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Source: The Auk, 128(3):531-542.
Published By: The American Ornithologists' Union
URL: http://www.bioone.org/doi/full/10.1525/auk.2011.10280

The Auk 128(3):531–542, 2011
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Printed in USA.

VEERY (*CATHARUS FUSCESCENS*) WINTERING LOCATIONS, MIGRATORY CONNECTIVITY, AND A REVISION OF ITS WINTER RANGE USING GEOLOCATOR TECHNOLOGY

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Abstract.—We used light-level archival geolocators to track five Veeries (*Catharus fuscescens*) for one annual cycle as they migrated from Delaware to South America and back. Southward migration commenced in late August and September 2009. Veeries arrived at wintering sites from 2 November to 2 December 2009. All birds initially wintered in the Amazon basin south of the Amazon River in Mato Grosso, Para, and Amazonas states, Brazil. All birds showed intratropical migration to a second winter site between 7 January and 7 March 2010. These second winter sites were in the interior, northern, and southern periphery of the Amazon basin and the Orinoco River headwaters, Venezuela. Northward migration commenced in mid-April 2010, and the Veeries returned to Delaware between 29 April and 20 May 2010. Despite variation in migratory patterns, several stopover regions were visited by multiple individuals: the coasts of the Carolinas, the coast of the Gulf of Mexico, Cuba and Jamaica, the north coast of Colombia and Venezuela, and southern Venezuela. Our spatial and temporal data necessitates that the Veery winter range include the entire Amazon basin and the headwaters of the Orinoco River, as well as two disjunct regions in Mérida state, Venezuela, and São Paulo state, Brazil. We hypothesize that Veeries initially settled in lowland forest and that intratropical migration was prompted by the ecological factors associated with the seasonal flood pulse of Amazonian rivers. If so, the Veery may be threatened by the recent, unprecedented proposed alteration of Amazonian lowland forests. *Received 10 December 2010, accepted 2 May 2011.*

Key words: *Catharus fuscescens*, geolocator, migratory connectivity, Nearctic–Neotropical migrant, South America, Veery.

Localidades de Invernada, Conectividad Migratoria y una Revisión de la Distribución Invernal de *Catharus fuscescens* con Base en Tecnología de Geolocalizadores

Resumen.—Empleamos geolocalizadores para seguir a cinco individuos de la especie *Catharus fuscescens* a lo largo de un ciclo anual mientras migraban desde Delaware hacia Sur América y de regreso. La migración hacia el sur comenzó a fines de agosto y septiembre de 2009. Las aves llegaron a sus sitios de invernada entre el 2 de noviembre y el 2 de diciembre de 2009. Todas las aves incialmente pasaron el invierno en la cuenca amazónica al sur del río Amazonas en los estados de Mato Grosso, Pará y Amazonas, Brasil. Todos los individuos realizaron migraciones intratropicales hacia un segundo sitio de invernada entre el 7 de enero y el 7 de marzo de 2010. Estos nuevos sitios de invernada estaban ubicados en el interior, norte y periferia sur de la cuenca amazónica y en la cabecera del río Orinoco, en Venezuela. La migración hacia el norte inició a mediados de abril de 2010 y las aves llegaron a Delaware entre el 29 de abril y el 20 de mayo de 2010. A pesar de la variación en patrones migratorios, varias regiones de parada fueron visitadas por múltiples individuos: las costas de las Carolinas, la costa del golfo de México, Cuba y Jamaica, la costa norte de Colombia y Venezuela, y el sur de Venezuela. Nuestros datos espaciales y temporales señalan que la distribución invernal de *C. fuscescens* abarca toda la Amazonía y las cabeceras del Orinoco, además de dos regiones disyuntas en el estado de Mérida, Venezuela y el estado de São Paulo, Brasil. Hipotetizamos que las aves inicialmente se establecieron en bosques de tierras bajas y que la migración intratropical fue promovida por los factores ecológicos asociados con el pulso estacional de inundación de los ríos amazónicos. Si es así, *C. fuscescens* podría ser una especie amenazada por la propuesta reciente y sin precedentes de alterar los bosques de tierras bajas amazónicos.

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The Auk, Vol. 128, Number 3, pages 531–542. ISSN 0004-8038, electronic ISSN 1938-4254. DOI: 10.1525/auk.2011.10280

Effective long-term conservation of Nearctic–Neotropical migrant (hereafter "Neotropical migrant") bird populations requires knowledge of all aspects of a species' biology, including breeding, migration, and wintering-season ecology. Determining the levels of connectivity among breeding, migratory, and wintering areas will lay a foundation upon which we can more fully understand population dynamics (Smith et al. 2005, Webster and Marra 2005). Once this connectivity has been established, conservationists will have the information necessary to focus action on specific problem areas that may limit populations (Faaborg et al. 2010b). However, to date, very few studies have definitively linked Neotropical songbird breeding populations to migratory routes and specific wintering areas to facilitate an understanding of migratory connectivity. In particular, few data exist regarding the migratory connectivity of species that winter in South America (Jones et al. 2008, Wilson et al. 2008).

For most Neotropical migrant songbirds, the temporal and spatial aspects of movements during the non-breeding season have been inferred from multiple sources, including reliable sight records, specimen collections, and banding records (e.g., Remsen 2001). Unfortunately, these data are subject to bias because of the heterogeneous geographic distribution of researchers and a lack of knowledge regarding the precise movements of the individuals in question (e.g., whether data are from transient or resident birds). More recently, stable isotope analysis has proved promising in its ability to reveal the origin of transient and wintering individuals (Wilson and Watts 1997, Boulet et al. 2006, Paxton et al. 2007, Wilson et al. 2008). For example, Hobson et al. (2001) linked wintering populations of Bicknell's Thrush (*Catharus bicknelli*) in the Dominican Republic with approximate breeding regions at longitudes north of New Brunswick or in Quebec. However, the ability to incorporate individual variation into the study of the migratory and wintering ecology of Neotropical migrant songbirds has remained elusive in part because of the constraints inherent with the use of most tracking devices (e.g., excessive weight, limited battery life).

Using light-level archival technology (geolocators), individual variation can now be examined within the broader contexts of migratory connectivity and behavior established from former research methods. Using geolocator technology, Stutchbury et al. (2009, 2011) recently tracked a Neotropical migratory songbird, the Wood Thrush (*Hylocichla mustelina*), from Pennsylvania to Central America, and Bächler et al. (2010) successfully determined the migratory routes and wintering regions of European Hoopoes (*Upupa epops*). The advent of technology small enough to use with larger migratory songbirds has ushered in an exciting new era of migratory songbird research (Stutchbury et al. 2009).

The Veery (*C. fuscescens*) is a Neotropical migrant that breeds in dense North American forests and winters in South America. The precise winter range of the Veery has been difficult to determine. Thus, although the Veery spends 8 months of its annual cycle outside of North America, virtually nothing is known about its wintering-season ecology. On the basis of reliable specimen records from migratory and wintering periods determined *a posteriori*, Remsen (2001) hypothesized that the Veery's winter range encompassed two separate areas of southern Brazil. Remsen's analysis was considered somewhat revolutionary (see Stouffer 2001) because former publications portrayed the Veery as occupying large areas of South and even Central America during wintering periods, a perspective that was not supported by Remsen's analysis. The source of the discrepancy between former published descriptions and Remsen's conclusion was the inclusion of Veery records from transient periods that had been used to determine the winter range rather than the use of records restricted to non-migratory periods. Remsen's intent was, in part, to prompt a call for the widespread reexamination of the wintering ranges of Neotropical migrant birds that breed in North America and winter in the tropics and has since been heralded as an example of how little ornithologists know about birds that winter in the tropics (Stouffer 2001; Faaborg et al. 2010a, b).

We used geolocator technology developed by the British Antarctic Survey (BAS) to record the daily locations of Veeries as they moved from their breeding grounds at a Delaware study site to South America and back. Our primary objectives were to (1) determine the wintering location, migratory patterns, and timing of migration of each individual in order to test Remsen's (2001) hypothesis that Veeries are restricted to two disjunct wintering areas of southern Brazil; (2) document the spatial and temporal aspects of migration; and (3) revise the species' known winter range on the basis of new spatial and temporal data. Building on the work of Stutchbury et al. (2009), an additional objective was to (4) determine whether geolocator technology can successfully track a terrestrial forest-dwelling songbird from its North American breeding site through dense tropical forests of equatorial South America where day length and night length are equal.

Methods

In June 2009, we captured Veeries at a long-term Delaware study site at White Clay Creek State Park, New Castle County (39.44°N, 75.45°W), using mist nets. We weighed, measured, and fitted them with an individually numbered federal band and a unique combination of color leg bands. We aged all banded birds as second-year (SY) or after-second-year (ASY) using criteria presented in Collier and Wallace (1989) and Pyle (2008). We attached archival light-level geolocator units (model Mk14S at 1.5 g, BAS) similar to those used by Afanasyev (2004) to 24 Veeries using a Rappole-Tipton leg-loop harness method with Teflon ribbon (Rappole and Tipton 1991). Mk14S geolocator units measure light level at 60-s intervals and store maximum values every 10 min. We calibrated geolocator units on the basis of a minimum of 9 clean dusk–dawn transitions obtained when the unit was affixed to the bird at a known location. We adjusted for clock drift and estimated the average sun elevation that corresponded to our chosen light threshold level using the program BASTRAK (BAS). We processed the data using a single-value threshold analysis, and we assumed that any natural light-attenuation effects (e.g., due to clouds, weather, foliage shading) during the calibration period were representative of those during the entire deployment period.

Shading obscures sunset and sunrise times and can produce errors in estimated latitude and longitude if different from that experienced at the time of calibration. After automatically matching sunrise–sunset times to our data, we examined each sunrise–sunset transition and rejected all that were obscured by shading events. The result was the inclusion of only unobscured transitions in final data analysis. We ignored all latitudinal estimates within 15 days of the autumn and spring equinoxes, when day length is similar in all regions. Longitude accuracy is largely unaffected by seasonal changes, so all longitudinal values obtained from clean transitions were included in analysis. Using BASTRAK, we obtained an estimated noon and midnight position for each 24-h period. Veeries migrate primarily at night (Cochran et al. 1967); therefore, we considered noon locations and ignored midnight locations.

Estimates of longitude are unaffected by day length. Therefore, we identified movement of birds in South America from abrupt shifts in longitude following stationary periods. We calculated these latitudes by taking a mean value during the period when longitude was static. We followed Stutchbury et al. (2009) in discarding obvious latitudinal outliers in the form of improbable round-trip movement of >3,000 km in a single night. We also calculated the mean and standard deviation of latitude and longitude from birds that remained stationary at stopover sites (≥2 days). We mapped mean values of latitude and longitude onto base maps using corresponding coordinates obtained from Google Earth. For points that fell over water, we mapped the location at the point of land closest to the mean location. Once mapped, we used the most direct route between locations to depict the minimum distance birds traveled and to measure distances (Figs. 1 and 2). Means are reported ± SD.

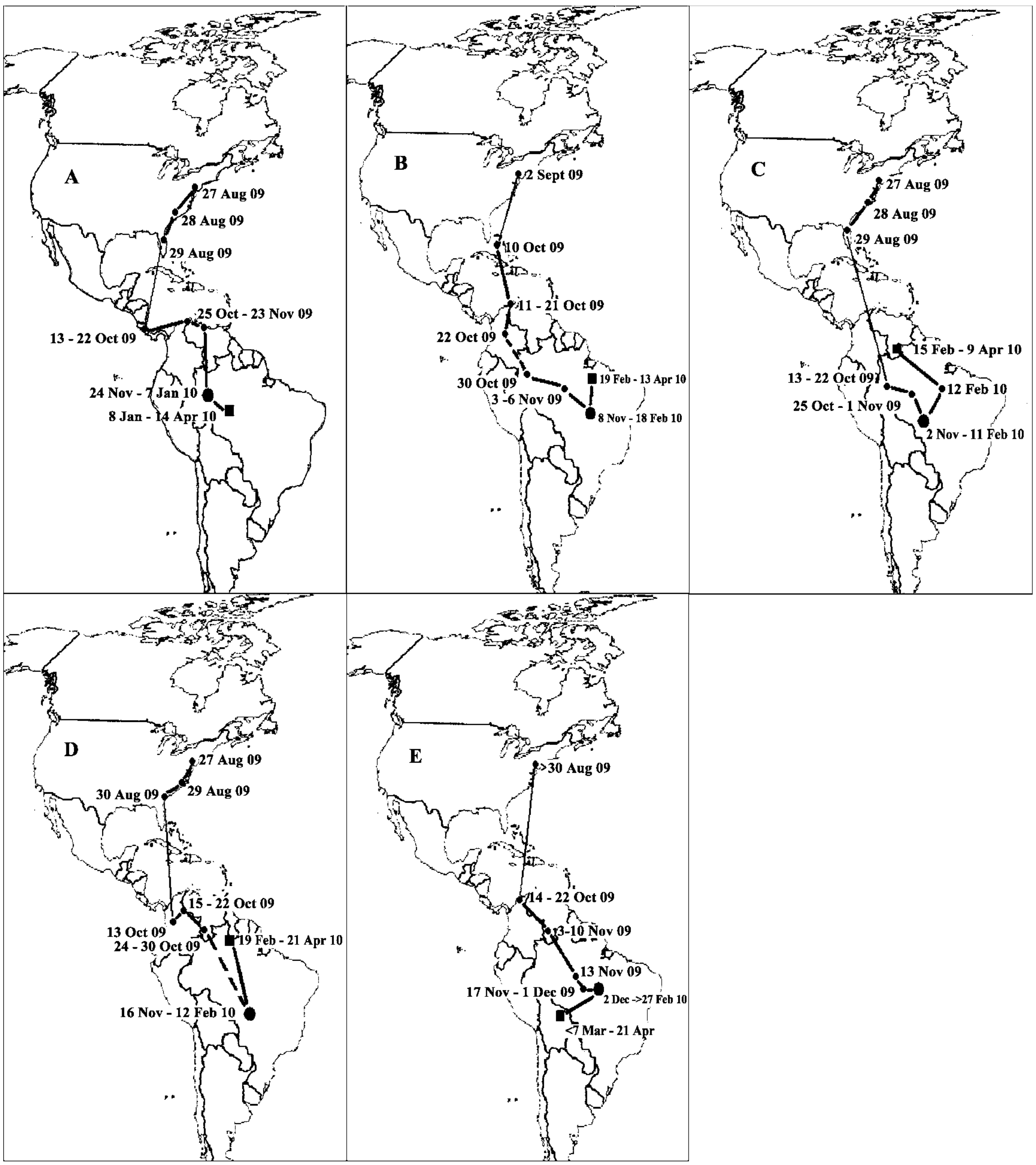

FIG. 1. Autumn migratory routes, dates, stopover sites, and first and second wintering locations of five Veeries (A–E) captured and fitted with light-sensitive geolocators in Delaware in 2009. Small circles represent stopover sites, large circles first winter sites, and squares second winter sites. Direct lines are used to indicate the movement between stationary points but do not necessarily reflect the routes taken by each individual. Thin lines represent concealed movement during equinox periods. Dashed lines indicate consistent leisurely movement. Missing dates indicate periods for which the location of the bird could not be established because of the equinox or shading events.

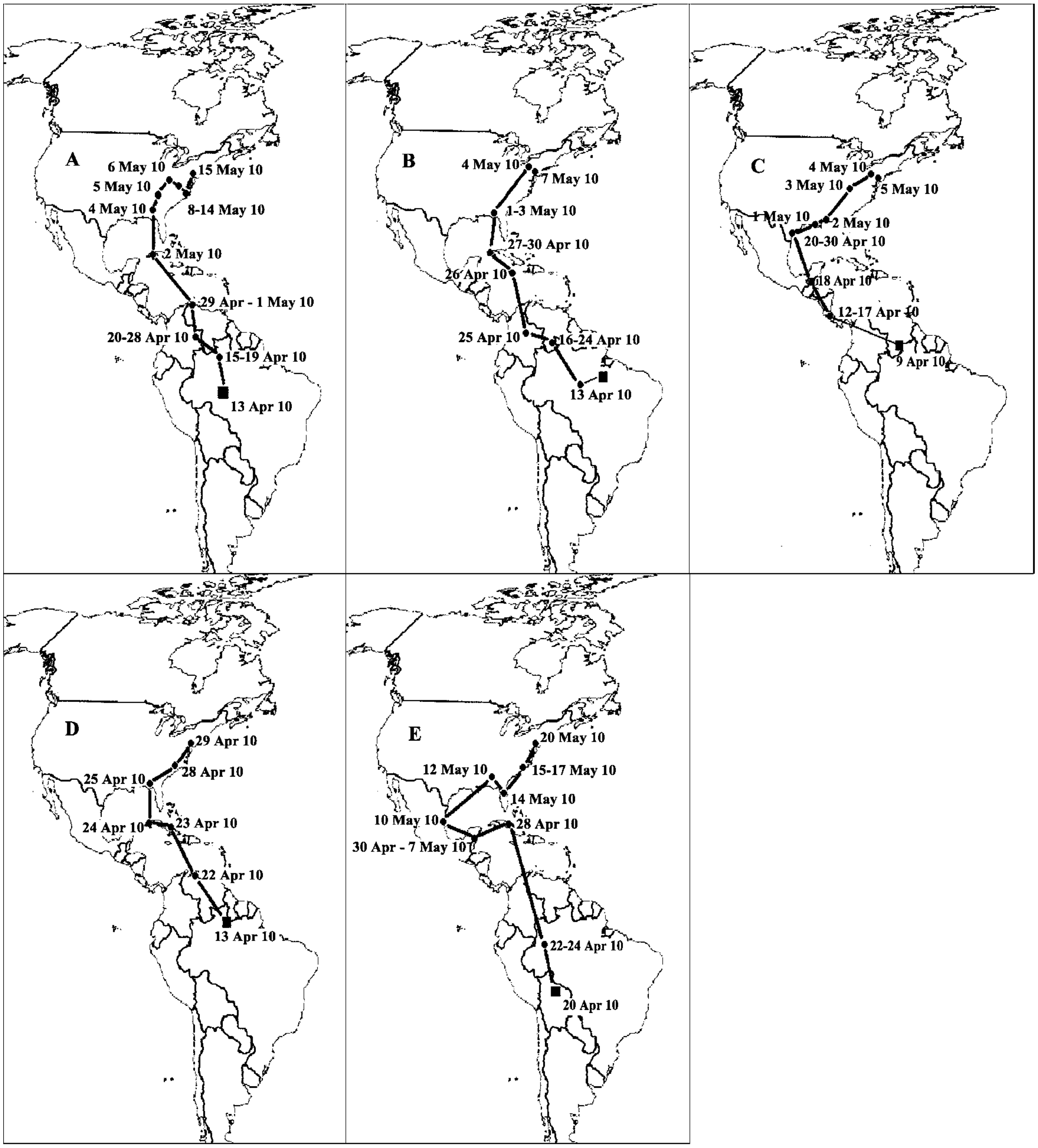

Fig. 2. Second wintering locations, with spring migratory dates, routes, and stopover locations, of five Veeries (A–E) fitted with geolocators in Delaware in 2009. Small circles represent stopover sites and squares second winter sites. Direct lines are used to indicate the movement between stationary points but do not necessarily reflect the routes taken by each individual. Thin lines represent concealed movement during equinox periods. Missing dates indicate periods for which the location of the bird could not be established because of equinox periods or shading events.

Results

Of the 24 Veeries that received geolocators in 2009, we relocated 16 at the study site in 2010. However, nine of these birds returned without their units. Of the seven that returned with their units, five were recaptured: four males (A–D) and one female (E; Table 1). Bird A was an SY male and bird B was in his third year (TY) in 2009. All others had been aged as ASY at initial capture (Table 1). The return rate of 67% was similar to the estimated return rate for the population as a whole over the 12-year study period (62%; C. M. Heckscher unpubl. data). All five units that we retrieved had complete data from the time the geolocator was deployed in 2009 to the 2010 retrieval date. At the study site, the average standard deviation of latitude and longitude in July was 1.8° and 1.0°, respectively, corresponding to a day-to-day accuracy of 200 km and 92 km, respectively. However, accuracy of latitude was expected to decrease as birds approached the equator and during periods that overlapped the spring and autumn equinoxes. Inferred stopover

Table 1. Age and summary statistics describing autumn migration for five Delaware Veeries as determined by light-senstive geolocators. Precise departure dates were not known for two birds because of shading events and the autumn equinox (see text). Additional stopover locations were likely concealed by shading events or the equinox. All birds migrated to a second winter site before initiating spring migration.

Bird	Age in 2009[a]	Departure date	Arrival date at first winter site	Straight-line distance (km)	Duration of migration (days)	Average distance per day (km day^{-1})	Number of inferred stopover locations (≥2 days)	Average number of days at stopovers (range)
A	SY	27 August	24 November	6,481	88	65	3	12 (10–14)
B	TY	>2 September	8 November	5,022	—	—	3	8 (3–11)
C	ASY	27 August	2 November	7,041	67	96	3	6 (2–9)
D	ASY	27 August	16 November	7,215	81	85	4	7.25 (2–14)
E (♀)	ASY	>30 August	2 December	6,320	—	—	3	11 (8–16)

[a]SY = second-year, TY = third-year, and ASY = after-second-year.

Table 2. Locations of the initial wintering sites of five Delaware Veeries as determined from light-sensitive geolocators, plus duration of stay and date of departure. All five birds established initial wintering sites in the southern Amazon River basin in Brazil before migrating to a second site prior to spring migration.

Bird	Location description at mean latitude and longitude	Mean latitude (± SD, km)	Mean longitude (± SD, km)	*n*	Departure date	Duration at site (days)
A	Jurua River, western Amazonas state	4.15°S (2.3, 253)	66.07°W (2.3, 280)	40	7 January	44
B	West side of the Xingú River, southern Para state	8.8°S (2.0, 220)	52.69°W (1.0, 109)	80	18 February	103
C	Headwaters of the Juruena River, NW Mato Grosso	11.5°S (2.0, 220)	58.37°W (0.9, 105)	96	11 February	109
D	Headwaters of the Xingú River, central Mato Grosso state	13.69°S (3.0, 330)	55.12°W (1.0, 107)	89	12 February	88
E (♀)	Iriri River, central Para state	6.8°S (2.6, 286)	54.65°W (0.8, 104)	80	≥27 February	88

locations and duration, as well as migratory routes and wintering locations, are depicted in Figures 1 and 2. Supporting data are presented in the Appendix.

Mean autumn migration travel rate was 82 ± 11 km day^{-1}, and the mean distance from Delaware to initial wintering sites was 6,415 ± 864 km (Table 1). All birds settled south of the Amazon River in Brazil at geographically separate locations (Fig. 1). Although widely spaced, three of the five birds settled within the Xingú River basin, including in the Iriri River watershed. The other two initial winter sites were northwest of the Xingú watershed in the Juruena and Jurua watersheds. Arrival dates ranged from 2 November to 2 December 2009 (Table 1). Duration at initial winter sites varied from 44 to 109 days ($\bar{x}$= 86 ± 25; Table 2). Departure dates ranged from 7 January to on or after 27 February 2010 (Table 2).

All five birds migrated to a second winter site (i.e., a second site with prolonged occupation prior to spring migration; Fig. 1). For most birds, light-level data from the second winter sites were largely obscured by shading events or overlapped with the spring equinox. Three second winter sites were located south of the Amazon River, and two were located north of the Amazon (Table 3 and Figs. 1 and 3). The duration at second sites ranged from 28 to 97 days ($\bar{x}$= 86 ± 25 days; Table 3).

Commencement of sustained northward movement ranged from 9 to 20 April 2010 (Table 4). Veeries averaged a spring migration rate of 287 ± 56 km day^{-1} (Table 4), and routes and stopover sites varied (Fig. 2). Distance traveled from second winter sites to the Delaware breeding site averaged 7,449 ± 1,664 km (Table 4). Delaware arrival dates ranged from 29 April to 20 May 2010 (Table 4).

Discussion

Wintering periods.—Neotropical migrants show a variety of nonbreeding-season life-history strategies, including site-faithful territoriality, local or short-distance movements, seasonal wandering, floating among territory holders, and nomadism (Newton 2008; for a brief review, see Faaborg et al. 2010b). However, to the best of our knowledge, our discovery of multiple wintering sites is the first report of individuals of a North American–breeding Neotropical migrant songbird showing prolonged occupation of two widely separated regions (i.e., >100 km) between autumn and spring migration. Because our discovery is novel, we provide the following to distinguish the movements of the birds in our study from other phenomena (e.g., movement to a stopover or staging area) and to validate the existence of two winter sites used by our subjects. First, settlement at the second winter site was independent from sustained movement toward breeding grounds; indeed, two of five Veeries flew hundreds of kilometers south to occupy their second sites. Second, regardless of the arrival dates at their second sites, all initiated sustained northward migration in mid-April. This synchronized movement north by all birds marked the commencement of spring migration similar to movement that has been used to designate the onset of migration in other avian species (e.g., Oppel et al. 2008). Third, among the five birds, all winter sites were geographically separate, suggesting a genetic or behavioral predisposition for each movement event. Finally, in one case, occupation of the second site exceeded the time spent at the initial winter site. Traditionally, sites are designated as migratory stopover locations because of their geographic position as a link

Table 3. Location of the second wintering sites of five Delaware Veeries as determined from light-sensitive geolocators, length of stay, and arrival and departure dates. Sample sizes for latitude and longitude differ because of uncertainties associated with measurement near the equinox (see text). All five birds settled at an initial location prior to migrating to their second winter site.

Bird	Location description at mean latitude and longitude	Arrival date	Straight-line distance from first winter site (km)	Duration from arrival to departure (Days)	Mean latitude ± SD	Mean longitude ± SD
A	Tapau River, central Amazonas state, Brazil	8 January	475	97	5.69 ± 3.2°S (352 km; n = 45)	62.2 ± 0.8°W (109 km; n = 45)
B	NE Para state, S of Amazon River, Brazil	19 February	758	28[a]	2.4 ± 2.7°S (297 km; n = 8)	52.51 ± 1.3°W (128 km; n = 28)
C	Ocamo River, Amazonas state, Venezuela	15 February	1,674	53	2.59 ± 3.0°N (330 km; n = 6)	64.38 ± 1.8°W (186 km; n = 50)
D	E Roraima state, Brazil	19 February	1,782	54	1.06 ± 3.3°N (363 km; n = 6)	59.36 ± 1.5°W (155 km; n = 50)
E (♀)	Mamore River, east-central Bolivia	<7 March[b]	1,350	≥ 45[b]	13.52 ± 5.0°S (550 km; n = 7)	62.8 ± 2.6°W (292 km; n = 20)

[a]This bird remained at one site from 19 February to 17 March but became unsettled thereafter, drifting slowly from east to southwest before initiating migration on 13 April.
[b]Precise arrival date and duration are unknown because of shading events.

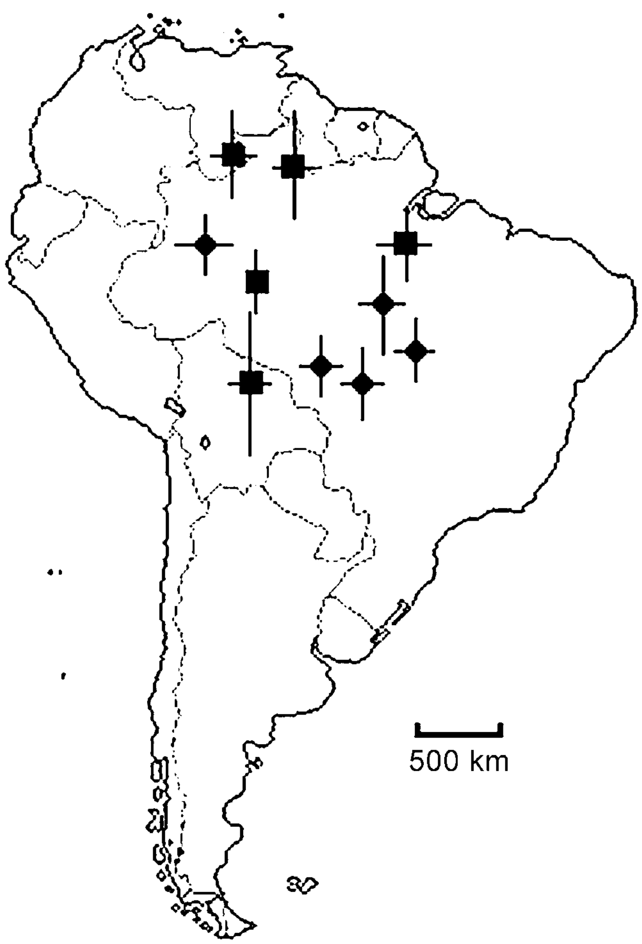

Fig. 3. First (diamonds) and second (squares) wintering locations of five Delaware Veeries in South America with respective latitude and longitude standard error bars. Some longitude error bars are concealed by the width of the respective symbols.

between wintering and summering locations for temporary occupation while the bird is on passage between the two regions (e.g., Moore and Simons 1989, McCann et al. 1993, Moore et al. 1995). It is clear that the Veery's movement to second sites is inconsistent with traditional definitions of migratory stopover behavior. Movements from first to second sites can also not be classified as local movements (e.g., shift in home range), short-distance movement (i.e., <100 km), seasonal wandering, or nomadism (Newton 2008, Faaborg et al. 2010b). Instead, the Veery's within-season long-distance movement qualifies as intratropical migration because it is identical to movements made by resident tropical species between the Tropic of Cancer and the Tropic of Capricorn (Remsen and Parker 1990, Petermann 1997, Faaborg et al. 2010b).

According to our spatial and temporal data, the cue prompting movement to a second winter site must be geographically broad but not synchronized. Veeries are primarily forest-litter foragers on the breeding grounds and during migration (Moskoff 1995) and, presumably, at winter sites. Food availability is thought to be a proximate determinant of the distribution and short-distance movement of nonbreeding Neotropical migrants in the tropics (Lefebvre and Poulin 1996, Strong and Sherry 2000, Brown and Sherry 2006). It thus seems reasonable to suspect that the predictable seasonal flooding of lowland forests in Amazonia may be the ultimate factor that prompted the Veeries to relocate. The predictable flood of Amazonia is indeed a geographically broad event that nevertheless remains unsynchronized because of variable local and regional conditions such as elevation, rainfall, topography, and positions in relation to headwater tributaries and larger rivers (Junk 1997). Veeries may have selected lowland forests (e.g., *várzea*, *igapó*) for initial winter sites and then relocated to higher elevations (e.g., *terra firme*) or unflooded regions. Thus, as the rainy season progressed, Veeries may have dispersed from lowland forests in a manner similar to that shown annually by resident lowland birds in Amazonia (Petermann 1997, Cintra et al. 2007). Our hypothesis also accounts for the movement of bird A from his initial site in western Amazonia 5 weeks prior to the movement of the birds in southeastern

Table 4. Summary statistics describing spring migration of five Veeries as measured by light-sensitive geolocators as they migrated from their second winter site in South America to Delaware. Additional stopover locations were likely concealed by shading events or the spring equinox (see text).

Bird	Initiation of spring migration	Arrival in Delaware	Straight-line distance to Delaware (km)	Duration of migration (days)	Average speed (km day^{-1})	Number of inferred stopover locations (≥2 days)	Average number of days at stopovers (range)
A	13 April	15 May	6,885	33	209	4	5.5 (3–8)
B	13 April	7 May	6,800	25	272	3	5.3 (3–9)
C	9 April	5 May	7,323	27	271	2	8 (6, 10)
D	13 April	29 April	5,950	17	350	0	0
E (♀)	20 April	20 May	10,290	31	332	3	4 (2–8)

Fig. 4. Revised winter range of the Veery (shaded), including two disjunct wintering areas (Mérida state, Venezuela, and southeast coastal forests of Brazil). The extent of the shaded area was determined by including the 10 wintering locations from the present study and by applying non-transient status to all Veery specimens reported in Remsen (2001) that were collected during non-transient periods (2 December–8 April). Question mark denotes a large region of the Brazilian highlands from which Veery winter records are lacking (Remsen 2001).

Amazonia, because comparable precipitation and rising river levels in eastern and interior Amazonia are typically 4 to 6 weeks later than those in western and peripheral regions (Irion et al. 1997).

Extreme dates of occupation of all winter sites ranged from 2 November to 20 April, a period of nearly 6 months. Remsen (2001) revised the Veery winter range on the basis of geographic distribution of specimen records from a more conservative timeframe: 2 December to 20 February. Thus, Remsen (2001) suggested that spring migration commenced about 21 February. However, that date is nearly 2 months before birds in the present study initiated synchronized northward migration. Furthermore, the individual that maintained the southernmost winter site did not initiate migration until 20 April. Therefore, the specimen records between 21 February and mid-April that Remsen (2001) mapped as spring transients were more likely winter residents. On the basis of our 10 wintering locations and the locations of all specimens collected between 2 December and 8 April that were reported in Remsen (2001), we propose a revised winter range that moves beyond the periphery of the Amazon basin to include the headwater region of the Orinoco River (Fig. 4). The collection of three specimens from high elevations in Mérida state, Venezuela, during non-transient periods is intriguing (see Remsen 2001) and may represent a disjunct northern wintering area for Veeries similar to the southern disjunct region of São Paulo, Brazil, initially established by Remsen (2001; Fig. 4).

Migratory periods.—Prior to our investigation, Veery spring migration was assumed to be nearly 3 months long (21 February to mid-May), similar to autumn migration (Remsen 2001). By contrast, Veeries initiated migration in mid-April and migrated rapidly to complete spring migration from wintering sites in Brazil to Delaware in as little as 17 days.

The location of migratory stopover sites that were visited multiple times by the five individuals may provide insight into potentially important stopover sites for transient Veeries. Notable sites included the Guyana Shield region of southern Venezuela, the northern coast of Colombia and Venezuela, the Greater Antilles, the coast of the Gulf of Mexico in North America, and eastern North and South Carolina. Despite earlier suggestions that Veeries are uncommon in Cuba and only casual in Jamaica (Arendt 1992), the northern coast of South America, Cuba, and Jamaica, may prove to be particularly important for Veeries that cross the Gulf of Mexico and Caribbean Sea.

From only five individuals, we documented three different migratory routes between South and North America and three different routes from the Gulf Coast to Delaware. Similarly, Bächler et al. (2010) recovered four geolocators from European Hoopoes that revealed three different trans-Saharan routes. Ornithologists studying the migratory patterns of Neotropical songbirds have often assumed that birds from the same population, and even those from the same region, follow the same migratory routes, to which they are presumably predisposed behaviorally and, to some degree, genetically (e.g., Ruegg et al. 2006, Wilson et al. 2008). For the Veery, our results suggest otherwise.

Implications for conservation.—All five Veeries used the southern Amazon basin in Brazil for initial winter sites. Three birds settled in or adjacent to the Xingú River basin. The Xingú River basin is the source of several Veery winter records (Remsen 2001) and lies within one of the most threatened regions in Amazonia (da Silva et al. 2005). Referencing da Silva et al.'s (2005) eight Amazonian conservation units, forests of the Xingú and Tapajós regions must now be recognized as among the most important to conserve for this species. In our opinion, all five Veeries showed intratropical migration from their initial winter site to a second winter site. We hypothesize that Veeries settled initially in seasonally inundated lowland forest and that the proximate cue that prompted relocation to a second site was related to the cyclical Amazonian flood pulse. The existence of two wintering areas of potentially equal ecological value will greatly complicate conservation planning for this species. Furthermore, forest communities in southern Amazonia are increasingly threatened by unprecedented deforestation and river damming, which now severely threatens the functioning of lowland forest ecosystems (Vale et al. 2008). If the birds in our study are typical for this species, the proposed ecological alteration of lowland forests may pose a serious threat to the Veery.

Acknowledgments

We thank the staff of the Delaware Division of Parks and Recreation, and especially White Clay Creek State Park, for cooperation and approval of permits. In particular, we thank Park Superintendant N. McFadden. C. Sun assisted with field work in 2010. K. Vulinec and four reviewers provided important editorial suggestions. B. Stutchbury provided invaluable advice and assistance in geolocator technology and field applications. Field supplies were funded from an internal Delaware State University funding source. Financial support for S. Taylor was provided by the Delaware NSF-EPSCoR Undergraduate Research Program administered by the Center for Integrated Biological and Environmental Research, College of Agriculture and Related Sciences, Delaware State University.

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Associate Editor: J. Jones

Appendix. Daily latitude and longitude with a general description of each location from five Veeries during (A) autumn migration and (B) spring migration. First winter sites are included as a termination point for autumn migration and second winter sites are included as a geographic reference point for the onset of spring migration. Sample sizes from second winter sites differ for latitude and longitude values because of uncertainties in location associated with the spring equinox (see text).

Bird	Date	Latitude or mean latitude (± SD) for sample sizes >1	Longitude or mean longitude (± SD) for sample sizes >1	Sample size	Approximate distance from previous location (km)	Location description
(A) Autumn migration						
A	27 August	39.44°N	75.45°W	—	—	Delaware
	28 August	72.97°N	72.97°W	1	671	Carolinas
	29 August	27.53°N	75.54°W	1	709	Florida
	13–22 October	10.31 ± 4.4°N (484 km)	83.28 ± 0.9°W (99 km)	7	1,800	Costa Rica
	25 October–7 November	11.15 ± 2.2°N (242 km)	72.5 ± 1.0°W (110 km)	8	1,231	North coast of Colombia
	12–23 November	11.18 ± 2.0°N (220 km)	69.67± 0.6°W (66 km)	12	320	North coast of Venezuela
	24 November–7 January	4.15 ± 2.3°S (253 km)	66.07 ± 2.3°W (253 km)	40	1,750	Western Amazonas State, Brazil
B	>2 September	39.34°N	75.44°W	—	—	Delaware
	10 October	24.01°N	77.39°W	1	1,752	Bahamas
	11–21 October	13.34 ± 4.6°N (506 km)	72.52 ± 1.6°W (176 km)	9	1,450	North coast of Colombia
	22–30 October	–	–	—	—	Continuous movement through eastern Colombia
	3–6 November	4.64°S	58.55°W	3	1,000	Southeast of Manaus, Brazil
	8 November–18 February	8.80 ± 2.0°S (220 km)	52.69 ± 1.0°W (110 km)	80	820	Southern Para State, Brazil
C	27 August	39.44°N	75.45°W	—	—	Delaware
	28 August	34.95°N	75.32°W	1	492	Outer Banks region, North Carolina
	29–30 August	28.95°N	80.54°W	2	852	Florida coast
	13–22 October	05.05 ± 2.4°S (264 km)	67.69 ±1.5°W (165 km)	6	4,037	W Amazonas state, Brazil
	25 October–1 November	04.75 ± 2.4°S (264 km)	60.25 ± 1.4°W (154 km)	6	835	Rio Madeira
	2 November–11 February	11.50 ± 2.0°S (220 km)	58.37 ± 0.9°W (99 km)	96	825	NW Mato Grosso, Brazil
D	27 August	39.44°N	75.45°W	—	—	Delaware
	29 August	34.79°N	76.37°W	1	541	Outer Banks region, North Carolina
	30 August	32.9°N	79.20°W	1	417	South Carolina
	13–14 October	3.02°N	73.98°W	2	3,385	Meta state, Colombia
	17–22 October	5.41 ± 2.0°S (220 km)	71.55 ± 0.9°W (99 km)	5	420	Casanare state, Colombia
	24–30 October	2.25 ± 1.8°S (198 km)	67.20 ± 0.7°W (77 km)	7	602	Amazonas state, Venezuela
	2–15 November	–	–	—	—	Continuous daily movement through central Brazil
	16 November–12 February	13.69 ± 3.0°S (330 km)	55.12 ± 1.0°W (110 km)	89	1,850	Central Mato Grosso, Brazil
E(♀)	>30 August	39.44°N	75.45°W			Delaware
	14–22 October	11.81 ± 3.7°N (407 km)	73.53 ± 0.7°W (77 km)	9	3,150	North coast of Colombia
	3–10 November	3.10 ± 2.4°N 264 km)	65.49 ± 0.8°W (88 km)	7	1,285	Southern Venezuela
	13 November	4.95°S	60.66°W	1	1,020	South of Manaus, Brazil

(*continued*)

APPENDIX. Continued.

Bird	Date	Latitude or mean latitude (± SD) for sample sizes >1	Longitude or mean longitude (± SD) for sample sizes >1	Sample size	Approximate distance from previous location (km)	Location description
	17 November–1 December	6.78 ± 5.0°S (550 km)	58.26 ± 1.5°W (165 km)	11	365	Southeast Amazonas state, Brazil
	2 December to >27 February	6.80 ± 2.6°S (286 km)	54.65 ± 0.8°W (88 km)	80	500	Central Para State, Brazil
(B) Spring migration						
A	8 January–13 April	5.69 ± 3.2°S (352 km)	62.2 ± 0.8°W (109 km)	45	—	Southern Amazonas state, Brazil
	15–19 April	0.56 ± 5.2°N (572 km)	63.61 ± 0.7°W (61 km)	4	780	Northern Amazonas state, Brazil
	20–28 April	3.78 ± 3.8°N (418 km)	68.53 ± 1.8°W (189 km)	8	600	Eastern Colombia
	29 April–1 May	10.99°N	70.11°W	3	780	Northwest Venezuela
	2 May	22.53°N	82.50°W	1	1,800	Western Cuba
	4 May	32.12°N	87.55°W	1	1,180	Alabama
	5 May	34.27°N	86.83°W	1	250	Northern Alabama
	6 May	37.14°N	83.59°W	1	400	Eastern Kentucky
	7 May	36.71°N	79.36°W	1	395	Central Virginia
	8–14 May	35.76 ± 1.1°N (121 km)	76.26 ± 0.5°W (50 km)	6	300	Eastern North Carolina
	15 May	39.34°N	75.00°W	—	400	Delaware
B	19 February–13 April	2.4 ± 2.7°S (297 km)	52.51 ± 1.3°W (143 km)	Lat: 8 Long: 28	—	Northeast Para State, Brazil
	16–24 April	5.64 ± 1.9°N (209 km)	63.18 ± 0.9°W (99 km)	9	1,400	Southern Venezuela
	25 April	5.09°N	69.76°W	1	570	Eastern Colombia
	26 April	17.98°N	79.80°W	1	1,600	Jamaica
	27–30 April	21.88 ± 4.7°N (517 km)	83.02 ± 0.8°W (88 km)	4	770	Western Cuba
	1–3 May	29.2°N	85.50°W	3	870	Florida panhandle
	4 May	40.25°N	77.55°W	1	1,400	Southcentral Pennsylvania
	7 May	39.34°N	75.00°W	—	190	Delaware
C	15 February–9 April	2.59 ± 3.0°N (330 km)	64.38 ± 1.8°W (198 km)	Lat: 6 Long: 50	—	Amazonas State, Venezuela
	12–17 April	9.11 ± 3.7°N (407 km)	86.89 ± 1.1°W (121 km)	5	2,400	Costa Rica
	18 April	16.72°N	89.17°W	1	890	Guatemala
	20–30 April	27.83 ± 3.3°N (363 km)	96.52 ± 0.5°W (50 km)	9	1,400	Texas coast
	1 May	30.09°N	91.98°W	1	530	Southern Louisiana
	2 May	29.63°N	89.75°W	1	207	Southeast Louisiana
	3 May	38.55°N	84.28°W	1	1,140	Northern Kentucky
	5 May	39.34°N	75.00°W	—	756	Delaware
D	19 February–13 April	1.06 ± 3.3°N (363 km)	59.36 ± 1.5°W (155 km)	Lat: 6 Long: 50	—	East Roraima State, Brazil
	22 April	11.78°N	67.87°W	1	1,500	Northern Venezuela coast
	23 April	21.28°N	77.42°W	1	1,400	Eastern Cuba
	24 April	22.36°N	83.72°W	1	680	Western Cuba
	25 April	31.13°N	84.76°W	1	1,000	Southwest Georgia
	28 April	33.94°N	78.13°W	1	700	Coastal North Carolina
	29 April	39.34°N	75.00°W	—	670	Delaware
E(♀)	<7 March–20 April	13.52 ± 5.0°S (550 km)	62.8 ± 2.6°W (292 km)	Lat: 7 Long: 20	—	East-central Bolivia

(*continued*)

Appendix. Continued.

Bird	Date	Latitude or mean latitude (± SD) for sample sizes >1	Longitude or mean longitude (± SD) for sample sizes >1	Sample size	Approximate distance from previous location (km)	Location description
	22–24 April	2.25°S	65.04°W	2	1,300	Western Brazil, north of the Amazon River
	28 April	22.0°N	75.13°W	1	2,800	Eastern Cuba
	30 April–7 May	16.26 ± 2.2°N (242 km)	87.07 ± 0.9°W (105 km)	6	1,150	Northern Honduras
	10 May	22.95°N	94.65°W	1	1,095	Mexico coast
	12 May	33.14°N	87.16°W	1	1,600	Central Alabama
	14 May	26.26°N	80.41°W	1	870	Central Florida
	15–17 May	34.41°N	76.28°W	2	950	Outer Banks, North Carolina
	20 May	39.34°N	75.00°W	—	525	Delaware