ORNITOLOGÍA NEOTROPICAL
(2021) 32: 1–9
ORIGINAL ARTICLE

Sociedad de Ornitología Neotropical

MINIATURE GPS DATA LOGGERS REVEAL HABITAT AFFILIATIONS AND MOVEMENT OF VEERIES (*CATHARUS FUSCESCENS*) DURING THEIR FIRST NON-TRANSIENT PERIOD IN SOUTH AMERICA

Christopher M. Heckscher[1] · Devin Mendez[1] · Keith A. Hobson[2] · Armando Alberto Aispuro[1,3] · Nicole Kleponis[1] · Alan H. Kneidel[1,4] · Melanie L. Mancuso[1,5] · Kevin J. Kardynal[6]

[1] Department of Agriculture and Natural Resources, Delaware State University. 1200 N. DuPont Highway, Dover, Delaware, USA, 19901.
[2] Department of Biology, University of Western Ontario. 1151 Richmond St. N., London, ON, Canada N6A 5B7.
[3] Konrad Lorenz Institute of Ethology, Department of Integrative Biology and Evolution, University of Veterinary Medicine. Savoyenstraße 1a, 1160, Vienna, Austria.
[4] Manomet, Inc., 125 Manomet Point Rd, Plymouth, Massachusetts, USA, 02360”
[5] Florida Fish and Wildlife Conservation Commission. 5285 N. Kenansville Rd. Saint Cloud, Florida, USA, 34773.
[6] Environment and Climate Change Canada, Science and Technology Branch. Saskatoon, SK, Canada.
E-mail: Christopher M. Heckscher · checkscher@desu.edu

Abstract · The ecology of Nearctic-Neotropical migrant songbirds in South America is largely unexplored. We used miniature global positioning system (GPS) data loggers to determine the broad habitat associations of nine Veeries (*Catharus fuscescens*) during their first non-transient period in South America. Because Veeries undertake an intra-tropical migration between two separate non-transient periods, the habitat used by settled birds in South America cannot be determined from field observation or the capture of single unmarked individuals. Using satellite images, we examined coarse habitat characteristics at GPS positions from the tagged birds during their first non-transient period (December to February). We also examined habitat descriptions from existing records (e.g., published literature, museum records) of multiple birds from single sites that we considered settled individuals. All records we accepted as birds settled during their first non-transient period, including birds we tagged, were associated with stunted forests on nutrient poor soils, primarily on elevated *cerrado* and white sand enclaves (~200 to 750 m) on the Brazilian Shield in southern Amazonia (*cerrado, cerradão, savana metalófita–canga*, *campinarana, sartenejal*). Notably, these forest communities are geographically limited and severely threatened due to anthropogenic conversion and occur largely in an ecologically distinct and highly threatened transitional biome between the Brazilian Cerrado and Amazonian lowlands (the Cerrado-Amazonia transition). Therefore, and considering the species’ recent population decline, we believe the Veery’s current global conservation status should be reconsidered. Following Nearctic-Neotropical migration, tagged individuals exhibited three behaviors prior to intra-tropical migration: (1) a prolonged stationary period at a single site, (2) shorter stationary periods with relocation events, and (3) apparent continual movement. Our results have significant importance in terms of understanding the ecology and conservation needs of this declining species and demonstrate the utility of GPS loggers in tracking songbirds through dense tropical vegetation in remote and inaccessible regions of South America.

Key words: Amazonia · Brazil · Nearctic-Neotropical migrant · White sand forest

INTRODUCTION

Nearctic-Neotropical passerine migrants spend more than half of their annual cycle on their non-breeding grounds, yet the ecology of these species, particularly those that spend the boreal winter in South America, has largely been an ornithological ‘black box.’ Basic information such as spatial and temporal patterns of movement and settlement, habitat affiliations, and species range limits have remained poorly understood for most species (e.g., Stouffer 2001, Callo et al. 2013, Ungvari-Martin et al. 2016). However, miniaturized tracking technology (e.g., archival light-level geolocators) has revolutionized our understanding of some aspects of the non-breeding season ecology of Nearctic-Neotropical migratory species in South America. Geolocation data has revealed that many species do not remain quiescent at a single site as previously assumed, but rather undertake periodic movement across large distances before initiating northward migration and returning to North America (Heckscher et al. 2011, Fraser et al. 2012, Callo et al. 2013, Renfrew et al. 2013).

The habitat occupied by many species during stationary periods in South America has remained unknown, partly because observations of unmarked birds may represent unsettled individuals rather than those settled for prolonged periods. Identifi-

Submitted 19 May 2020 · First decision June 18 2020 · Acceptance August 18 2020 · Online publication 18 June 2021

cation of the habitat types used during periods of settlement (as opposed to transience) is critically important as these areas may fulfill specific needs upon which the species depend. An understanding of the specific habitat needs of Nearctic-Neotropical migratory passerine species during their time in the Neotropics will be necessary to understand the biology of the full annual cycle and, consequently, the threats faced by migrant songbirds, which has been identified as a research priority (Marra et al. 2015). In addition, Nearctic-Neotropical songbirds may play significant ecological roles while settled in tropical ecosystems. Therefore, a fine scale approach to determine habitat use is now desirable as the error associated with geolocator resolution in the tropics can be excessive, sometimes reaching ± 500 km under certain circumstances (McKinnon et al. 2012), being at an insufficient scale to parse the specific habitat types used by individuals.

Miniaturized global positioning system (GPS) data loggers have become available for use on small songbirds (Hallworth & Marra 2015, Siegel et al. 2016, Fraser et al. 2017, Pedersen et al. 2018) and offer unprecedented spatial resolution of ~10 m error on single satellite fixes for small passerines despite a dense forest understory. This allows birds to be tracked using a high level of resolution and has enabled the remote assessment of the general habitat types used by individuals during sedentary periods (Hallworth & Marra 2015). Thus, we can now gain preliminary information regarding habitat use of small songbirds during sedentary periods in South America, including those periods between substantial intra-tropical movement. Although GPS loggers have drawbacks, such as a limited number of annual fixes due to limited battery life, they offer a unique opportunity to obtain precise spatial information from multiple stages of the annual cycle of small migratory birds (Hallworth & Marra 2015, Siegel et al. 2016, Fraser et al. 2017).

The Veery (*Catharus fuscescens*) is a Nearctic-Neotropical, trans-hemispheric migratory thrush that breeds in northern temperate and boreal forests of North America. Most Veeries spend the winter in southern Amazonia and undertake a mid-season intra-tropical migration, usually to northern portions of the basin or the Orinoco watershed (Heckscher et al. 2011, Hobson & Kardynal 2015). However, precise geographic limits remain poorly understood and habitat use during settlement has not been determined. Subsequent tracking studies have shown that other Nearctic-Neotropical migratory forest songbirds may relocate from primary wintering sites to a pre-migratory staging site prior to exiting South America (e.g., Callo et al. 2013). Nonetheless, the Veery's movement to a second overwintering site usually occurs mid-season, is substantial (often > 1500 km), and can be spatially and temporally separated from the onset of northward migration —the mid-season migration is considered a life history event separate from Nearctic-Neotropical migration (Heckscher et al. 2015, Hobson & Kardynal 2015, Kardynal & Hobson 2017). Thus, the Veery's non-breeding season in South America includes a southward migration, a first non-transient period, an intra-tropical migration, a second non-transient period (presumably stationary), and a northward migration (Heckscher et al. 2015).

To complement information gained from geolocators (e.g., Heckscher et al. 2011, Hobson & Kardynal 2015), we deployed miniaturized GPS data loggers (Lotek Wireless, Inc., Ontario, Canada) on Veeries in Delaware, USA, and British Columbia, Canada. Our objectives were: (1) to determine the precise locations and corresponding habitat use of our study subjects during their first sedentary period in South America, and (2) supplement these data with information from literature and voucher collections to provide a more complete understanding of the species' full life cycle and conservation needs in South America.

METHODS

In 2015–2017, we deployed miniaturized Lotek Wireless, Inc., PinPoint 10 GPS loggers on 40 Veeries at White Clay Creek State Park, Delaware, USA (39˚44'19.80˚N, 75˚45'39.12˚W), and 14 Veeries in Pemberton Valley in British Columbia, Canada (50˚27'55.27˚N, 122˚56'19.12˚W), using the Rappole Tipton harness method (Rappole & Tipton 1991). Each logger is ~1 g and they have shown spatial resolution of ~10 m accuracy in prior studies (Hallworth & Marra 2015). At the time of deployment, PinPoint 10 tags averaged 8–10 GPS locations ("fixes") per unit before the battery expired. The same tags can also be pre-programmed by the manufacturer to obtain up to 80 fixes (hereafter SWIFT tags). PinPoint GPS tags attempt to obtain satellite information for 70 s before the unit shuts down to save battery power. However, SWIFT tags limit the time used to collect information on satellite positions (12 s), thereby saving battery power and enabling up to 80 pre-programmed fixes. The loggers are archival and must be retrieved from each bird in order to access the data. After retrieval, GPS fixes were determined using the PinPoint Host software (Lotek Wireless, Inc., Ontario, Canada) and were subsequently mapped using Google Earth. To examine topography at each GPS fix, we applied three-dimensional elevation model imagery using the 3D Imagery tool in Google Earth, with Elevation Exaggeration set to 3, and supplemented the imagery with elevation models obtained from NASA and the Land Processes Distributed Active Archive Center, USGS/EROS, Sioux Falls, SD. Google imagery is often outdated and may not convey the ecological conditions of the sites as they were when occupied by the tagged Veeries. Therefore, we obtained Planet imagery (San Francisco, CA) for the date the GPS fixes were taken to confirm that the sites occupied by Veeries had not been ecologically altered after the Google imagery was obtained. We performed an unsupervised classification of the imagery to identify similar habitat types within a 500 m buffer around each GPS fix. This enabled the comparison of different land cover types using consistent image resolution from the immediate landscape. We then interpreted general habitat features of each GPS position.

For the Delaware sites, we deployed 40 total PinPoint tags during the 2015 (N = 15), 2016 (N = 10) and 2017 (N = 15) breeding seasons. We programmed the units to record locations from the species' first winter site using dates reported by Heckscher et al. (2015) in an attempt to obtain the precise location and general environmental features occupied by individual Veeries. This included pre-programmed fixes between 25 December and 22 February (approximate first winter period). Positions were considered stationary if fixes were obtained within 500 m in two separate 24 h periods. Hallworth & Marra (2015) programmed their units to take points at night, while the subject is most likely to be

Table 1. Summary data from GPS fixes and their corresponding coordinates, obtained from archival GPS loggers deployed on nine Veery (*Catharus fuscescens*) at a Delaware, USA, breeding site (Birds A, B, D – I) and a British Columbia, Canada, breeding site (Bird C). All units were recovered at the site of deployment. DOP refers to Dilution of Precision and indicates the accuracy of the GPS location (scale 0 – 20): the lower the number, the more accurate the fix. The slope aspect indicates the direction the occupied slope faces. Sex and age (SY = second-year bird, ASY= after-second-year bird) are given for each bird. [1]Obtained from NASA and the Land Processes Distributed Active Archive Center, USGS/EROS, Sioux Falls, SD, USA. [2]British Columbia male.

GPS fixes	Latitude	Longitude	DOP	Date	Local Time of Fix (h)	Elevation From Logger (m)	Corresponding Ground Elevation (m)[1]	Slope Aspect (˚)
Male A	**ASY**							
Fix 1	-10.742	-56.459	2.8	25 Dec 2015	10:48	232	322	230 (SW)
Fix 2	-10.742	-56.459	2.6	1 Jan 2016	07:05	251	321	315 (NW)
Fix 3	-10.742	-56.459	2.0	1 Jan 2016	11:05	324	321	315 (NW)
Fix 4	-10.742	-56.460	2.2	2 Jan 2016	11:00	319	321	315 (NW)
Female B	**ASY**							
Fix 1	-8.7089	-54.938	6.8	24 Dec 2015	19:41	359	380	20 (N)
Fix 2	-8.7088	-54.938	4.2	24 Dec 2015	22:00	393	380	122 (SE)
Fix 3	-8.7084	-54.940	7.4	31 Dec 2015	20:01	7	427	65 (E)
Fix 4	-8.7094	-54.938	1.8	1 Jan 2016	18:00	363	386	-
Fix 5	-8.7093	-54.938	3.8	2 Jan 2016	18:00	416	386	91 (E)
Male C[2]	**ASY**							
Fix 4	-14.090	-59.108	3	15 Nov 2015	00:57	627	646	286 (W)
Fix 5	-14.090	-59.108	7.4	15 Jan 2016	00:55	609	646	308 (NW)
Male D	**SY**							
Fix 1	-8.787	-50.165	3.6	24 Dec 2016	00:48	202	219	329 (NW)
Fix 2	-8.787	-50.166	6.8	25 Dec 2016	00:38	215	219	329 (NW)
Fix 3	-8.788	-50.167	2.2	31 Dec 2016	20:00	204	215	62 (NE)
Fix 4	-8.787	-50.167	2.6	1 Jan 2017	00:38	207	200	329 (NW)
Fix 5	-8.787	-50.165	1.2	1 Feb 2017	19:58	205	219	329 (NW)
Fix 6	-8.787	-50.166	2.2	2 Feb 2017	01:08	228	200	329 (NW)
Fix 7	-8.787	-50.166	1.0	21 Feb 2017	19:59	227	200	329 (NW)
Fix 8	-8.788	-50.166	1.6	22 Feb 2017	00:00	217	215	62 (NE)
Male E	**SY**							
Fix 3	-14.326	-59.539	0.8	31 Dec 2016	20:00	662	623	201(S)
Fix 4	-14.355	-59.530	1.0	1 Jan 2017	00:00	695	638	19 (N)
Fix 5	-14.333	-59.506	1.6	1 Feb 2017	19:58	660	660	73 (E)
Fix 6	-14.333	-59.506	2.0	2 Feb 2017	00:00	692	660	73 (E)
Female F	**ASY**							
Fix 1	-9.078	-60.797	0.8	24 Dec 2017	23:59	231	215	193 (S)
Fix 2	-9.078	-60.797	0.8	1 Jan 2018	00:00	224	215	193 (S)
Fix 3	-9.078	-60.796	2.0	4 Jan 2018	00:00	214	204	344 (N)
Fix 4	-9.079	-60.796	2.4	22 Feb 2018	00:00	208	212	266 (W)
Fix 5	-9.078	-60.797	4.8	28 Feb 2018	00:00	199	215	193 (S)
Male G	**SY**							
Fix 1	-14.210	-57.008	1.8	24 Dec 2017	23:52	480	525	230 (SW)
Fix 2	-14.211	-57.008	2.8	1 Jan 2018	00:00	539	525	230 (SW)
Fix 3	-14.212	-57.008	2.4	4 Jan 2018	00:00	513	525	230 (SW)
Fix 4	-14.027	-57.119	1.2	21 Feb 2018	23:58	537	539	56 (NE)
Fix 5	-14.027	-57.119	1.4	28 Feb 2018	00:00	556	539	56 (NE)
Female H	**ASY**							
Fix 1	-11.172	-56.068	2.2	24 Dec 2017	23:47	433	456	56 (NE)
Fix 2	-11.172	-56.068	2.4	1 Jan 2018	00:00	450	456	56 (NE)
Fix 3	-11.172	-56.067	1.6	4 Jan 2018	00:00	482	462	205 (SW)
Fix 4	-11.172	-56.066	2.6	21 Feb 2018	23:57	98	456	56 (NE)
Fix 5	-11.173	-56.068	1.4	28 Feb 2018	00:00	454	456	56 (NE)
Male I	**SY**							
Fix 1	-10.667	-56.335	2.0	24 Dec 2017	23:53	320	300	241 (SW)
Fix 2	-10.667	-56.336	0.8	1 Jan 2018	00:00	301	300	241 (SW)
Fix 3	-10.667	-56.335	2.0	4 Jan 2018	00:00	314	298	307 (NW)
Fix 4	-10.667	-56.336	2.2	21 Feb 2018	23:58	307	300	241 (SW)
Fix 5	-10.667	-56.336	1.4	28 Feb 2018	00:00	304	300	241 (SW)

stationary. However, we thought nighttime roosts might be within exceptionally dense tropical vegetation and perhaps among complex topography, making effective satellite fixes impossible. Conversely, we expected daytime foraging locations to be in a less dense cover, making successful fixes more likely despite the possibility of active movement. Therefore, in 2015—the first year of our study—, we arbitrarily varied the time of day in which we attempted fixes, programming both daytime and nighttime fixes to maximize the probability of at least some fixes being obtained. In 2016 through 2017, we programmed all units to obtain fixes only at or near midnight after confirming that nighttime fixes were adequate for our study objectives.

For the Canadian site, we deployed 14 units in 2015 and programmed the GPS tags to record one location near the breeding ground, three locations on migration, and four locations on the presumed wintering grounds. We assumed satellite reception would be optimal during roosting periods, as per Hallworth & Marra (2015), and programmed the devices to fix locations only at midnight (local time).

We undertook a literature search using the key terms of Veery, *Catharus*, *fuscescens*, Brazil, and South America to obtain location and habitat information from Veeries reported in published sources. We limited our search to records of

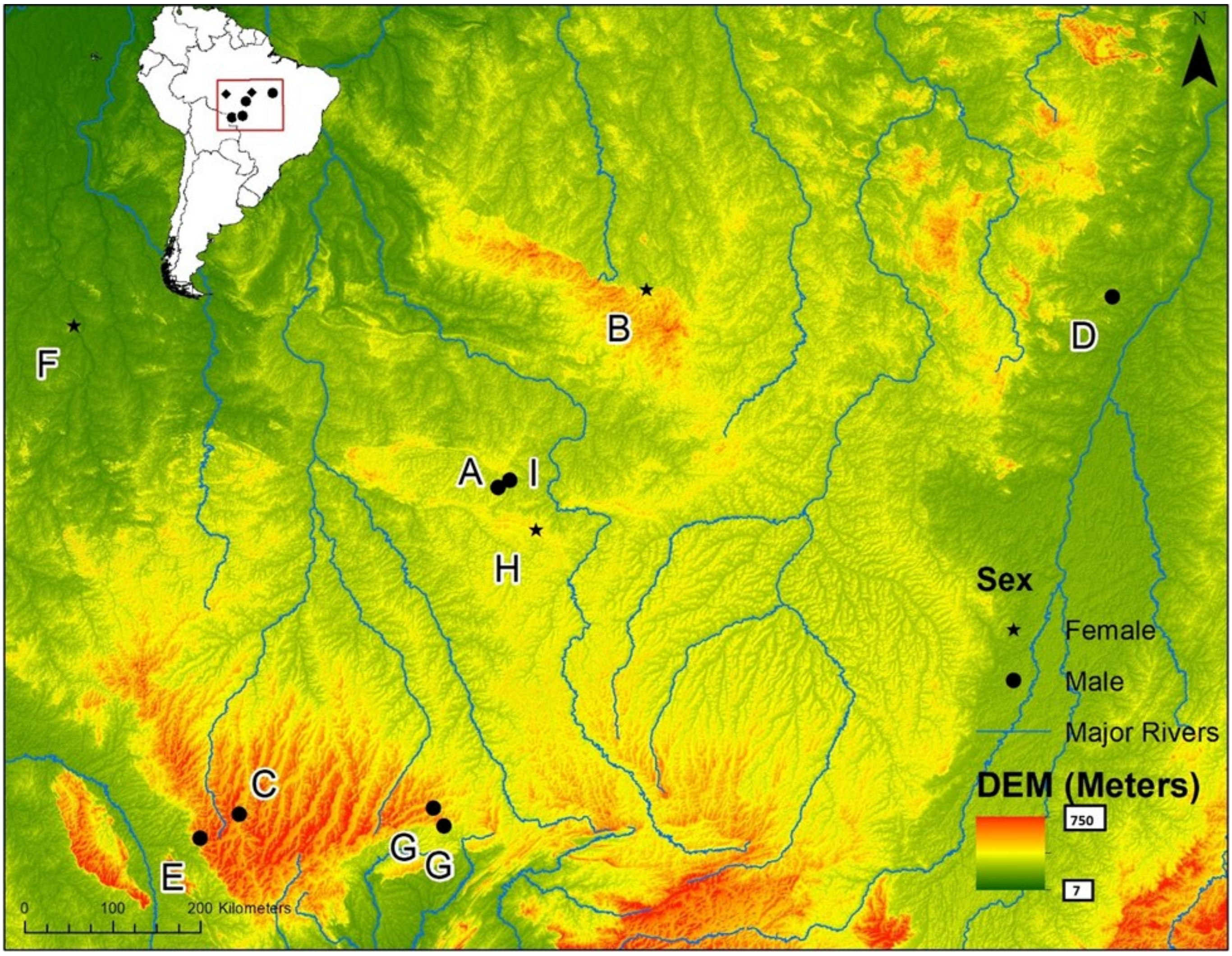

Figure 1. Digital elevation model (DEM) showing the distribution of elevated southern Amazonian *cerrado* and white sand enclaves (orange) in Mato Grosso and Pará states, Brazil. Locations of GPS fixes from nine Veeries (A – I) mark initial non-transient sites in the southern Amazon Basin. All Veeries settled at relatively high elevations on *cerrado*, white sand enclaves and associated outlying elevated formations (~200 – 750 m). Points G represent a single bird occupying multiple sites resulting from a relocation event. Point C represents the Veery tagged in British Columbia, Canada. All other points represent birds tagged in Delaware, USA.

multiple birds observed or taken from single sites during mid-December to early January —the time period within which Veeries are most likely to be settled. Remsen (2001) provided an exhaustive list of South American Veery voucher specimens. We queried the Instituto Nacional de Pesquisas da Amazônia (INPA) and the Museu Paraense Emilio Goeldi with multiple specimen records from single sites within our time period of interest in an attempt to obtain spatial coordinates and associated habitat information from specimen labels. We are aware of only one significant unpublished collection effort that resulted in multiple Veery specimens collected from a single site in South America during our targeted time period since the 2001 list was published. However, we were unable to obtain the pertinent habitat information from that effort. We also searched the eBird database (Cornell Laboratory of Ornithology). We filtered our search to December and January reports including multiple birds from the same site and photos to ensure accurate identification. Unfortunately, eBird records are often mapped to local "hotspots" that may be many kilometers from the observation or collection site.

RESULTS

In May and June 2016–2018, we retrieved data from nine recovered GPS units (8 from Delaware and 1 from British Columbia), with 45 total GPS fixes from first non-transient periods (Table 1). This included fixes from four second-year (SY) birds and five after-second-year (ASY) birds, aged according to Pyle (1997). Seven (2016 N = 3, 2017 N = 3, 2018 N = 1) birds returned with units that did not successfully store data; this included our SWIFT tags deployed in 2016 (N = 3), none of which obtained satellite fixes—possibly due to the short time the units were programmed to obtain fixes (12 s) from within dense tropical vegetation (M. Van del Tillaart, Lotek Wireless, Inc. pers. comm.). Indeed, data from all three SWIFT tags revealed the units attempted to collect satellite information, but timed out at 12 s prior to completion. One bird that returned with a unit was not re-captured. A unit's antennae was lost on another bird, so it did not provide meaningful data. Thus, 18 of 43 deployed units (42%) returned to our study sites, but only nine of 17 recovered units had meaningful data (53%).

All tagged birds settled on the Brazilian Shield from western and central Mato Grosso State to southeastern Pará State, Brazil. The use of Planet imagery revealed that none of our GPS fixes were obtained from sites that were ecologically altered or underwent significant ecological succession after the Google Earth imagery we used for analyses was obtained

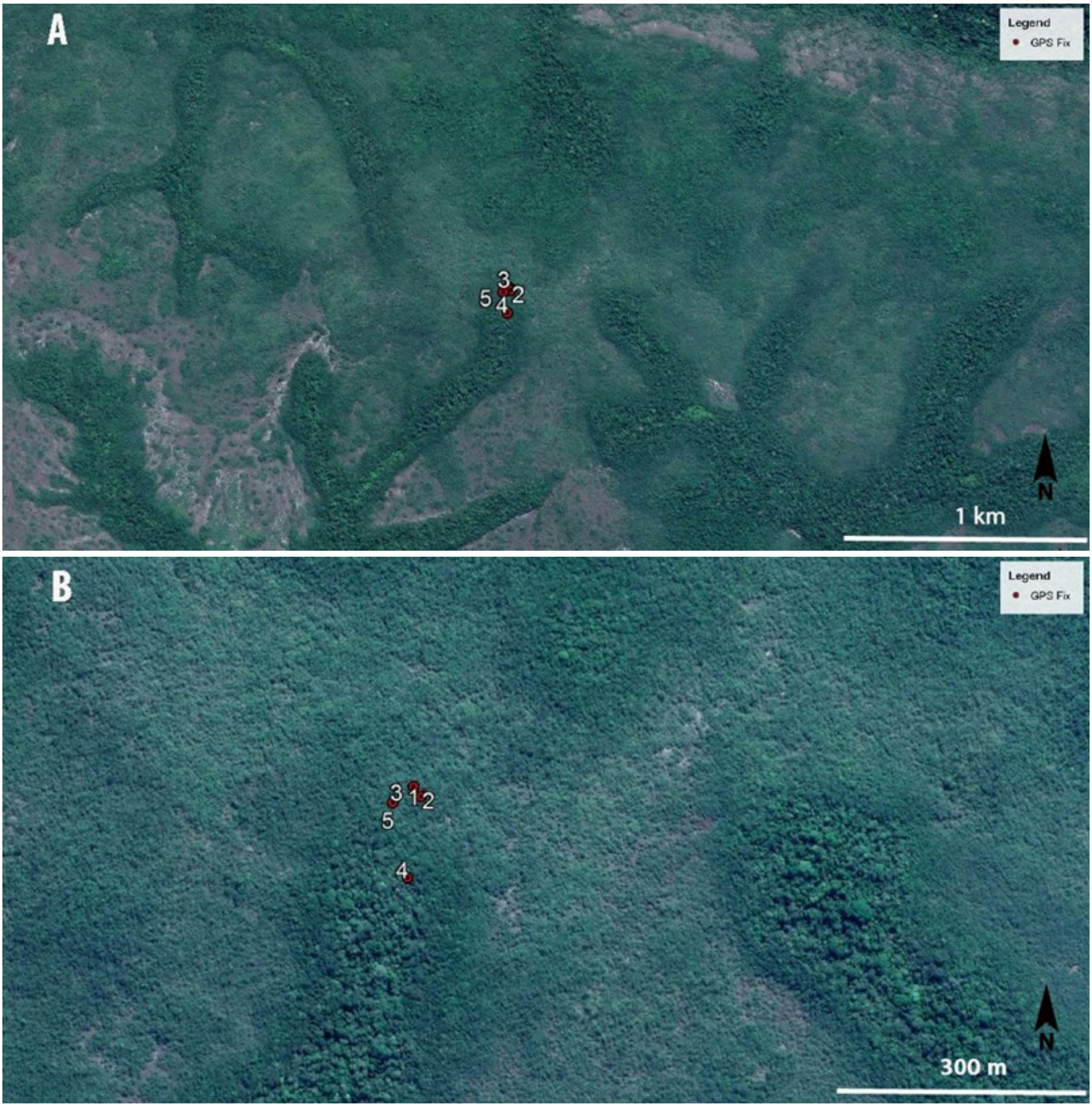

Figure 2. GPS fixes in southern Mato Grosso State, Brazil, showing five fixes (1-5) from Veery F (after second-year female) from 24 December 2017 (fix 1) to 28 February 2018 (fix 5). (A) A broad perspective showing the network of gallery forest amid a landscape of stunted vegetation and nutrient poor soils, and (B) the same fixes within a 20 m radius circle showing that points occur in a physiognomic transition zone of stunted forest, between open shrubland vegetation and closed canopy gallery forest. The Veery remained stationary throughout the two-month period in which fixes were obtained. Numbers correspond to the GPS coordinates presented in the paper's accompanied table (image source: Google Earth, Mountain View, CA. Imagery 2014).

from the same location. All Veeries occupied sites at comparatively high elevation (range 200–660 m) relative to intervening lowland areas on the Brazilian Shield (Table 1, Figure 1). Collectively, these broad isolated elevated regions are referred to as southern Amazonian *cerrado,* or "white sand" enclaves, and they support a resident avifauna distinct from lowland Amazonia and the dominant *terra-firme* forests of the region (e.g., Aleixo & Poletto 2007, Guilherme et al. 2018). Thus, all nine birds from two widely separated (>4,000 km) North American breeding sites settled at various elevated Amazonian enclaves on the Brazilian Shield. Satellite imagery revealed that most (66%) stationary sites were on upper slopes of ravines or otherwise on hillsides. Vegetation structure and geology inferred from Google Earth and corroborated with Planet imagery suggests that all sites were in areas of nutrient-poor soil, as evidenced by sandy substrate with dominant vegetation consisting of dense forest of low to medium stature (Figures 2–4). Four subjects (44%)—including the individual from British Columbia—occupied narrow bands of ecological transition zones on slopes above comparatively mature gallery or gallery-like forest, but below what appeared to be shorter shrubby or sparsely vegetated areas at slightly higher elevations (Figure 2). For this region, the term "stunted forest" has been used to describe mature but low stature forests on various nutrient-poor soil types, either semi-xeric or poorly drained (e.g., Tobias & Seddon 2007, Whitney et al. 2013). We adopt this term to refer generally to Veery habitat occupied by birds tracked in this

Figure 3. Five GPS fixes from Veery G (second-year male) Mato Grosso State, Brazil, showing two stationary sites separated by ~24 km: (1) 24 December 2017, (2) 1 January 2018, (3) 4 January 2018, (4) 21 February 2018, (5) 28 February 2018. Numbers correspond to the GPS coordinates presented in the paper's accompanying table (image source: Google Earth, Mountain View, CA. Imagery 2014).

study, as site-specific data regarding forest plant communities and specific soil types are not available.

GPS fixes revealed three types of behavior during the first non-transient period: (1) a prolonged stationary period at a single site (birds A–D, F, H, I; Table 1, Figure 2); (2) two stationary periods separated by a relocation event (Male G; Figure 3), and (3) apparent continuous unsettled movement over large distances (Male E; Figure 4). All five ASY birds remained stationary, while two of four SY birds showed movement prior to intra-tropical migration. Male E is the only bird that appeared to remain unsettled, but did so primarily in a ~4 km radius of contiguous forest. Male G was stationary at two separate sites (Table 1, Figures 1, 3). To the best of our knowledge, all other birds remained settled during their first non-transient period (Table 1).

Our literature search revealed three publications that detailed the habitat at sites where multiple Veeries were taken or observed during our periods of interest (Tobias & Seddon 2007, Whitney et al. 2013, de Lima Pereira et al. 2019). We believe these reports represented settled birds between Nearctic-Neotropical migration and intra-tropical migration. One publication reported an inter-annual recapture from a single site—possibly the first such confirmation for this species in South America (de Lima Pereira et al. 2019). In addition, four specimens at the INPA collection, collected from a single site during our target period, had accompanying habitat notes. None of the eBird records for mid -December to early January met our search criteria of multiple birds observed or collected with photographic documentation or voucher specimens (last accessed 1 October 2020).

DISCUSSION

Our results show that after completing the Nearctic-Neotropical migration, and prior to the intra-tropical migration, the Veeries we tracked from Delaware and British Columbia were associated with the higher elevations of the Brazilian Shield in areas of dense, naturally stunted vegetation overlying nutrient-poor soils. These sites were often in transition zones along gallery forests (i.e., *cerradão*) amid elevated *cerrado* and white sand enclaves, but also included topographically level areas of expansive naturally stunted forest. One bird settled on a steep, sparsely-vegetated slope amid a topographically diverse area, yet apparently consistent in vegetative physiognomy with habitat used by other birds, showing additional variation in habitat use. Similarly, Ungvari-Martin et al. (2016) reported an association of the closely related Gray-cheeked Thrush (*C. minimus*) with Peruvian white sand (i.e., nutrient poor) forests of the upper Amazon basin.

Our literature and specimen search provided specific habitat information from the species' first non-transient period that we could not obtain remotely from tagged individuals. These habitat descriptions are otherwise consistent with our GPS results: (1) a notable remark by Whitney et al. (2013) that multiple Veeries were observed in nutrient-poor stunted *campinarana* (white sand) forest near the Rio Madeira in Rondônia State, Brazil, in mid-December; (2) four Veery specimens in the INPA collection that were taken on 18–20 December from habitat consistent with a low-stature transition vegetation profile on nutrient-poor soils (*savana metalófita–canga*) in southeastern Pará State (Mario Cohn-Haft pers. comm.); (3) de Lima Pereira et al. (2019) report a Veery captured on 11 December 2015 in *cerradão* forest (8–15 m height) in Maranhão state, Brazil. Another bird was captured nearby and banded on 10 December 2013 and recaptured on 6 December 2014. This latter bird showed inter-annual site fidelity –possibly the first such confirmation for this species in South America– and was captured both years at the same site in *cerrado* vegetation; (4) Tobias and Seddon (2007) re-

Figure 4. Four GPS fixes from Veery E (second-year male) showing repeated movement: (3) 31 December 2016, (4) 1 January 2017, (5) 1 February 2017, (6) 2 February 2017. GPS fixes 1 (24 December 2016) and 2 (25 December 2016) are together and out of frame, ~47 km to the southwest. Note all habitat occupied consists of low-stature forest, and the adjacent un-paved roadways show exposed sandy substrate. Numbers correspond to the GPS coordinates presented in the paper's accompanying table (image source: Google Earth, Mountain View, CA. Imagery 2014).

ported five Veeries caught in mistnets in "lightly logged" *terra firme* (N = 1) and in nearby stunted forest (N = 4) in Pando Dept., Bolivia, on 23 October and 1–2 November, respectively. The authors suggested that the high number of individuals caught in that short period were likely indicative of an important non-transient population, but acknowledged that the dates of capture were prior to the species' presumed stationary period at the time (2 December–20 February; Remsen 2001). Geolocator tracking data from past studies shows that the mean date of arrival at the first non-transient sites by Delaware Veeries is 3 November (Heckscher et al. 2017). Given the number of individuals captured, and considering that the habitat described by Tobias & Seddon (2007) is consistent with our GPS fixes and at the extreme southern edge of the species' non-breeding range, we concur with their conclusion that their observations were likely of settled birds. Tobias & Seddon (2007) report dominant vegetation at one site (four of five reported Veeries) as ~12 m height. Alverson et al. (2003) provide more detail from this area, reporting it to be a low-stature (5–20 m high) forest, damp, poorly drained, with a thick spongy mat of raised humps (*monticulos*), or ridges, each from one to a few meters in diameter and separated by lower channels that seem to represent seasonal waterways. Some areas are described as a "spongy mass of leaves and roots" on the forest floor. This forest type is classified by Alverson et al. (2003) as *sartenejal* forest. It covers a relatively small area and has a patchy distribution in the region. On satellite images, it appears similar to the nearly topographically level habitat used by Male D in southeast Pará State, Brazil, herein reported. Tobias & Seddon (2007) conclude that northeastern Pando Dept. likely maintains significant areas of stunted forest important for the Veery and we agree with that assessment. Additional records of multiple birds from single sites were found in museum collections or mentioned in the literature, but are not included here because they lack precise site and habitat information or such information was not available for our use.

Collectively, these records show an association with various recognized naturally stunted forest types, including *cerrado, cerradão, savana metalófita–canga*, *sartenejal,* and *campinarana.* All are stunted vegetation overlying nutrient-poor soils. The occupied sites occur within a climatic zone between southern lowland Amazonia and the elevated Brazilian Plateau, and stretch from northwest Pando Dept., Bolivia, through Mato Grosso State and southern Pará State, to southwest Maranhão State, Brazil. Importantly, this transition zone has recently been identified as a unique and highly threatened biological region (Marques et al. 2020). Of note, there are several Veery records from eastern Brazil, including the Brazilian Atlantic forest (e.g., Remsen 2001, Pereira et al. 2012, Kardynal & Hobson 2017, Souza et al. 2018), which suggest the species settles there as well. The breeding origin, their duration in eastern Brazil, and habitat associations of these birds warrants further study.

Our results showing the Veery's association with stunted forests of the southern Amazon basin differ from prior published remarks. Heckscher et al. (2011) hypothesized that the Veery settled in lowland rainforests (e.g., *várzea*, *igapó*) prior to initiating its intra-tropical migration, and suggested that this was prompted by the concurrent cyclical flood pulse of the Amazon basin. As suggested by Heckscher et al. (2015), there may be an indirect effect of the flood pulse that prompts intra-tropical migration (e.g., interspecific competition with species emigrating from lowland areas), or perhaps the movement may be related to precipitation events in the southern basin, but GPS points show that none of the nine birds tagged in our study settled in lowland riverine floodplains.

Our subjects used three different behaviors during their first stationary period: (1) a prolonged stationary period, (2) multiple stationary periods separated by significant movement, and (3) apparent continuous unsettled movement.

These patterns may be age-related, as all five ASY birds remained stationary while two of four SY birds exhibited movement; however, a larger sample size will be needed before definitive inference can be drawn about age-related effects. It is perhaps notable that the bird that remained unsettled concentrated within a ~4 km radius of contiguous unfragmented forest over a minimum 34-day period.

Our findings have important implications for the conservation of this species. The Veery is declining at an alarming rate of -1.13% per year (Heckscher et al. 2020) and declined by 40% between 1979 and 2014 (Partners In Flight 2016), but the causes of the decline are unclear. It appears that the species is a facultative obligate of both damp (e.g., *sartenejal*) and more xeric (e.g., *campinarana*), naturally stunted nutrient-poor forest presumably <15 m height and perhaps often <10 m height. Of particular importance, we believe that Veeries may be largely dependent upon vegetative transition zones on slightly elevated terrain between lower mature gallery forests and more open scrub-shrub xeric sites. These narrow riparian ecotones, which are typical of much of the elevated enclaves, may be of particular importance to Veeries during their first non-transient period. The Veery's affiliation with specific and uncommon natural community types (e.g., c*erradão, savana metalófita – canga*, *campinarana*) among the isolated *cerrado* and white sand enclaves of the southern Amazon Basin indicate that the area occupied by Veeries during their first non-transient period may be far smaller than that spanned by their current known range in South America —particularly considering that these stunted forest communities cover only a small portion of the elevated enclaves. Adeney et al. (2016) report that approximately 165,000 km^2 of white sand forest occurs in Brazil, with <50% of that occurring south of the Amazon River. Of that percentage, only a small fraction consists of medium-stature vegetative ecotones (i.e., c*erradão*) between open shrubland and high stature forest –a frightening prospect considering the entire North American Veery population may be largely dependent on these narrow ecotones. Importantly, *cerrado* and white sand enclaves are highly threatened by deforestation and habitat alteration (e.g., Adeney et al. 2016, Marques et al. 2020), and these forests may take many decades or even centuries to recover from anthropic disturbance (Adeney et al. 2016). From a broad perspective, most of the region occupied by Veeries lies within the cerrado-Amazonia ecological transition zone, an expansive region that warrants renewed recognition by conservationists for its unique species assemblages and threatened status (Marques et al. 2020). The region is known as the "Arc of Deforestation" due to expanding agriculture, ranching, logging, and forest fires, and may be near ecological collapse (Marques et al. 2020). Marques et al. (2020) report >52,000 km^2 (42%) of ecotonal *cerradão* forest lost in this region between 1984 and 2019. Taken in sum, and in combination with recent annual Veery decline, these findings are alarming. Our results warrant the further study of Veery habitat use with a larger sample of individuals but suggests the Veery's global conservation status should be reconsidered; for example, the species is considered of Least Concern by BirdLife International (2020) and does not appear on the most recent Partners In Flight Watch List (Partners In Flight 2016).

We found three possibly age-related behavior patterns during the species' first non-transient periods in southern Amazonia, including permanent settlement, multiple sedentary periods, and continuous unsettled movement. Research to refine the ecological requirements during this period and the possible ecological role Veeries fulfill in tropical ecosystems is warranted. In addition, studies to determine precise habitat associations at second non-transient sites (post intratropical migration), movement patterns, age, and sex-related differences, as well as habitat affiliations in eastern Brazil, should be additional research priorities to fill knowledge gaps in the Veery's full-cycle biology and to inform future conservation efforts.

ACKNOWLEDGEMENTS

We thank Mike van den Tillaart, Lotek Wireless, Inc., for technical assistance and advice, and Mario Cohn-Haft for providing information about South American Veery specimens. The Delaware Division of Parks and Recreation allowed access to the Delaware study site and approved research permits. In particular, we thank Chris Bennett, Susan Staats, Angel Burns, Vincent Porcellini, and Rob Line. Limited funding was provided by the NOAA-EPP Environmental Cooperative Science Center award NA11SEC4810001 to CMH and by an operating grant to KAH from Environment and Climate Change Canada.

REFERENCES

Adeney, JM, NL Christensen, A Vicentini & M Cohn-Haft (2016) White-sand ecosystems in Amazonia. *Biotropica* 48: 7–23.

Aleixo, A & F Poletto (2007) Birds of an open vegetation enclave in southern Brazilian Amazonia. *The Wilson Journal of Ornithology* 119: 610–630.

Alverson, WS, DK Moskovits & C. Halm (2003) Bolivia: Pando, Federico Roman. Rapid Biological Inventories: 06. The Field Museum, Chicago, USA.

BirdLife International (2020) Species factsheet: *Catharus fuscescens*. Available at http://www.birdlife.org [Accessed 13 April 2020]

Callo, PA, ES Morton & BJ Stutchbury (2013) Prolonged spring migration in the Red-eyed Vireo (*Vireo olivaceus*). *The Auk* 130: 240–246.

de Lima Pereira, KD, G de Avila Batista, V Sousa, L D'avila Della Coletta e Ferreira & LB Monteiro (2019) First records of Veery, *Catharus fuscescens*, for the state of Marahao, northeast Brazil. *Biota Amazônia* 9: 59–60.

Fraser, KC, BJM Stuchbury, C Silverio, PM Kramer, J Barrow, D New stead, N Mickle N, NBF Cousens, JC Lee JC, DM Morrison, T Shaheen, P Mammenga, K Applegate & J Tautin (2012) Continent-wide tracking to determine migratory connectivity and tropical habitat associations of a declining aerial insectivore. *Proceedings of the Royal Society B* 279: 4901–4906.

Fraser, KC, A Shave, A Savage, A Ritchie, K Bell, J Siegrist, JD Ray, K Applegate & Pearman M (2017) Determining fine-scale migratory connectivity and habitat selection for a migratory songbird by using new GPS technology. *Journal of Avian Biology*, 48: 339–345.

Guilherme, E, EL Marques & GS Santos (2018) Avifauna of a white-sand enclave in north-west Rondônia, Brazil: relevant records, body mass and morphometrics. *Bulletin of the British Ornithologists Club* 138: 286–306.

Hallworth, MT & PP Marra (2015) Miniaturized GPS tags identify non-breeding territories of a small breeding migratory songbird. *Scientific Reports* 5: 11069.

Heckscher, CM, SM Taylor, JW Fox & V Afanasyev (2011) Veery (*Catharus fuscescens*) wintering locations, migratory connectivity, and a revision of its winter range using geolocator technology. *The Auk* 128: 531–542.

Heckscher, CM, MR Halley & PM Stampul (2015) Intratropical migration of a Nearctic-Neotropical migratory songbird (*Catharus fuscescens*) in South America with implications for migration theory. *Journal of Tropical Ecology* 31: 285–289.

Heckscher, CM, M Gutierrez Ramirez & AH Kneidel (2017). Reproductive outcomes determine the timing of arrival and settlement of a single-brooded Nearctic-Neotropical migrant songbird (*Catharus fuscescens*) in South America. *The Auk: Ornithological Advances* 134: 842-856.

Heckscher, CM, LR Bevier, AF Poole, W Moskoff, P Pyle & MA Patten (2020) Veery (*Catharus fuscescens*), v. 1.0. *In* Rodewald, PG (ed) *Birds of the World*. Cornell Lab of Ornithology, Ithaca, N.Y. https://doi.org/10.2173/bow.veery.01

Hobson, KA & KJ Kardynal (2015) Western Veeries use an eastern shortest-distance pathway: New insights to migration routes and phenology using light-level geolocators. *The Auk: Ornithological Advances* 132: 540–550.

Kardynal, KJ & KA Hobson (2017) The pull of the central flyway? Veeries breeding in western Canada migrate using an ancestral eastern route. *Journal of Field Ornithology* 88: 262–273.

Marra, PP, EB Cohen, SR Loss, JE Rutter & CM Tonra (2015) A call for full annual cycle research in animal ecology. *Biology Letters* 11: 20150552.

Marques, EO, B Hur Marmon-Junior, BS Marimon, EAT Matricardi, HA Mews & GR Colli (2020) Redefining the Cerrado-Amazonia transition: implications for conservation. *Biodiversity and Conservation* 29: 1501-1517.

McKinnon, EA, CQ Stanley, KC Fraser, MM MacPherson, G Casbourn, PP Marra, CE Studds, N Diggs & BJM Stutchbury (2012) Estimating geolocator accuracy for a migratory song bird using live ground-truthing in tropical forest. *Animal Migration* 2: 1–8

Partners In Flight (2016) Partners In Flight 2016 Landbird Conservation Plan Revision. Available at https://partnersinflight.org/wp-content/uploads/2017/03/SPECIES-OF-CONT-CONCERN-from-pif-continental-plan-final-spread-2.pdf [Accessed 19 May 2020]

Pedersen, L, K Thorup & AP Tøttrup (2018) Annual GPS tracking reveals unexpected wintering area in a long-distance migratory songbird. *Journal of Ornithology* 160: 265–270.

Pereira, GA, LW Lobo-Araújo, S Leal, J Medcraft, CA Marantz, MTF Toledo, HFP Araujo, C Albano, T Pinto, CHA Santos, LCH Serapião, GBM Silva & D Pioli (2012) Important bird records from Alagoas, Pernambuco and Paraíba, north-east Brazil. *Cotinga* 34: 91–95.

Pyle, P (1997) *Identification guide to North American birds, part 1: Columbidae to Ploceidae*. Slate Creek Press, Bolinas, USA.

Rappole, JH & AR Tipton (1991) New harness design for attachment of radio transmitters to small passerines. *Journal of Field Ornithology* 62: 335–337.

Remsen, JV (2001) True winter range of the Veery (*Catharus fuscescens*): Lessons for determining winter ranges of species that winter in the tropics. *The Auk* 118: 838–848.

Renfrew, RB, D Kim, N Perlut, J Smith, J Fox & PP Marra (2013) Phenological matching across hemispheres in a long-distance migratory bird. *Diversity and Distributions* 19: 1008–1019.

Siegel, RB, R Taylor, JF Saracco, L Helton & S Stock (2016) GPS-tracking reveals non-breeding locations and apparent molt migration of a Black-headed Grosbeak. *Journal of Field Ornithology* 87: 196–203.

Souza JL, AC Queiroz, GA Pereira, V Leandro-Silva, ACR Souza & SM Azevedo-Júnior (2018) Documented records of two migratory bird species in the State of Pernambuco, North-East Brazil. *Brazilian Journal of Biology* 78: 588–590.

Stouffer, PC (2001) Do we know what we think we know about winter ranges of migrants to South America? The case of the Veery (*Catharus fuscescens*). *The Auk* 118: 832–837.

Tobias, JA & N Seddon (2007) Nine bird species new to Bolivia and notes on other significant records. *Bulletin of the British Ornithologists' Club* 127: 49–84.

Ungvari-Martin, J, CM Heckscher & KA Hobson (2016) Inter-annual site fidelity and breeding origins of Gray-cheeked Thrushes in white sand forests of the Peruvian Amazon. *Journal of Field Ornithology* 87:55–87.

Whitney, BM, M Cohn-Haft, GA Bravo & LF Silveira (2013) A new species of *Herpsilochmus* antwren from the Aripuanã-Machado interfluvium in central Amazonian Brazil. Pp. 277-281 *in* del Hoyo, J, A Elliott, J Sargatal, D Christie (eds) *Handbook of the Birds of the World. Special volume: new species and global index.* Lynx Edicions, Barcelona, Spain.