60 d (n = 30)
C) 61-90 d (n = 49)
D) 91-120 d (n = 92)
Latitude (°)
Longitude (°)
5
0
-5
-10
-15
-20
-25
-70
-65
-60
-55
-50
-45



Sedentary Wood Thrush

ITM Bobolink

ITM Purple Martin