

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

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Online enhancements: appendix, video. Dryad data: <http://dx.doi.org/10.5061/dryad.785sc>.

ABSTRACT: New discoveries from direct tracking of temperate-breeding passerines show that intratropical migration (ITM) occurs 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, something 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 need to incorporate ITM to properly address seasonal carryover effects and identify which wintering regions are most important for conservation.

Keywords: migration, wintering grounds, intratropical migration, seasonality, temperate bias.

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 nonbreeding 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 two or three 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 2,500-km ocean crossing in autumn requiring up to 3 days of nonstop flight (DeLuca et al. 2015). Northern wheatears (*Oenanthe oenanthe*) breeding in the eastern Canadian arctic travel over 14,000 km to their nonbreeding (wintering) grounds in western Africa (Bairlein 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 intratropical migration (ITM), which until recently has been a term used to describe the seasonal migration of tropical

* This issue originated as the 2015 Vice Presidential Symposium presented at the annual meetings of the American Society of Naturalists.

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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 diets (fruit, soil arthropods, seeds, aerial insects), winter social organization (solitary, flocking, large nocturnal roosts), and winter habitats (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, modeling population dynamics, and 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 that birds physiologically switch from hyperphagia and migratory restlessness to a sedentary nonbreeding lifestyle (Newton 2008). Indeed, the wintering period of temperate-tropical migrants has been referred to as the "stationary" period (Sillert and Holmes 2002) to avoid the inaccuracy of labeling 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 nonbreeding season—through band resighting (Sillert and Holmes 2002) or short-distance radio tracking (Kresnik and Stutchbury 2014). Many species that do exhibit ITM (table 1) are gregarious and nonterritorial 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 bobolinks (*Dolichonyx oryzivorus*) 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 bobolinks 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. On arrival at their wintering grounds, veeries (*Catharus fuscescens*) first occupy lowland forest in southern Amazonia, and the generally northward ITM that occurs from December to March in this ground-foraging bird may be prompted by the seasonal flood 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 northwestern South 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 payoffs for migrants and residents. In a tropical lekking bird, the white-ruffed manakin (*Corapipo altera*) males who migrate altitudinally during the nonbreeding 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 six to 15 times

Table 1: Passerine species in which long-distance intratropical migration (ITM) has been documented on the wintering grounds using direct tracking

Species	Nonbreeding diet	Nonbreeding social system	n	Fall migration distance (km)	Winter grounds	Timing of ITM	ITM distance (km)	% ITM	References
Eastern kingbird	Frugivore	Small flock	7	7,000	South America	December–March	1,200	86	Jahn et al. 2013a
Western kingbird	Frugivore	Small flock	5	1,500	Central America	October	2,500	100	Jahn et al. 2013a
Fork-tailed flycatcher	Frugivore	Small flock	6	3,500	South America	April–May ^a	800	83	Jahn et al. 2013b
Purple martin	Aerial insectivore	Roost	191	6,000	South America	September–March	800	44	This article
Tree swallow	Aerial insectivore	Roost	11	>2,700	Southern Mexico	?	~500	9	Laughlin et al. 2013
Barn swallow	Aerial insectivore	Roost	66	4,000	Central Africa	?	~750	15	Liechti et al. 2015
Veery (eastern)	Omnivore	Solitary	25	6,400	South America	January–March	1,400	100	Heckscher et al. 2011, 2015
Veery (western)	Omnivore	Solitary	9	9,000	South America	March–April	1,400	89	Hobson and Kardynal 2015
Swainson's thrush	Omnivore	Solitary	9	4,000	South America	December–January	420	30	Delmore et al. 2012
Swainson's thrush	Omnivore	Solitary	12	2,500	South America	November–December	900	18	Cormier et al. 2013
Bobolink	Granivore	Roost	15	6,000	South America	November	4,000	100	Renfrew et al. 2013
Tawny pipit	Insectivore	Solitary	6	4,230	Western Africa	November–January	472	83	Briedis et al. 2016
Great reed warbler	Insectivore	Solitary	7	6,300	Central Africa	December–January	700	100	Lemke et al. 2013

^a Austral migrant.

higher compared with their sedentary period on the breeding or wintering grounds (Sillert and Holmes 2002; Klaassen 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, which results in lower fitness for migrants than for residents. Altitudinal migration in American dippers (*Cinclus mexicanus*) 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 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 this could trigger ITM in some species.

Purple Martins: Testing Hypotheses for ITM

Our direct tracking has shown that 44% of 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 article). 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 (Davidar and Morton 1993; Hill 1993).

First, we test whether 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 young 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) may be more likely to exhibit ITM than individuals from 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 (Davidar and Morton 1993; Hill 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. Purple martin breeding abundance is about three times higher in the southern half of their range (table A1; fig. A1, available online), which could put later arriving northern populations at a disadvantage. 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, and MK20, and Biotracker equivalent models) during the nesting period (2007–2014, $N = 987$

geolocators) at multiple breeding sites in Canada (Alberta) and the United States (Florida, Minnesota, New Jersey, Pennsylvania, South Carolina, South Dakota, Texas, and 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 geocator (Fraser et al. 2012). Most geolocators (80%) were deployed on birds in at least their second year of breeding, as identified by their distinct adult plumage characteristics that differ from 1-year-old birds (Tarof and Brown 2013). The exact age of adults ≥ 2 years old was deter-

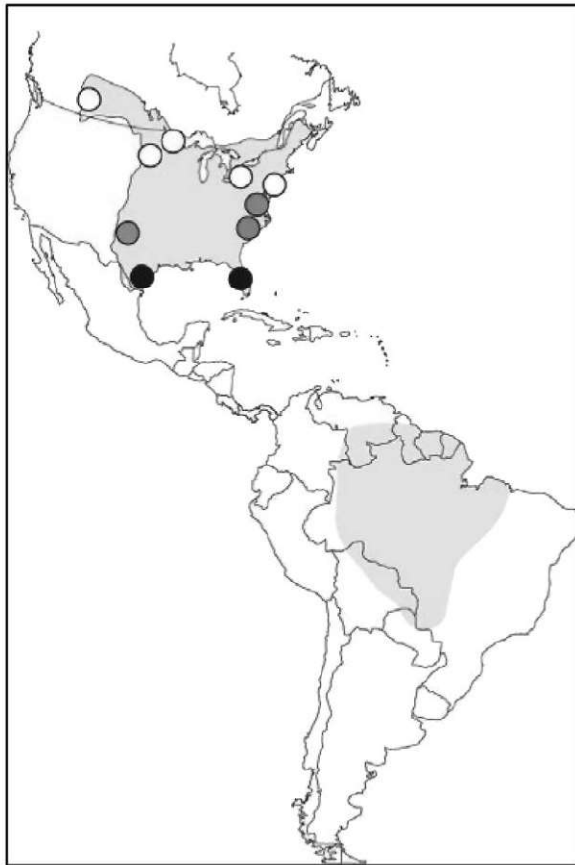


Figure 1: Breeding and wintering range of the purple martin (*Progne subis subis*) showing breeding ground sites where geolocators were deployed. Southern populations ($<30^{\circ}\text{N}$; black circles): southern Texas, Florida; central populations (30° – 40°N ; gray circles): northern Texas, South Carolina, Virginia; northern populations ($>40^{\circ}\text{N}$; white circles): Alberta, South Dakota, Minnesota, Pennsylvania, New Jersey. Winter range is determined from wintering sites occupied for at least 30 days ($N = 191$ unique individuals, 332 roost sites).

mined if they were first banded as nestlings or 1-year-olds, and minimum age was 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. Geocator 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 days on its wintering site and in which the bird occupied the new winter roost for at least 30 days. This definition of ITM ensures that the movements fall far outside geocator measurement error for individuals.

To map roost sites of ITM and non-ITM birds, we determined kernel densities at 20%, 40%, 60%, and 80% 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 (Fraser et al. 2012). We calculated the percentage 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 geocator error) around each winter roost. We also obtained weather data using the European Centre for Medium-Range Weather Forecasts Global Atmospheric Reanalysis through Movebank (<http://www.movebank.org>) for average daily temperature and rainfall for each individual 2 weeks prior to ITM and at the second site for 2 weeks after ITM.

We combined the observed purple martin tracking data with breeding region population estimates (table A1; fig. A1) to create a migratory network that included ITM movements between winter regions. A migratory network estimates the percentage of the North American population (of the eastern subspecies, *Progne subis subis*) that moves between different breeding and winter regions (Stanley et al. 2015).

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 (>30 d) roost site (fig. 2). The first ITM was a mean distance of 776 ± 43 km (SE) from the first roost site. Average duration of roost occupancy was 66 ± 3 days at the first wintering site and 77.6 ± 3.4 days at the second site (paired t -test, $t = -2.06$, $N = 85$, $P = .042$). Only 18 of these 85 ITM martins underwent a second ITM. Average distance from the second to the third site was 763 ± 47.5 km (maximum 1,100 km), and occupancy duration of the third site was 58.1 ± 4.6 days. Data underlying figure 2 (and figs. 3–5) are deposited in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.785sc> (Stutchbury et al. 2016).

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 was a significant predictor of which individuals exhibited ITM (year: Wald's $\chi^2 = 0.37$, $P = .54$; latitude: $\chi^2 = 0.36$, $P = .54$; age: $\chi^2 = 0.08$, $P = .77$; sex: $\chi^2 = 0.06$, $P = .80$).

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 first roost sites similar to those of birds that did not undergo ITM (fig. 2). First roost sites were primarily concentrated in the northwestern Amazon, and second sites were primarily concentrated in the eastern Amazon. However, at a population level there was much geographic overlap in regions occupied by first versus second roosts (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 with bobolinks (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. However, average forest cover within 50 km of roosts for non-ITM birds was $82.1\% \pm 2.1\%$ ($N = 106$) and did not differ significantly from first roosts of ITM birds ($85.2\% \pm 2.2\%$, $N = 85$; t -test: $t = -1.0$, $df = 189$, $P = .32$). For ITM birds, second roosts had significantly less forest cover ($70.4\% \pm 2.9\%$) than first roosts (fig. 4A; paired t -test: $t = 3.98$, $df = 84$, $P < .001$). After ITM, birds occupied regions with more agricultural land use

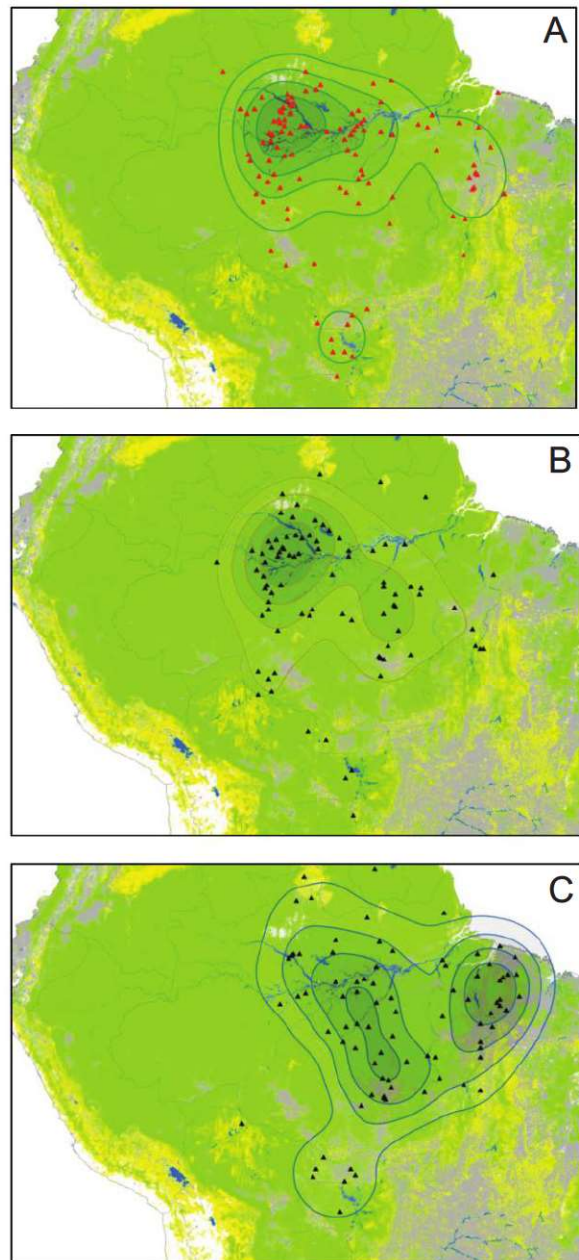


Figure 2: A, Average position of winter roost site (estimated from geolocator tracking) of purple martins ($N = 106$) that did not undergo intratropical migration (ITM). B, First winter roost sites of ITM birds ($N = 85$). C, Second roost sites of ITM birds. ITM was defined as moving at least 500 km between roost sites that were occupied for 30 days or more. Maps show kernels of 20%, 40%, 60%, and 80% of the total density. The background shows forest cover (green) and agricultural landscapes (yellow).

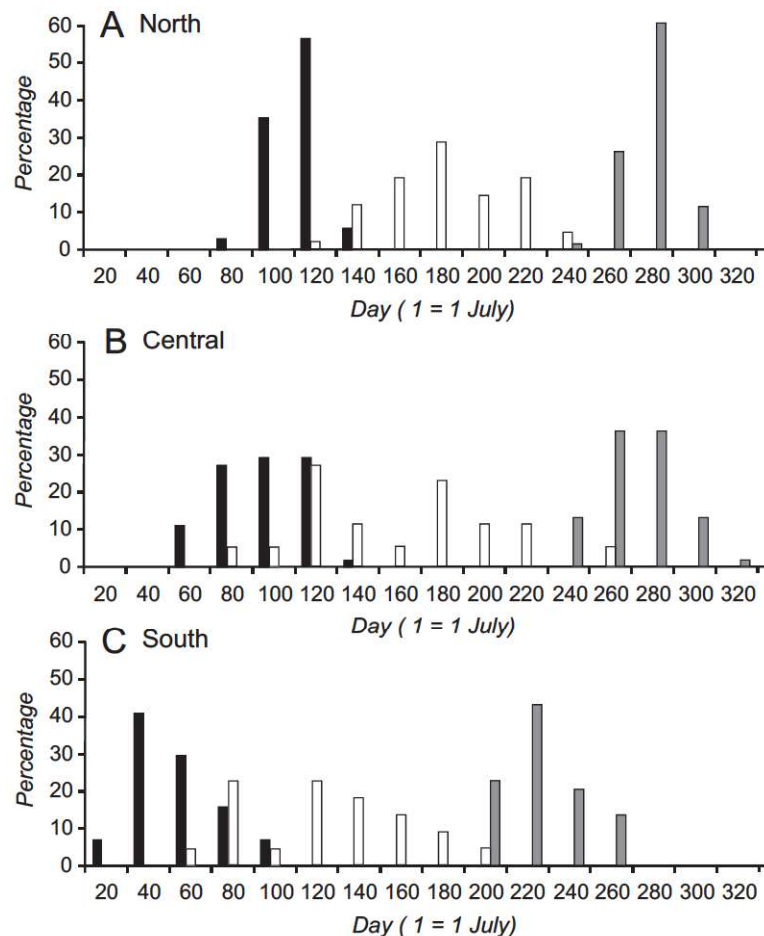


Figure 3: Variation in the timing of arrival on the wintering grounds (black bars), intratropical migration (ITM; white bars), and departure on spring migration (gray bars) within and between breeding regions. A, Northern populations ($>40^{\circ}\text{N}$; $N = 103$, $N = 41$). B, Central populations (30° – 40°N ; $N = 44$, $N = 17$). C, Southern populations ($<30^{\circ}\text{N}$; $N = 44$ for arrival/departure, $N = 23$ ITM).

(fig. 4A; first site: $5.1\% \pm 1.3\%$ vs. second site: $19.1\% \pm 2.5\%$). 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. 4B, 4C) between first and second roost sites (paired t -test, temperature: $t = -1.6$, $df = 84$, $P = .10$; rainfall: $t = 1.54$, $P = .13$).

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 30 days of this winter season settled almost exclusively (90%) in the core winter range of the northwestern Ama-

zon (fig. 4A; video A1, available online), 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 4-month species-wide arrival window settled in the core (fig. 4D).

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 (figs. 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

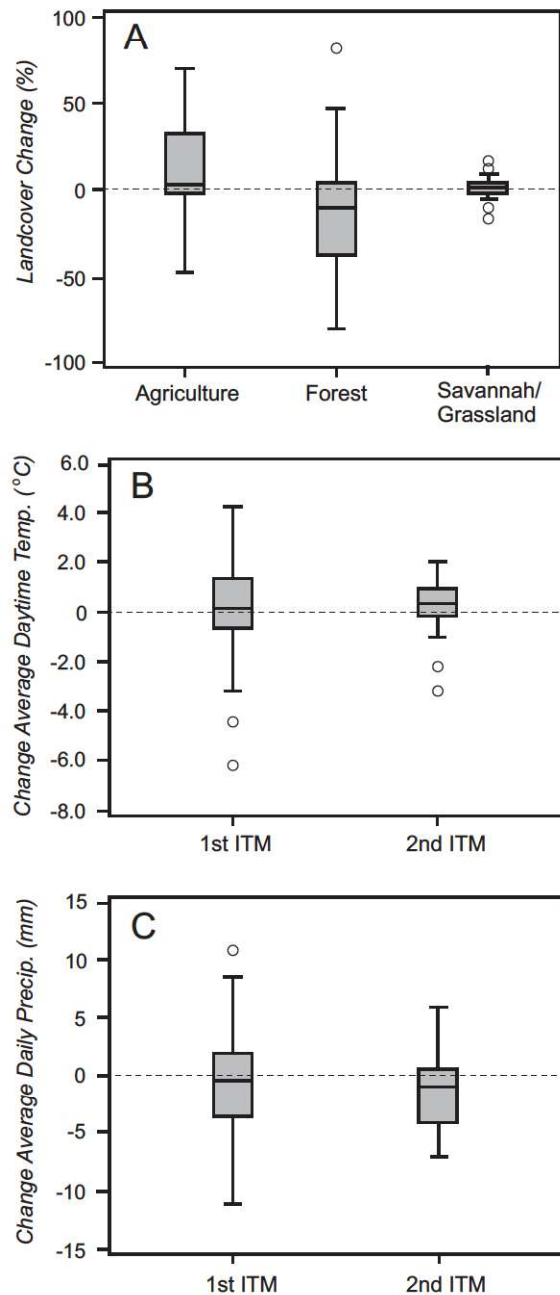


Figure 4: Boxplots showing the difference in landscape cover (A) between the first and second winter site ($N = 85$) and the difference in average daily temperature (B) and average daily precipitation (C) for individuals before and after their first ($N = 85$) and second ($N = 18$) ITM movements. Precip.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

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 core wintering region in the western Ama-

zon 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 southward and eastward shift toward drier regions, but movements occurred over a broad time period (October–March), and second sites did not have more rainfall than 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 reoccupied 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 also play a role, because *Progne* roosts in Brazil are described as being comprised mostly of gray-breasted martins (*Progne 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

Intratropical 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; ITM movements cover short distances 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 conduct removal experiments to test how territory quality affects fitness (Studds and Marra

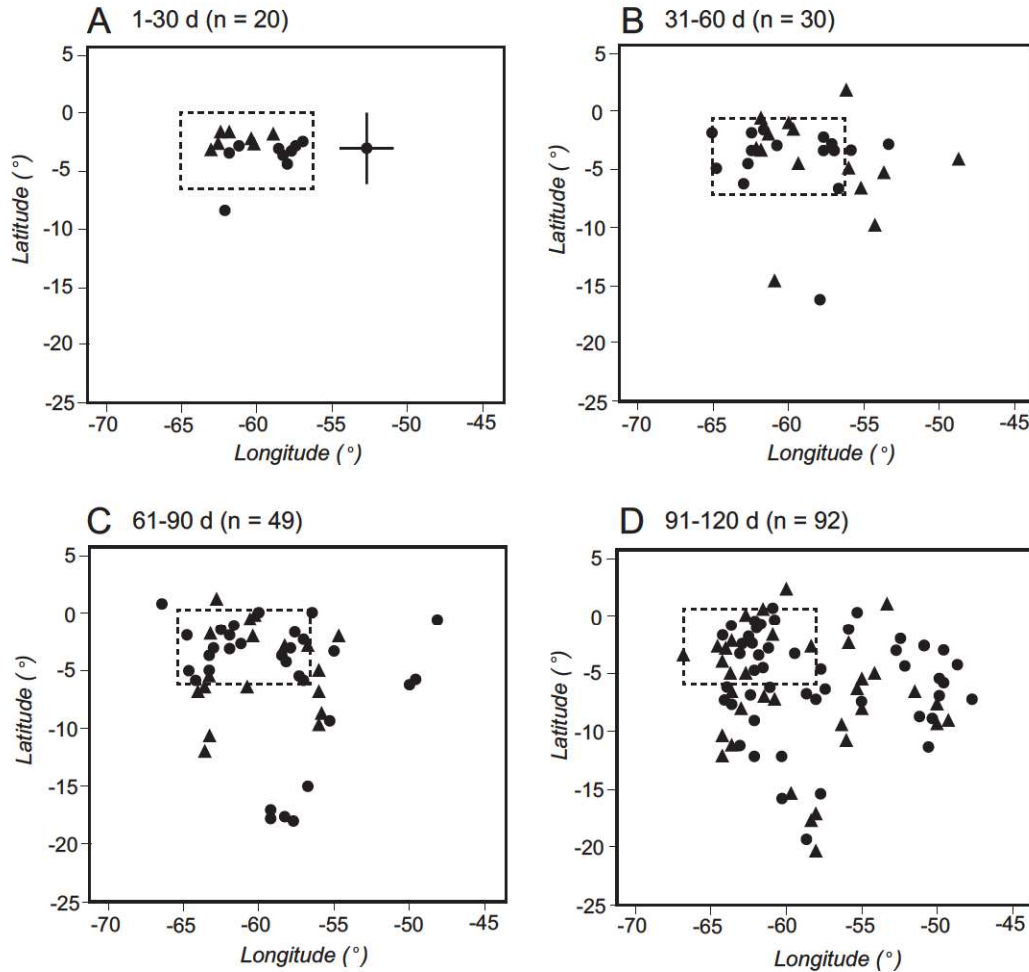


Figure 5: Relationship between the arrival date on the wintering grounds and the location of the first prolonged (≥ 30 days) winter site ($N = 191$) for all birds tracked with geolocators. Panels A–D show the arrival date in 30-day intervals from the first observed arrival (July 7 = day 1). Dashed rectangles show the core winter range based on kernel density (-7° to 0° latitude, -57° to -65° longitude). Circles indicate no subsequent intratropical migration (ITM). Triangles indicate subsequent ITM (second location not shown). The typical standard deviation in latitude and longitude of a winter roost site (error bars around the roost site) is shown with lines for one winter roost site in A.

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 whether individuals physiologically prepare for ITM. Migratory birds enter a distinct physiological state to prepare for and execute fall and spring migration that 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 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 (Sillert and Holmes 2002; Klaassen et al. 2013) and 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 support 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 have 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 whether 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.

Intratropical 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 under way to gather sufficient demographic data on reproduction and survival and to measure seasonal carryover effects to create full life cycle models that better predict population dynamics of migratory birds (Harrison

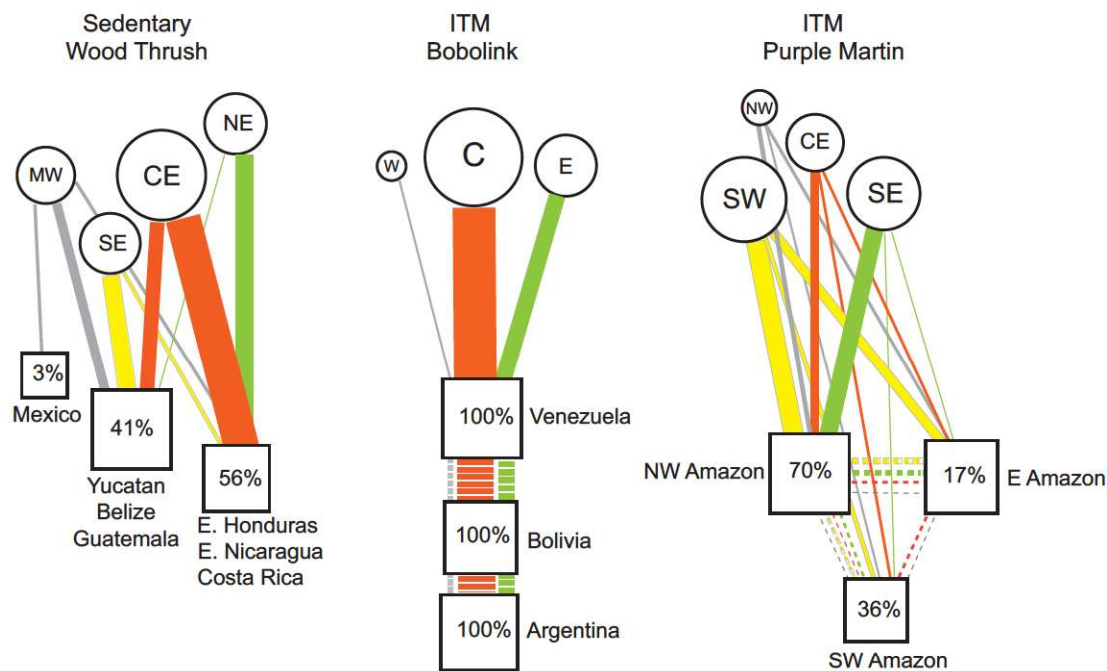


Figure 6: Migratory connectivity networks for species where individuals are sedentary on their wintering grounds (wood thrush; from Stanley et al. 2015; A), all individuals undergo intratropical migration (ITM; dashed lines) between the same distinct regions (bobolink; B), and ITM occurs in only a portion of the population (purple martin; C). Circles indicate breeding regions, with the size of the circle relative to the abundance of the species within each region. Squares indicate wintering regions, with the size of the square relative to the geographic area of the region. Percentages given in the winter regions indicate the estimated proportion of the North American population that occupies a given winter region. The widths of lines (color coded for each breeding region) are relative to the frequency of all birds (North American population estimate) moving between sites.

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 subpopulations even in regions that are not directly connected (Taylor and Norris 2010). For instance, Taylor and Stutchbury (2016) 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. 6A), and this species does not undergo intratropical migration. This network model suggests that species-level declines in wood thrushes 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 for species that are sedentary on the wintering grounds, such as the wood thrush, quantifying the migratory network and then developing a network model to predict population dynamics is difficult (Taylor and Stutchbury 2016).

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 bobolinks, all breeding populations apparently converge in northern Venezuela and also share the same subsequent ITM movements (fig. 6B). This does not overly complicate population dynamic modeling, because the migratory network is relatively simple. However, for other species, such as purple martins, migratory connectivity is very low (Fraser et al. 2012; fig 6C). ITM is partial migration; movements are variable both spatially or temporally, and the migratory network becomes more complex (fig. 6C). Nevertheless, tracking many birds from across the breeding range combined with Breeding Bird Survey estimates of population size in each breeding region (table A1) allows us to quantify the percentage of the eastern purple martin subspecies (*Progne subis subis*) population that occupies each of three Amazonian wintering regions. The northwestern Amazon is an important wintering region (minimum occupancy 30 days) 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 need to incorporate ITM to properly address seasonal carryover effects and identify which wintering regions are most important for conservation.

Acknowledgments

We thank E. Brockwell and J. Tautin of the Purple Martin Conservation Association for long-term project support. For field work we thank B. Aeppli, J. Barrow, J. Beatson, J. Hovis, P. Kramer, D. Newstead, B. Ortego, and C. Silverio. At Disney's Animals, Science, and Environment we thank R. Lindborg, J. Mejeur, L. Moscar, and M. Pearson as well as other team members. We also thank the dozens of dedicated volunteers at all our study sites who assisted with geolocator deployment and retrieval and other support. R.S. was supported by a Natural Sciences and Engineering Research Council Undergraduate Student Research Award. Major sources of funding for this research include the Natural Sciences and Engineering Research Council of Canada; a Liber Ero Postdoctoral Fellowship to K.C.F.; the National Geographic Society; the Kenneth M. Molson Foundation; the North American Bluebird Society; the Purple Martin Conservation Association; Ellis Bird Farm; the Red Deer and District Community Foundation; TD Friends of the Environment; Bird Studies Canada (James L. Baillie Memorial Fund); Dow Canada Community Grant Program; Alberta Sport, Recreation, Parks, and Wildlife Foundation; Disney's Animals, Science, and Environment; and the US Department of Energy/National Nuclear Security Administration in cooperation with Consolidated Nuclear Security (Pantex).

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Symposium Editor: Marlene Zuk



Adult male purple martin (*Progne subis*) in flight. Photo credit: Harold Stiver.