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ORIGINAL ARTICLE

Migratory stopover timing is predicted by breeding latitude, not habitat quality, in a long-distance migratory songbird

A. Van Loon[1] · J. D. Ray[2] · A. Savage[3] · J. Mejeur[3] · L. Moscar[3] · M. Pearson[3] · M. Pearman[4] · G. T. Hvenegaard[5] · N. Mickle[6] · K. Applegate[7] · K. C. Fraser[1]

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Abstract The timing of migration can have important survival impacts, as birds must synchronize their movements with favourable environmental conditions to reach their destination. The timing of arrival at and duration of migratory stopover may be largely governed by environmental conditions experienced en route as well as by endogenous factors, but our understanding of these processes is limited. We used light-level geolocators to collect start-to-finish spatio-temporal migration data for a declining aerial insectivore, the Purple Martin (*Progne subis*), that travels seasonally between North and South America. Using data obtained for birds originating from range-wide breeding populations, our objectives were to test intrinsic and extrinsic hypotheses for migration stopover duration as well as to identify important stopover regions during fall migration. We examined whether breeding latitude, fall migration timing, age, sex or habitat quality at stopover sites (measured using Normalized Difference Vegetation Index) influenced the duration of stopovers. We found that most individuals rely on the eastern coast of the Yucatan Peninsula, Honduras, and Nicaragua for stopovers during fall migration, where duration ranged from 1 to 36 days (average 6.8 ± 8.2). Stopovers in these regions were later and of longer duration for more northern breeding populations. Only breeding latitude predicted stopover duration, and not habitat quality at stopovers, lending support to the hypothesis that duration is prescribed by endogenous factors. The important core stopover regions we documented could be targeted for conservation efforts, particularly for steeply-declining, more northern breeding populations that have greater stopover duration in these areas.

Keywords Migration phenology · Migration behaviour · Aerial insectivore · Direct-tracking · Geolocator

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✉ K. C. Fraser
kevin.fraser@umanitoba.ca

1 Department of Biological Sciences, University of Manitoba, R3T 2N2 Winnipeg, MB, Canada

2 Consolidated Nuclear Security, LLC, Pantex Plant, Amarillo, TX 79120, USA

3 Disney's Animals Science and Environment, Lake Buena Vista, FL 32830, USA

4 Ellis Bird Farm, T4L 1W7 Lacombe, AB, Canada

5 Department of Geography and Environmental Studies Augustana Campus, University of Alberta, Camrose, AB T4V 2R3, Canada

6 1501 Spoonbill Court, Woodbridge, Virginia 22191, USA

7 Mille Lacs Band of Ojibwe Department of Natural Resources, 43408 Oodena Drive, Onamia, MN 56359, USA

Zusammenfassung

Der Breitengrad des Brutgebietes und nicht die Habitatqualität liefert bei einem langstreckenziehenden Singvogel Vorhersagen über den zeitlichen Ablauf der Rastpausen auf dem Zug

Die zeitliche Abstimmung des Zuggeschehens kann wichtige Auswirkungen für das Überleben haben, da die Vögel ihre Bewegungen mit günstigen Umweltbedingungen synchronisieren müssen, um ihr Ziel zu erreichen. Der Zeitpunkt der Ankunft und die Verweildauer am Rastplatz können zum großen Teil von den unterwegs erlebten Umweltbedingungen als auch von endogenen Faktoren bestimmt werden, allerdings ist unser Verständnis dieser Prozesse begrenzt. Wir setzten Hell-Dunkel-Geolokatoren ein, um zwischen Abflug und Ankunft räumlich-zeitliche Zugdaten eines im Bestand abnehmenden insektenfressenden Flugjägers, der Purpurschwalbe (Progne subis), zu sammeln, welche saisonal zwischen Nord- und Südamerika wechselt. Anhand von Daten, die von Vögeln aus Brutpopulationen des gesamten Verbreitungsgebietes stammten, wollten wir intrinsische und extrinsische Hypothesen zur Dauer von Zwischenstopps auf dem Zug überprüfen sowie wichtige Rastgebiete auf dem Herbstzug ausfindig machen. Wir untersuchten, ob der Breitengrad des Brutgebietes, der zeitliche Ablauf des Herbstzuges, Alter, Geschlecht oder die Habitatqualität an den Rastplätzen (gemessen anhand des normalisierten differenzierten Vegetationsindex; Normalized Difference Vegetation Index) die Rastdauer beeinflussten. Wir stellten fest, dass die meisten Individuen die Ostküste der Yucatan-Halbinsel und Honduras sowie Nicaragua für Zwischenstopps auf dem Herbstzug nutzten, wobei die Verweildauer zwischen 1 und 36 (im Mittel 6.8 ± 8.2) Tagen betrug. Weiter nördlich brütende Populationen machten später in dieser Region Rast und blieben länger. Allein der Breitengrad des Brutgebietes, nicht die Habitatqualität der Rastplätze, lieferte Voraussagen über die Verweildauer, was die Hypothese stützt, dass die Dauer von endogenen Faktoren bestimmt wird. Die von uns dokumentierten wichtigen Kernrastgebiete könnten als Fokus für Schutzmaßnahmen dienen, insbesondere für rapide abnehmende nördlichere Brutpopulationen, die länger in diesen Gebieten rasten.

Introduction

How songbirds time their migration, i.e., when to travel and how long to remain at stopover sites, and to what degree they are phenotypically flexible to environmental conditions they encounter during the journey, is an active area of investigation (Fraser et al. 2013b; Knudsen et al. 2011; McKinnon et al. 2013; Stanley et al. 2012; Tottrup et al. 2012a). Spring migration may be under strong time-selection, driven by breeding arrival date and its subsequent fitness benefits (Kokko 1999, Nilsson et al. 2013). In contrast, constraints during fall migration have been less well-studied, but timing may be governed by environmental conditions encountered en route or factors tied to the previous breeding season and location (Nilsson et al. 2013). Determining key stopover areas during fall migration, and factors driving stopover duration, could yield important insights into fall migration strategies and limitations. Factors contributing to variation in fall stopover duration may include extrinsic factors such as habitat quality and weather encountered at stopover locations, or intrinsic factors such as breeding site origin, age, or sex.

Most recent work based upon direct tracking has examined extrinsic hypotheses for how environmental factors influence stopover timing and duration in songbirds (e.g., Tottrup et al. 2012a). Environmental conditions at stopover sites can vary depending on the time of year an individual arrives at the site (Both 2010) and enact two potential phenotypic responses in birds: (1) stopover duration may be prolonged in response to poor (drought) conditions, because birds take longer to refuel for subsequent migration (Tottrup et al. 2012a), or, (2) stopover duration may be prolonged in response to good (wet) conditions with higher prey availability as birds may delay departure and put on more fat to fuel a faster subsequent migration (Tottrup et al. 2012b). Combining spatio-temporal data from direct-tracking with remote sensing of local or regional environmental factors enables tests of phenotypic hypotheses for migration stopover duration.

Recent research using direct-tracking methods has revealed that breeding latitude is an important factor driving timing around the full annual cycle (Conklin et al. 2010), including the initiation of spring migration from overwintering sites, timing en route, and arrival at breeding sites (Conklin et al. 2010; Fraser et al. 2013b; McKinnon et al. 2015). However, whether breeding latitude is an endogenous harbinger that also predicts the spatio-temporal aspects of fall migratory stopover behaviour has never been examined.

The elucidation of migratory stopover behaviour and important stopover locations can also have important implications for our understanding of population dynamics and can support conservation initiatives for species at risk (Laughlin et al. 2013). Many songbird species are experiencing steep rates of population decline, particularly long-distance migrants (Both et al. 2010) and aerial insectivores (North American Bird Conservation Initiative Canada 2012, North American Bird Conservation Initiative USA 2014; Sauer et al. 2014), where more northern breeding populations are also experiencing the highest rates of decline (Nebel et al. 2010; Smith et al. 2015; Michel et al. 2016). By investigating fall stopover locations, timing and duration we can gain a better understanding of how factors during the little-studied migration period may contribute to population declines. Recent evidence from a Palearctic-African long-distance migrant shows that stopover habitat quality in fall can have carry-over effects to breeding productivity in the subsequent spring (Schaub et al. 2011) and a study of eight migratory species using long-term annual survival probabilities reveals that species using more humid non-breeding areas had higher adult annual survival probabilities and that survival was positively correlated with rainfall for some populations/species (Johnston et al. 2016).

We tested both extrinsic and intrinsic hypothesis for migratory stopover behaviour in Purple Martin (*Progne subis*), a long-distance migratory aerial insectivore that breeds across eastern North America, and overwinters in South America. Martins travel 10,000 km to over 20,000 km annually during migration (Fraser et al. 2012b, 2013a, b), and are experiencing high rates of population decline across much of their northern range (Fraser et al. 2012a; Nebel et al. 2010). However, rates of decline vary widely by population and since both declining and stable breeding populations share overwintering sites in non-agricultural landscapes in the Amazon rainforest in Brazil (Fraser et al. 2012b), factors on migration or at breeding sites contributing to these high rates of decline have yet to be identified. Previous work in this study system found that the longitude of breeding sites predicted fall migration route but not stopover duration (Fraser et al 2013a). Our current study builds upon this knowledge, to determine core, fall stopover regions and to determine whether environmental conditions in these regions predict stopover duration.

Our specific objectives were to, (1) identify fall stopover locations for individuals originating from range-wide breeding locations and determine where fall stopover habitat use is concentrated spatially and temporally, (2) test the environmental quality hypothesis for stopover duration, by examining whether habitat quality predicted the duration of stay at core stopover regions, (3) test intrinsic hypotheses for stopover duration by examining the influence of breeding latitude of origin on stopover duration, and (4) identify whether declining and more stable populations have overlapping stopover regions or timing. This study represents the first test of the influence of intrinsic and environmental factors on stopover duration in a Neotropical aerial insectivore using journey-long direct tracking data. This research also provides important insight into the stopover locations for a species experiencing steep population declines, which could be used to inform conservation initiatives.

Methods

Geolocator deployment and analysis

Migration data ($n = 187$ individuals) for Purple Martins were collected (2009–2015) at six breeding sites ranging from 26°N to 53°N across the North American breeding range (Online Resource 1). Purple Martins were caught in their nest boxes using both trap doors and pole trap methods during the summer breeding season (May–August) and archival light logger tracking tags (geolocators) were attached to each individual using a leg-loop backpack harness made of Teflon ribbon (Stutchbury et al. 2009). Geolocators provided daily geographical locations by measuring the intensity of visible light, providing estimates of sunrise and sunset times, which can be used to determine latitudinal and longitudinal positions. During the following breeding season, geolocators were retrieved from the same sites where they were deployed. Additionally, breeding arrival date, sex, and age were recorded for each individual. Purple Martins were sexed and classified into one of two age categories [second year (SY) and after second year (ASY)] based on plumage and colouration (Pyle 1997).

Light level data were used to determine sunrise and sunset times, by using the TransEdit British Antarctic Survey (BAS), which were then translated into latitude and longitude coordinates with Locator software (BAS) (See methods in (Fraser et al. 2012b). We defined a stopover as a cease in migration where daily latitude and longitude positions (Purple Martins are diurnal migrants) did not fluctuate >2° for two or more consecutive days. Latitude could not be determined for 15 days before and after the fall equinox when day length is similar everywhere, and; therefore, the location of fall migration stopovers could be determined for 59 individuals (of 187) and migration timing at crossing the Tropic of Cancer (23.4°N) could not be determined for 158 individuals. Accuracy of geographical positions determined by using geolocators ranged from 0 to 210 km latitude and 0–196 km longitude (Fraser et al. 2012b, 2013a). We averaged latitudinal and longitudinal positions for each stopover to determine all fall stopover locations for each individual and identified core stopover regions during migration by using kernel density analysis run in ggplot2 (Wickham 2009).

Stopover habitat analyses

The normalized difference vegetation index (NDVI) is a measure of primary productivity (Pettorelli et al. 2005), and, thus, also reflects rainfall/moisture (Schultz and Halpert 1993). Since rainfall is correlated with insect abundance (Wolda 1978), NDVI has been used as an important proxy of habitat quality for insectivorous migrants (Tottrup et al. 2012a). We used NDVI analyses to estimate habitat quality at core stopover regions that we identified in Mexico and Central America during fall migration. High NDVI values indicate increased leaf area and productivity (better habitat quality) thus, greater insect abundance (Pettorelli et al. 2005; Wolda 1978), while low NDVI values suggest low leaf area (lower habitat quality), and, thus, lower insect abundance. NDVI files were downloaded in 16-day increments from NASA Earth Observations (http://www.neo.sci.gsfc.nasa.gov). A 200 km radius buffer (size of average geolocator error) was drawn around each stopover site (Fraser et al. 2012b), and an average NDVI value was determined within this buffer. We used the average NDVI value 16 days prior to arrival date for each individual at a given stopover sites to reflect conditions and insect availability leading up to passage dates (Fraser et al. 2013b).

Statistical analyses

To determine the influence of multiple factors on stopover duration in core regions, we used a Generalized Linear Mixed Model using the "lme4" package in R (Bates et al. 2015). The number of stopover days in Mexico and Central America was the response variable and random effects that were individual (to account for multiple stops per individual) and population nested within year (to account for different size of sample by population in different years). We included migration distance (number of km on individual migration routes from breeding site to 23.4°N/Tropic of Cancer) as a fixed effect, as the distance traveled prior to stopover may influence the number of stopover days needed to refuel. Breeding latitude was also included as a fixed effect, as this has been shown as an important predictor of timing around the annual cycle (Conklin et al. 2010) and may also predict stopover timing. NDVI was included as a fixed factor to examine whether habitat quality was an important predictor of stopover duration (Tottrup et al. 2012a, b). Fall departure date and stopover initiation date were included as indicators of migration timing. While migration timing is not a direct indication of the influence of environmental variability on timing, if conditions vary by date, these could be reflected in the number of stopover days taken as birds journey toward, and arrive at, tropical latitudes. Age and sex were included to account for potential differences between sex and age classes in migration behaviour. The number of different stops (locations) in Central America was included to account for a strategy whereby birds may make multiple shorter stops in the region, rather than one of longer duration. We used the function "step" in the package "lmertest" (Kuznetsova 2014) to perform a backward elimination of non-significant effects in our model to arrive at the top model. All statistical analyses were conducted using R (R Core Team 2016). Means are reported ± standard error, unless otherwise noted.

Results

Between their North American breeding sites and South American overwintering sites, Purple Martins had an average of 21 ± 14 total stopover days during fall

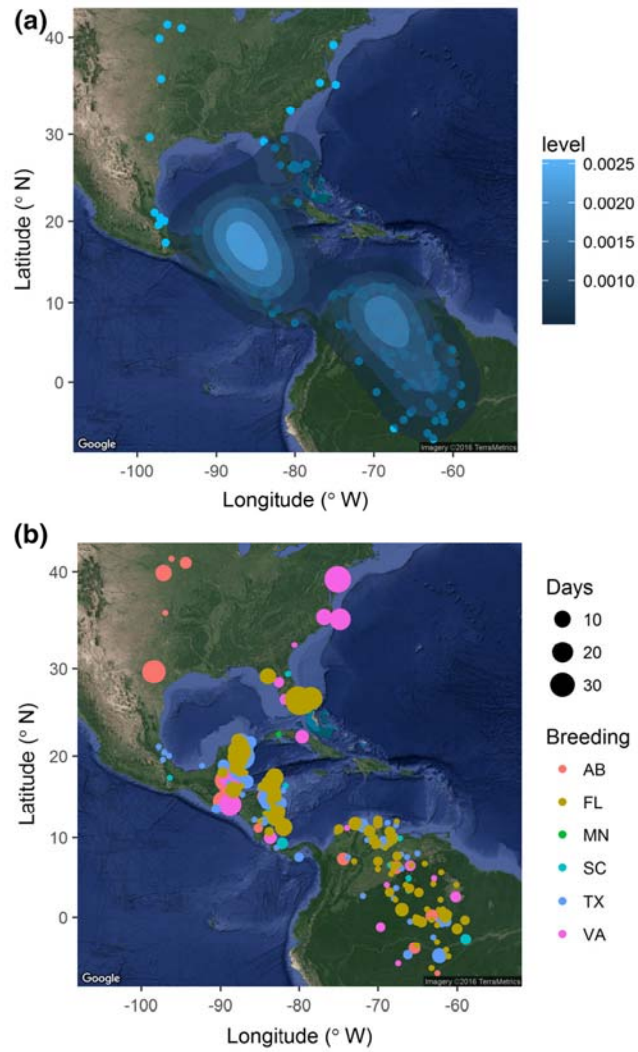

Fig. 1 Fall migration stopover locations for Purple Martins tracked with light-level geolocators from range-wide breeding populations. Map **a** shows fall stopover locations (*blue circles*) and the kernel density of all fall stopover locations (*blue shading*), and **b** shows individual stopover locations where size of circle reflects the duration of stopover days

migration (range 1–62) partitioned into 1–7 different stopovers (Fig. 1a, Online Resource 2). While stopover locations extended into South America as birds approached their overwintering sites, kernel densities reveal that the highest concentration of stopover sites were on the eastern coast of the Yucatan Peninsula, Honduras, and Nicaragua, and most breeding populations used these areas as main stopover regions during fall migration (Fig. 1a. Stopover duration was also the greatest in this region, ranging from 1 to 36 days with an average of 6.8 ± 8.2 days (Fig. 1b). The total number of fall migratory stopover days was predicted by migration distance ($p < 0.0001$, $F_{1,168} = 84.62$, $r^2 = 0.331$) (Fig. 2a. We found that populations of martins breeding at more northern (e.g., Alberta) and more southern (e.g., Texas) latitudes both

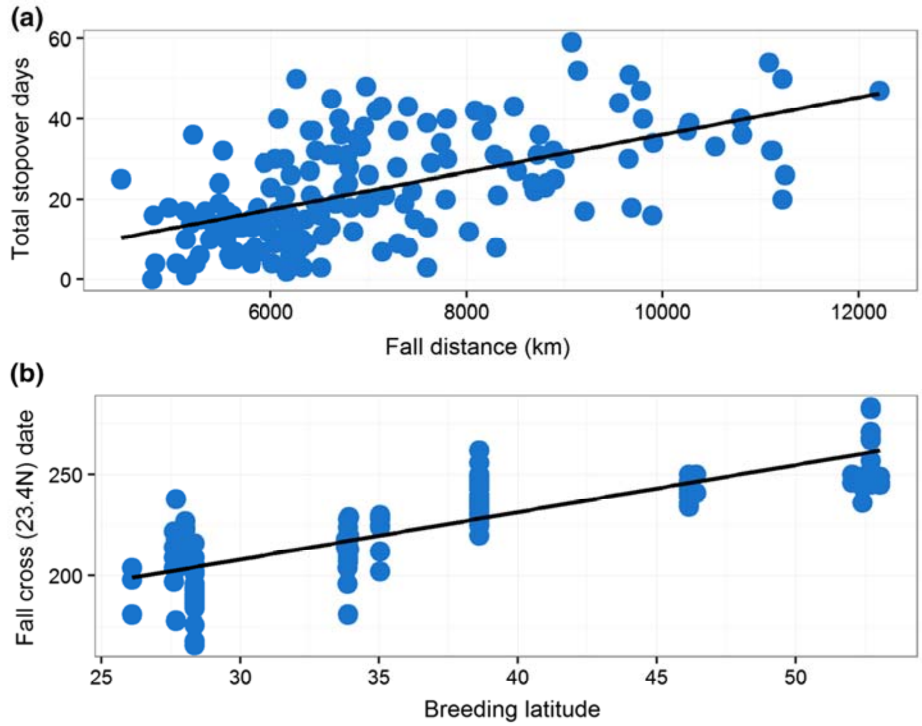

Fig. 2 Spatio-temporal comparisons of fall migration data for Purple Martins originating from range-wide breeding populations. **a** Total number of fall migration stopover days compared with migration distance, **b** timing of Gulf of Mexico (23.4°N) crossing (Julian date where Jan1 = 1) during fall migration compared with breeding latitude for individuals

used the Yucatan/Central American region for stopovers, but more northern populations arrived in this region much later in the season ($p < 0.0001$, $F_{1,156} = 317$ $r^2 = 0.68$) with the earliest arrivals June 17 and latest arrivals October 9 (Fig. 2b).

Factors predicting stopover duration in the Yucatan/Central America

Stopover duration was best explained by a single fixed effect, breeding latitude (estimate ± SE 0.4452 ± 2.736, $p < 0.017$) after accounting for random variation by year and population (variance ± SD 27.83 ± 5.28, $p < 0.048$). There was no relationship between NDVI values and stopover duration in Central America. Despite birds from northern breeding latitudes crossing the Gulf of Mexico at later dates than those originating from southern latitudes, these large differences in timing did not predict the duration that birds stopped over in Central America.

Discussion

We revealed spatio-temporal patterns of journey-long fall migration strategies for a Neotropical migratory songbird for the first time. Purple Martins from across the breeding range had the highest density of fall migratory stopovers in the eastern Yucatan Peninsula, Honduras, and Nicaragua, where stopovers were also of the longest duration. Despite highly variable timing of migration through this region (spanning ~115 days), environmental quality did not predict the duration of stopovers, or contribute to the long periods (some >20 days) in this region. Only breeding latitude predicted stopover duration in Central America, lending support to endogenous hypotheses for migration stopover duration.

Geographic locations of fall stopover sites

Considering the high density and long duration of stopover sites in the Yucatan Peninsula, Honduras, and Nicaragua, these regions could be considered migratory stopover "hot spots" for range-wide breeding populations. These areas have experienced extreme habitat degradation, which based upon our results, could impact birds from across the breeding range. The southern Yucatan has experienced significantly high rates of deforestation since the 1960s (Archard et al. 1998) and Nicaragua has lost more than half of its forest cover in the past 50 years (Gourdji et al. 2015). We recommend that future conservation planning for Purple Martins, and possibly other species that use these areas for stopover (Stanley et al. 2015), include these key stopover regions. Conservation of habitat in these regions may be particularly important for more northern breeding populations of Purple Martins, as these groups are declining the most steeply (Nebel et al. 2010; Smith et al. 2015; Michel et al. 2016) and also had the greatest stopover duration in these areas. New tracking technology with greater precision, such as archival GPS tags, could be used to identify habitat use at a finer, sub-regional scale (Fraser et al. 2017), which may be of particular benefit in such conservation planning. The stopover areas we identified could also be better considered in population dynamic models, as stopover behavior and locations can have important fitness consequences when they carry-over to affect subsequent stages, such as breeding (Schaub et al. 2011; Tottrup et al. 2012a).

Fall stopover duration, migration timing and habitat quality

We found that more northern breeding populations arrive at stopover locations in Central America significantly later during the fall migratory period and that all populations had the longest stopover duration in this region. Purple Martins stop for long periods after crossing the large, ecological barrier of the Gulf of Mexico. They did not exhibit long stopovers before the crossing, as reported for other songbird species preparing to cross ecological barriers (e.g., Skrip et al. 2015). Martins may be using long fall stops after crossing the Gulf of Mexico to recover from the crossing and fuel the remainder of the journey to the overwintering grounds. However, this is not consistent with our result that migration distance between breeding sites and the tropics did not predict the duration of stopovers in Central America with both northern and southern breeders exhibiting long fall stopovers in this region, and that distance to shared overwintering areas after long stopovers is similar for all populations, due to winter range overlap (Fraser et al. 2012b). Also, most individuals from a southern Texas population on fall migration go out of their way to stop at the Yucatan peninsula, even though it entails a short reverse migration (i.e., they head north after coming south) (Fraser et al. 2013a) suggesting this area is important other than simply for refueling post-Gulf of Mexico crossing. The long stopover duration in Central America that we documented supports the pattern that Purple Martins, like several other species for which direct-tracking data are available (McKinnon et al. 2013), do not exhibit the expected stop-refuel-resume strategy of songbird migration (Alerstam and Lindstrom 1990), but have long periods of residency during fall migration (Fraser et al. 2013a; Stach et al. 2012; Nilsson et al. 2013). Long stationary periods between breeding sites and overwintering sites have been identified in other long distance migrants, and due to their apparent inconsistency with migration refueling models (Alerstam and Lindstrom 1990), have been considered additional residency or itinerancy periods, rather than extra-long migratory stopovers (Moreau 1972; Tottrup et al. 2012b). For example, Red-backed Shrikes journeying from Europe to African overwintering sites had long stops after crossing the Sahara desert (Tottrup et al. 2012b), and Wood Thrushes had long periods of residency in the Yucatan peninsula after crossing the Gulf of Mexico (Stutchbury et al. 2011).

Surprisingly, we did not find support for the habitat quality hypotheses for stopover duration. We found that habitat quality (as measured by NDVI) was not a significant predictor of stopover duration. This is in contrast to the findings of other recent works in Palearctic-African migratory systems, where stopover duration was prolonged due to poor (drought) conditions, presumably because birds take longer to refuel for the subsequent journey (Tottrup et al. 2012b). This contrast could be due to inherent differences between Palearctic-African and Nearctic-Neotropical migratory systems, where fluctuations in rainfall, and thus habitat quality, may vary less in the latter. Our results of long fall stopover duration do match patterns found for Red-backed Shrikes journeying from European breeding sites to Central Africa in fall, where they also exhibited prolonged stopovers after crossing a different ecological barrier, the Sahara desert. The authors inferred that birds may have stayed for long durations at stopovers in response to favourable, wet conditions at these locations (Tottrup et al. 2012b); however, we found this was not an important factor in determining Purple Martin stopover duration after crossing the Gulf of Mexico. How differences between Nearctic-Neotropical and Palearctic-African systems may influence migratory behaviour is an important area for future research attention.

Although we did not find support for the habitat quality hypothesis, it cannot be eliminated as a possible influential factor on stopover duration. In this study, habitat quality was measured at a large-scale geographical scale (limited by $\sim$ 200 km error of geolocators and correspondingly-scaled NDVI values). To further assess how environmental factors (such as insect availability) affect aerial insectivores during stopovers, a multi-scale approach would be ideal. Including more fine-scale spatial measurements may help to avoid incorrectly evaluating the relationship between habitat quality and stopover duration (Buler et al. 2007). Additionally, using tracking technology that provides greater precision in spatial positions (e.g., recently miniaturized GPS devices with $<$10 m accuracy) would support the inclusion of more local/fine scale influences on stopover duration.

An additional aspect of habitat quality that would not be captured by our NDVI values is insect prey that has migrated, like the martins, from more northern regions to the Yucatan Peninsula and other southward stopover locations. Many species of dragonflies are long-distance migrants and large numbers may arrive to the Yucatan during the period this area is used for stopover by martins (May 2012). Martins consume large numbers of dragonflies, which constituted the majority of biomass fed to nestlings during a nesting cycle at northern breeding site (Jones et al. in prep.). This remains to be explored, but because local availability of migratory dragonflies at the Yucatan would be based on productivity both locally and with a contribution from northern sites, this could be an unmeasured habitat quality feature that could contribute to phenotypically driven stopover duration in this region.

Prolonged stopovers of martins in this region may be caused by other unmeasured factors. While moult patterns are little known for martins, with most moult likely accomplished on the overwintering grounds (Niles 1972), it is possible that individuals with prolonged stays in Central America pause to complete feather moult, as has been shown recently in a long-distance migratory songbird with long residency periods mid-migration (Pillar et al. 2015). However, other species that are known to moult outside of the migratory period also have long stopovers (Tottrup et al. 2012b). Constraints imposed by prevailing wind patterns in the Gulf of Mexico region could explain long stopover duration in these areas (Erni et al. 2005). However, our result that the date of arrival was not a significant factor predicting duration is suggestive, and further investigation of how wind and other local environmental variability may impact stopover duration in this region may further illuminate these patterns.

In conclusion, this study represents the first test of factors that influence stopover behaviour in a declining, long-distance migratory aerial insectivore by using direct tracking methods. We found strong evidence that stopover locations are concentrated spatio-temporally in core areas in Mexico and Central America, for individuals originating from range-wide breeding populations. Climate change scenarios for the Yucatan and Central America are predicted to be more dry (Hidalgo et al. 2013), thus determining how changing habitat quality impacts migration behaviour will be important for predicting future impacts for populations of Purple Martin and other insectivorous migrants passing through this region. Future research should be aimed at examining additional factors that influence variation in stopover duration such as migratory-moult, weather patterns and fine-scale habitat quality.

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