



CONSISTENT RANGE-WIDE PATTERN IN FALL MIGRATION STRATEGY OF PURPLE MARTIN (*PROGNE SUBIS*), DESPITE DIFFERENT MIGRATION ROUTES AT THE GULF OF MEXICO

KEVIN C. FRASER,^{1,10} BRIDGET J. M. STUTCHBURY,¹ PATRICK KRAMER,¹ CASSANDRA SILVERIO,¹
JOHN BARROW,² DAVID NEWSTEAD,³ NANETTE MICKLE,⁴ TIM SHAHEEN,⁵ PAUL MAMMENGA,⁶
KELLY APPLGATE,⁷ ELI BRIDGE,⁸ AND JOHN TAUTIN⁹

¹Department of Biology, York University, Toronto M3J 1P3, Canada;

²4146 Congressional Drive, Corpus Christi, Texas 78413, USA;

³Coastal Bend Audubon Society, Corpus Christi, Texas 78401, USA;

⁴1501 Spoonbill Court, Woodbridge, Virginia 22191, USA;

⁵15 Wigwam Road, Locust, New Jersey 07760, USA;

⁶South Dakota Department of Game, Fish and Parks, Aberdeen, South Dakota 57401, USA;

⁷Mille Lacs Band of Ojibwe Department of Natural Resources, Onamia, Minnesota 56359, USA;

⁸Oklahoma Biological Survey, University of Oklahoma, 111 E. Chesapeake Street, Norman, Oklahoma 73019, USA; and

⁹Purple Martin Conservation Association, Erie, Pennsylvania 16505, USA

ABSTRACT.—The migration rate of Nearctic–Neotropical songbirds is expected to be influenced by whether the route is around or across migration barriers such as the Gulf of Mexico. To examine factors that influence fall migration strategies, we used light-level geolocators to track the journeys of 91 Purple Martins (*Progne subis*) originating from breeding colonies across the eastern range of the species. We expected individuals that crossed the Gulf of Mexico to have slower migration rates, and more stopover days in Central America to refuel after the crossing, than birds that took routes around the gulf. Owing to expected variability in conditions experienced by individuals en route, we anticipated that departure date would be a poor predictor of arrival date within and among populations. Despite widely separated breeding origins, one-way journeys of >7,000 km, and high variability in departure dates and routes, individuals showed a strikingly similar fall migration strategy. Fall migration featured a rapid (450 km day⁻¹) initial migration covering ≥2,000 km, followed by prolonged stopovers and a slower rate of travel before the birds continued to South America. Contrary to predictions, route explained little of the variation in the overall migration rate or the rate to Central America. Stopover duration in Central America was unrelated to whether birds crossed or circumnavigated the Gulf of Mexico. As expected, breeding location (primarily longitude) was the strongest predictor of the routes that birds took at this barrier. Within-breeding-region departure date alone predicted much of the variation in arrival date at the first winter roost, but route was not a significant factor. Our results reveal a consistent range-wide pattern in fall migration strategy, with route and migration timing predicting little of the variation in rate or stopover duration. Received 1 December 2012, accepted 19 March 2013.

Key words: autumn migration, geolocator, migration rate, migration schedule, *Progne subis*, Purple Martin, songbird, South America, stopover.

Patrón Consistente Todo El Rango En La Estrategia De Migración De La Caída De Púrpura Martin (*Progne Subis*), A Pesar De Las Rutas Migratorias Diferentes En El Golfo De México

RESUMEN.— Se espera que la tasa de migración de aves canoras Nearctic–Neotropical ser influenciado por la ruta sea alrededor o a través de barreras de migración como el Golfo de México. Para examinar los factores que influyen estrategias de migración de otoño, utilizamos geolocalizadores de nivel de luz para realizar un seguimiento de los viajes de 91 púrpura Martins (*Progne subis*) procedentes de las colonias de cría a través de la cordillera oriental de la especie. Esperábamos a individuos que cruzaba el Golfo de México para tener tasas de migración más lentas y más días de parada en Centroamérica para repostar después del cruce, que las aves que tomaron rutas alrededor del Golfo. Debido a la variabilidad esperada en las condiciones vividas por los individuos en el camino, nos anticipó que la fecha de salida sería un pobre predictor de fechas dentro y entre poblaciones. A pesar de ampliamente separados orígenes de cría, viajes de ida o vuelta de > 7.000 km y la alta variabilidad en las fechas de salida y rutas, individuos demostraron una sorprendentemente similar

¹⁰E-mail: fraserkev@gmail.com

estrategia de migración de otoño. Migración de otoño aparece una rápida migración inicial (450 km day⁻¹) cubriendo $\geq 2,000$ km, seguido por escalas prolongadas y un ritmo más lento del viaje antes de que las aves continúan en América del sur. Contrariamente a las predicciones, ruta poco de la variación en la tasa de migración o la tasa explicó a Centroamérica. Duración de la escala en Centroamérica estaba relacionada con si aves cruzan o rodeó el Golfo de México. Como era de esperar, cría ubicación (principalmente longitud) fue el predictor más fuerte de las rutas que aves tuvieron en esta barrera. Fecha de salida de la región dentro de cría solo predijo gran parte de la variación en la fecha de llegada en el primer dormitorio de invierno, pero ruta no era un factor significativo. Nuestros resultados revelan un patrón constante de todo el rango en la estrategia de migración de otoño, con la ruta y el tiempo de migración predecir a poco de la variación en duración tarifa o escala. Nuestros resultados revelan un patrón constante de todo el rango en la estrategia de migración de otoño, con la ruta y el tiempo de migración predecir a poco de la variación en duración tarifa o escala.

ROUTE SELECTION AND migration rates of birds may be shaped by selection pressure to avoid risk and arrive optimally at both stopover locations and final destinations (Alerstam 2003, Newton 2008). Large open-water crossings, such as the Gulf of Mexico, may serve as migration barriers and influence migration rates if birds require greater refueling time before or after crossing (Newton 2008). Factors that affect individual decisions to either cross or circumnavigate large barriers, and subsequent effects of that decision on migration rate and arrival date at wintering sites, are poorly understood. For passerines, other factors such as departure date and migration distance may also affect migration rate. Birds that depart breeding sites later in the year may be able to accumulate larger fat stores prior to migration that support a faster migration rate and effectively allow them to “catch up” to birds that departed earlier (Fransson 1995, Newton 2008). Birds with longer overall migration distances may also travel at a faster rate; passerines traveling through Europe to destinations 1,000 km away traveled at about half the rate of those with journeys of 5,000–6,000 km (Alerstam 2003). Owing to variability in migration speed, stopover duration, and routes, departure date alone is expected to be a poor predictor of arrival date at the destination (Newton 2008, Both 2010).

Previous estimates of fall migration strategy (here referring to rate, departure date, arrival date, and stopover duration or timing) have been based largely on band recovery data, providing only a snapshot of behavior. Direct tracking using geolocators allows an examination of migration strategies for many individuals over the whole of the migratory journey. We tracked the trans-hemispheric migration of individual Purple Martins (*Progne subis*) that originated from seven breeding populations spanning the eastern part of the species' North American breeding range. We expected, given the wide spread in latitude and longitude between breeding populations, that the fall migration route would differ among populations, particularly at the Gulf of Mexico. We predicted greater stopover duration and a slower rate of travel in Central America for individuals crossing the Gulf of Mexico (800–1,000 km) because birds presumably require more refueling time after a nonstop flight across a large open-water barrier than after they follow an overland route around the barrier (Newton 2008). Because en route factors experienced by individual birds are expected to uncouple the relationship between departure and arrival date within and among populations (Newton 2008, Both 2010), we predicted that departure dates in fall would explain little of the variation in arrival dates at winter roosts in South America.

METHODS

Geocator deployment.—Purple Martins were captured and fitted with geolocators in different years during the breeding season in seven regions across the eastern range of the

species: Pennsylvania (2007–2011; 41°53'08"N, 80°07'46"W), Texas (2009–2010; 27°41'N, 97°24'W), Virginia (2010–2011; 38°36'47"N, 77°15'46"W), South Dakota (2011; 45°36'00"N, 96°42'00"W and 45°36'59"N, 98°17'59"W), Minnesota (2011; 45°23'59"N, 94°12'00"W; 46°08'59"N, 93°43'11"W; 45°15'36"N, 92°57'22"W; and 45°16'43"N, 92°59'6"W), New Jersey (2011; 40°23'59"N, 74°00'00"W), and Oklahoma (2011; 33°52'51"N, 96°48'1"W). All birds tracked on fall migration were at least 1 year old (after-second-year). See Fraser et al. (2012) for details regarding geocator type and mounting procedures by population and year. Geolocators were retrieved at the same breeding sites in the year after deployment, and battery failure prior to completion of fall migration reduced the sample size to 91, with lower sample sizes for some variables owing to the equinox (when day length is similar across latitudes) or poor-quality sunrise–sunset transitions because of shading or light pollution.

Analysis of light data from geolocators.—Raw light data were corrected for clock drift using BASTRAK and analyzed using TRANSEdit (British Antarctic Survey). We manually verified a sharp transition at each sunrise and sunset and ignored obvious shading events during the daytime. Transitions with light peaks or nonlinear transitions before sunrise or after sunset were rejected from further analysis. We used a light-level threshold of 32 (MK16, MK10) or 5 (MK12, MK20) 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 threshold at the breeding site (for additional methods specific to Oklahoma geolocators, see Fraser et al. 2012). Latitude was not determined for 15 days before and after the fall equinox, when day length is similar everywhere. Latitude and longitude coordinates were calculated with LOCATOR software (British Antarctic Survey), using midnight locations because Purple Martins are diurnal migrants. Locations that were clearly anomalous (i.e., >1,000 km from previous location) were rejected as outliers. Sun elevation was calculated separately for different geocator models, after birds finished nesting but before migration, and averaged across individuals within each year to better represent average conditions for migrating birds at unknown locations. Average geocator accuracy at each breeding location was assessed prior to fall migration. Average accuracy ranged from 49 to 60 km in latitude (range: 0–210 km) and from 38 to 48 km in longitude (range: 0–196 km) for different breeding sites; see additional details and return rates of birds with and without geolocators in Fraser et al. (2012). Movements of >200 km in latitude and >100 km in longitude away from the breeding site, and from one stopover location to another, were defined as migratory movements. Movements during the fall equinox, when latitude could not be determined, were based on longitude alone. Locations that remained consistent for ≥ 2 days and were within the location error of stationary birds were defined as stopover locations.

Arrival at the wintering ground was considered to have occurred when the latitude and longitude were consistent with a stationary bird; that is, latitude and longitude (1) ceased to shift in a direction consistent with fall migration, (2) fluctuated around a narrow range of values ($<2^\circ$ longitude), and (3) fluctuated around a similar value for ≥ 10 days. To explore migration rate and stopover duration in the vicinity of the Gulf of Mexico, we analyzed the migration rate within each breeding population separately for three stages of fall migration: breeding site to the tropics (Gulf of Mexico, $\sim 24.5^\circ\text{N}$), travel within Central America, and entry into South America to first night at the winter roost. Migration rate is defined as the number of kilometers traveled divided by the total number of days traveled, including stopover days. Migration distance was calculated as the straight-line distance between breeding sites, stopover locations, and winter sites.

Statistical analyses.—To test predictors of circum- versus trans-Gulf crossing, we fit general linear models (GLMs) with breeding latitude, breeding longitude, fall departure date, and sex as factors. Using hypothesis-testing procedures, we dropped the least significant explanatory variables one-by-one on the basis of t and P values to arrive at an optimal model (Zuur et al. 2009). We used similar methods to explore factors that influenced the overall fall migration rate (km day^{-1}) and the rate on the first leg of the journey (between the breeding site and arrival in Central America), with route at Gulf of Mexico (across, east route around, or west route around), departure date, distance (overall and between breeding site and Central America), and sex as factors. We expected the migration rate (overall and first leg) to be faster for birds that traveled a greater distance (Alerstam 2003) and departed later from breeding colonies (Newton 2008). We expected a slower rate of travel for birds that made a direct crossing of the Gulf, owing to greater stopover duration for fueling before and after crossing. We also examined variation in stopover duration (days) in Central America, the ratio of days spent in flight to days spent at stopover, and the arrival date at first winter roost in South America. Because of the presumed greater stopover time needed to fuel before and after a crossing of the Gulf of Mexico, we expected birds taking this route to have a longer stopover in Central America, a lower ratio of flight to stopover nights, and later arrival at winter roosts. To compare variation in migration rate by stage of migration (breeding site to tropics, through Central America, to South America) and breeding region, we fit general linear mixed-effects models with region and stage as fixed factors and individual as a random factor. We grouped breeding regions by longitudinal proximity because we expected longitude to predict route and migration rate. Because of large latitudinal differences between Texas–Oklahoma and South Dakota–Minnesota that might also influence migration strategy, these colonies were grouped separately despite longitudinal similarity. Some migration variables were not available for all birds because of equinox, missing days, and battery failure. All analyses were conducted using R (R Development Core Team 2011). Results are presented as means \pm SE unless otherwise noted.

RESULTS

As expected, once birds reached the Gulf of Mexico, the fall migration route varied widely among populations across the breeding range (Fig. 1) and, in some cases, also varied within populations. However, migration routes of Purple Martins at the Gulf

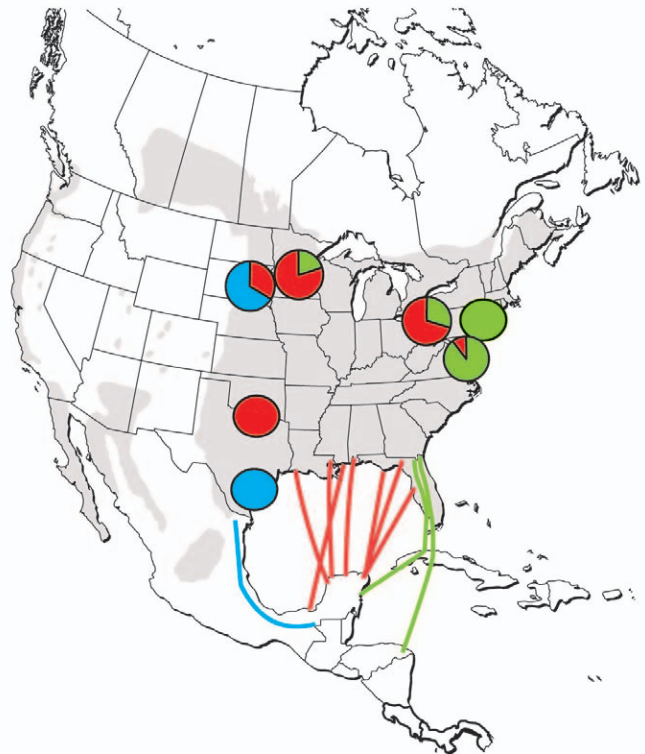


FIG. 1. Breeding sites and fall migration routes at the Gulf of Mexico of birds originating from seven breeding colonies (South Dakota, $n = 9$; Minnesota, $n = 5$; Pennsylvania, $n = 34$; New Jersey, $n = 11$; Virginia, $n = 20$; Oklahoma, $n = 3$; and Texas, $n = 8$). Pie charts show the percentage of birds from each breeding colony that used one of three major routes at the Gulf of Mexico (blue = western route around the gulf, red = direct crossing of the gulf, and green = eastern route around the gulf). Lines illustrate tracks taken by individuals for each of the three major routes.

of Mexico were predicted reasonably well by breeding longitude. Birds from more western breeding populations (Minnesota, South Dakota, Texas, Oklahoma) were much more likely to take a western route around the gulf, whereas those from breeding populations nearer to the Atlantic coast (New Jersey, Virginia) took a mostly overland route eastward around the gulf, traversing the Florida panhandle and crossing a shorter open-water distance to Cuba, followed by a flight to either the Yucatan Peninsula or Central America. Birds that bred directly north of the Gulf of Mexico (Pennsylvania) were the most likely to make a direct gulf crossing to the Yucatan Peninsula. In the GLM fitted to describe the route taken at the Gulf of Mexico, only breeding latitude (model estimate = -0.065 ± 0.021) and longitude (model estimate = 0.079 ± 0.012) were retained in the top model ($F = 37.3$, $df = 2$ and 88 , $r^2 = 0.46$, $P < 0.0001$), illustrating that departure time and sex did not predict whether birds crossed or went around the gulf.

Despite different breeding origins and migration routes across or around the gulf (Fig. 1), individuals from widely separated populations ($\leq 2,500$ km) and with different migration routes showed a strikingly similar fall migration strategy (Fig. 2). The migration rate was very rapid for the first 2,000 km for all populations (mean breeding population rate = $360\text{--}473$ km day^{-1}), after which individuals had a slower overall migration rate during the

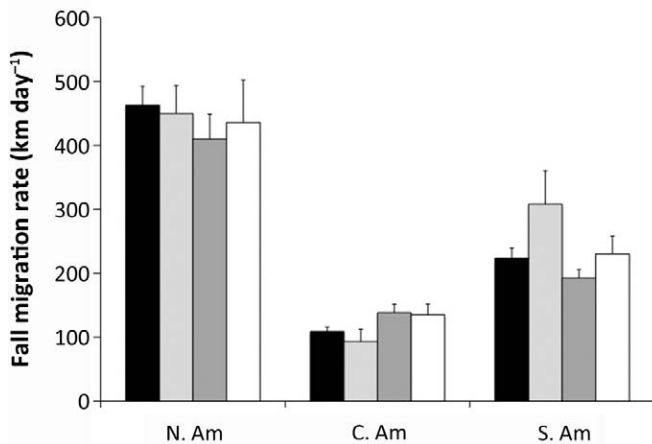


FIG. 2. Mean (\pm SE) fall migration rate by zone (North America, Central America, and South America) and grouped by breeding region (black bars = Pennsylvania, $n = 31$; light gray = Oklahoma and Texas, $n = 11$; dark gray = New Jersey and Virginia, $n = 27$; and white = South Dakota and Minnesota, $n = 14$).

second leg of their journey (68–157 km day⁻¹) owing to long stopovers (average [\pm SD] stopover duration = 16 ± 9 ; $n = 84$) in the Yucatan peninsula, Cuba–Caribbean, and Central America before reaching Panama. The migration rate then increased across northern South America (180–361 km day⁻¹) to the first wintering site (Fig. 2). The migration rate varied significantly with stage of migration (North, Central, and South America; $t = -8.39$, $df = 163$, $P < 0.0001$), but breeding region was not a significant predictor of rate ($t = -0.34$, $df = 86$, $P = 0.73$). The route taken at the Gulf of Mexico (across, east route around, or west route around) did not influence the migration rate from the breeding site to the first night at the roost in South America; migration rate was also independent of distance from the breeding colony, departure date from the breeding grounds, and sex ($F = 0.43$, $df = 4$ and 83 , $R^2 = 0.03$, $P < 0.82$). For the first rapid leg of the journey between the breeding site and arrival in the tropics, migration route did not influence rate. Fall departure date and distance were retained as significant factors in the top model but, overall, were poor predictors of migration rate because they explained just 13% of the variation in migration rate (km day⁻¹) between the breeding site and Central America ($F = 4.03$, $df = 3$ and 78 , $R^2 = 0.13$, $P < 0.01$). Fall departure date and migration rate over the entire route were positively correlated (model estimate = 5.95 ± 2.3 , $t = 2.6$, $P < 0.01$), as were distance from the breeding colony and rate (model estimate = 0.18 ± 0.06 , $t = 2.97$, $P < 0.004$).

Birds that crossed the Gulf of Mexico were expected to have a greater stopover duration in Central America; however, our GLM results showed that stopover duration was independent of route at Gulf of Mexico, rate and distance from breeding site to Mexico, and sex, in that none of these factors examined to explore variation in stopover duration (days) was significant. Route also did not account for variation in the ratio of flight to stopover days over the whole journey, showing that birds crossing the Gulf did not take a proportionally greater number of stopover days to compensate for the long open-water crossing.

Departure date from the breeding colony alone predicted much of the variation in arrival date at the first winter roosts in South America (Fig. 3). The GLM analysis of arrival date on the winter grounds

included departure date from the breeding ground, route at Gulf of Mexico, overall migration distance, and sex, but only fall departure date (model estimate = 0.881 ± 0.0991) and distance (model estimate = 0.0061 ± 0.0017) were retained in the top model, which explained 56% of the variation ($F = 54.42$, $df = 2$ and 86 , $r^2 = 0.56$, $P < 0.0001$).

DISCUSSION

Purple Martins have been described as leisurely diurnal migrants that forage while migrating (Brown 1997), but our results show that individuals that originated from breeding populations across eastern North America had very rapid migration (440 ± 188 [SD] km day⁻¹) during the first days of fall migration, followed by a prolonged stopover in Central America. It is not known how food supply (aerial insects) varies along the journey or affects stopover duration, or whether stopover sites used in Central America are locations with regionally abundant food resources. Purple Martins do not exhibit the expected stop–refuel–resume strategy thought to be typical of migrating songbirds (Hedenström and Ålerstam 1997). Instead, Purple Martins gather at premigratory roosts near their breeding sites for 4–6 weeks prior to fall migration, then travel ~2,000 km in less than 1 week. The prolonged Central American stopover could also be a staging site for subsequent rapid migration to Brazil.

Within species, migration rate is generally predicted to be highly flexible and influenced by the availability of fueling resources at stopover sites, migration routes, migration barriers, distance of migration, weather, molt strategies, and distance to the final destination (Newton 2008). Contrary to predictions, our results reveal that fall route at Gulf of Mexico, departure date, and migration distance were not significant predictors of Purple Martins' start-to-finish migration rate and explained little of the variation in the migration rate to Central America. Whether birds crossed or took an overland route around the Gulf of Mexico also did not influence stopover duration in Central America, which suggests that “barrier” crossing did not require greater time to refuel after an extended migratory flight. It is surprising that our data reveal similar migration rates among widely separated breeding populations and that the overall migration rate is largely independent of breeding origin, timing, route, and distance.

We speculate that the subsequent stopover by many individuals in the Yucatan Peninsula, which includes birds breeding in Texas that made a detour to this region (Fig. 1), is a staging area to refuel for the longer migration to the Amazon basin and/or serves as a location to continue their annual molt. Purple Martins may begin flight feather molt in premigratory roosts that form throughout eastern North America in late summer and early fall (Russell et al. 1998), but museum records suggest that this molt is interrupted during migration (Niles 1972). In some western songbirds, long stopovers in coastal western Mexico are associated with molt (Rohwer et al. 2005, 2009) during the seasonal flush in food resources with monsoon rains. The Yucatan Peninsula may serve Purple Martins in a similar manner; it remains to be determined whether a seasonal abundance of aerial insects there might support the nutritional and energetic costs of molt.

That winter arrival dates in the Amazon basin can be predicted largely from departure dates from breeding sites >6,000 km away is surprising, especially given the different migration routes across (or around) the Gulf of Mexico and long stopovers during

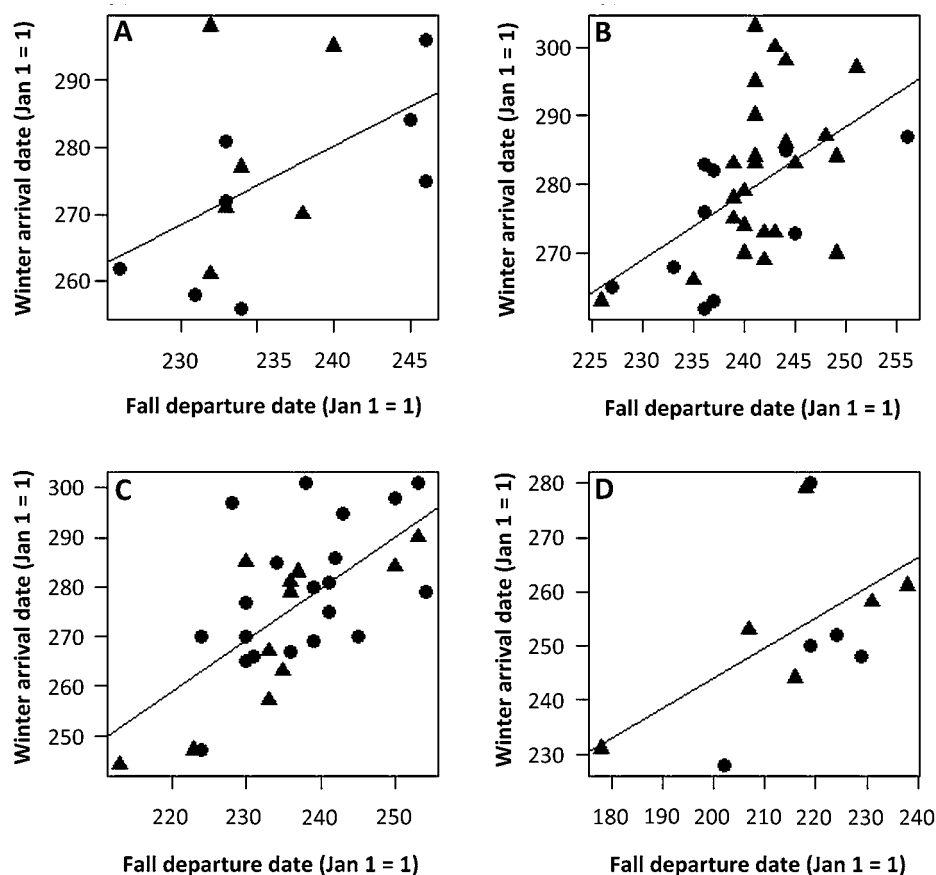


FIG. 3. Within-population patterns of fall departure versus winter arrival date for birds of four breeding regions: (A) South Dakota and Minnesota ($n = 14$, $r^2 = 0.27$, $P = 0.06$), (B) Pennsylvania ($n = 34$, $r^2 = 0.28$, $P = 0.001$), (C) New Jersey and Virginia ($n = 31$, $r^2 = 0.43$, $P < 0.0001$), and (D) Oklahoma and Texas ($n = 11$, $r^2 = 0.30$, $P = 0.08$) (triangles = males; circles = females).

autumn migration (Tøttrup et al. 2012). Even within populations, departure date was a strong predictor of arrival date. A predictable trans-hemispheric migration schedule that includes long stationary periods en route has been described for shorebirds (Hedenström and Alerstam 1997, Conklin et al. 2010) but has not been previously documented in songbirds. We suggest that the range-wide migration strategy described here is more similar to shorebird migration, in which individuals have prolonged staging periods to refuel, followed by rapid migration to the next refueling site (Newton 2008). As in shorebirds and waterbirds (Baker et al. 2004), the convergence of widely separated breeding populations on predictable staging areas during migration increases vulnerability to localized reduction in food resources due to habitat loss or climate change.

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