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SHORT COMMUNICATION

Intratropical migration of a Nearctic-Neotropical migratory songbird (Catharus fuscescens) in South America with implications for migration theory

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Abstract: Recent advances in tracking technology have revealed significant intratropical movement of Nearctic–Neotropical migratory songbirds during their non-breeding season. We report the movement of 25 veeries (Catharus fuscescens) over multiple seasons (2009–2013) through equatorial rain forests of South America. Veeries initially settled on the Brazilian Shield geological formation but undertook an intratropical migration to a second South American region in January, February or March. Consequently, our study is the first to track individual forest passerines to document an annual migration from the Brazilian Shield to the Guiana Shield and into lowland regions of Amazonia. The movement and settlement patterns showed no spatiotemporal relationships with Nearctic–Neotropical migration, remained in accordance with the flood pulse of the Amazon basin, and were spatially and temporally complex suggesting relatively ancient ancestral origins. The ability to isolate the migration event from Nearctic–Neotropical migration is an important contribution to the ongoing discourse regarding the evolution of trans-hemispheric migration in the genus Catharus.

Key Words: Amazonia, avian migration, Brazilian Shield, Catharus, geolocators, Guiana Shield, Levey–Stiles model, veery

Nearctic-Neotropical migrant songbirds spend most of their annual cycle in the Neotropics, yet we understand little about the non-breeding season ecology of most species especially those that settle in South America (Gómez et al. 2014). With the advent of miniature light-archival technology (hereafter, geolocators), it has become apparent that the inability to determine the spatial and temporal movements of individuals in the tropics has concealed significant life-history events for many species. Recent studies have revealed that significant seasonal patterns of intratropical movement and settlement are not uncommon (Callo et al. 2013, Fraser et al. 2012, Heckscher et al. 2011). Importantly, as birds move among and within tropical ecosystems, they likely fulfill important ecological roles unaccomplished by sedentary residents (Cotton 2007, Levey 1994, Rodrigo de Castro et al. 2012).

Four distinct types of avian tropical movement have been widely recognized by ornithologists: altitudinal (Loiselle & Blake 1991), nomadic including itinerancy (i.e. facultative movement of birds in relation to shifting resources; Kristensen et al. 2013), short-distance (e.g. shift in home range <100 km; Lefebvre & Poulin 1996) and intratropical latitudinal or longitudinal migration (Morton 1977). Intratropical migration is the annual long-distance movement (≥100 km) of individuals that takes place between the Tropic of Cancer and the Tropic of Capricorn (Hayes 1995, Heckscher et al. 2011). Of the four, it is the least understood. Unlike nomadic movement, intratropical migration is temporally and spatially predictable and therefore presumably more obligatory than facultative. Significant non-breeding season migratory movements of Palaearctic–African passerine migrants in tropical regions have been recognized for some time (Lack 1983, Moreau 1972), yet until recently New World intratropical migration of passerines, as defined here, was recognized

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Table 1. Descriptive statistics for veeries (Catharus fuscescens) in South America from date of first entry into the continent to departure. Data are from geolocators retrieved from veeries at a breeding site in Delaware, USA, from 2010 to 2013. Sample size differs due to differences in shading events and the failure of some units in March 2011.

<table>
<thead>
<tr>
<th>Variable</th>
<th>N</th>
<th>Mean ± SE</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Date into South America</td>
<td>25</td>
<td>8 October</td>
<td>11 September–1 November</td>
</tr>
<tr>
<td>Arrival at first site</td>
<td>25</td>
<td>11 November</td>
<td>15 October–8 December</td>
</tr>
<tr>
<td>Latitude (°S) of first site</td>
<td>25</td>
<td>10.42 ± 3.6</td>
<td>2.3–16.8</td>
</tr>
<tr>
<td>Longitude (°W) of first site</td>
<td>25</td>
<td>56.4 ± 4.3</td>
<td>50.8–66</td>
</tr>
<tr>
<td>Duration at first site (d)</td>
<td>25</td>
<td>92.4 ± 20.3</td>
<td>36–121</td>
</tr>
<tr>
<td>Distance of intratropical migration (km)</td>
<td>21</td>
<td>1382 ± 584</td>
<td>461–2617</td>
</tr>
<tr>
<td>Arrival at second site</td>
<td>19</td>
<td>12 February</td>
<td>5 January–4 March</td>
</tr>
<tr>
<td>Latitude of second site</td>
<td>21</td>
<td>1.6 ± 5.9 °S</td>
<td>2.9 °N–17.5 °S</td>
</tr>
<tr>
<td>Longitude (°W) of second site</td>
<td>21</td>
<td>60.1 ± 4.2</td>
<td>50.3–68.7</td>
</tr>
<tr>
<td>Duration at second site (d)</td>
<td>11</td>
<td>62 ± 15.8</td>
<td>38–97</td>
</tr>
<tr>
<td>Date of initiation of northward migration</td>
<td>13</td>
<td>15 April</td>
<td>6 April–30 April</td>
</tr>
</tbody>
</table>

only in tropical residents and was largely without confirmation – observers noticed the disappearance of bird populations in one region followed by the appearance of individuals of the same species in another (Cotton 2007, Morton 1977). However, since 2011, at least three Nearctic-breeding species have shown some form of significant intratropical movement between Nearctic–Neotropical migrations (Swainson’s thrush Catharus ustulatus, Cormier et al. 2013; purple martin Progne subis, Fraser et al. 2012; veery C. fuscescens, Heckscher et al. 2011).

The veery is a Nearctic-breeding species that spends most of its annual cycle in South America. Using geolocators, Heckscher et al. (2011) tracked five individuals from North to South America. Once in South America, veeries settled at non-breeding sites yet subsequently migrated to a second South American region prior to the initiation of northward migration, possibly prompted by the flood pulse of the southern Amazon basin (Heckscher et al. 2011). The veery’s movement from first to second sites is inconsistent with stopover or staging behaviour yet meets the definition of intratropical migration (Heckscher et al. 2011). The behaviour is not isolated in our study population and occurs in individuals from across the species range as nine veeries recently tracked from British Columbia, Canada, show essentially the same pattern of spatial and temporal movement (Keith Hobson, pers. comm.). Thus, the species appears to be both a Nearctic–Neotropical migrant and an intratropical migrant. We report data on the movement of 25 individual veeries over multiple years to refine our knowledge of this complex system. Specifically, we tested two hypotheses: (1) The veery’s intratropical movement is independent from Nearctic–Neotropical migration and (2) the movement remains spatially consistent with the cyclical flood pulse of the Amazon basin as previously hypothesized by Heckscher et al. (2011). Finally, the Catharus lineage has been a model system for examining the evolution of migration (Outlaw et al. 2003, Voelker et al. 2013). Our study of intratropical migration contributes a unique perspective to the ongoing dialogue regarding the role of the tropics in the evolution of migration in the Catharus lineage.

From 2010 to 2013, we retrieved geolocators (British Antarctic Survey models Mk10 and Mk12, and Lotek model Mk40C) from 25 individuals (2010–2013: N = 4, 11, 7, 3, respectively; male: N = 15; female: N = 10) at a Delaware, USA, breeding site (39°44′N, 75°45′W), that revealed their South American movement and approximate non-breeding season locations. We mapped the mean locations of each individual during stationary periods. Descriptive statistics with standard errors are reported in Table 1. Straight-line distances between stationary locations were measured in Google Earth (Google, Inc., Mountain View, CA, USA). Linear regressions were run using the R statistical program version 3.0.1 (R Development Core Team). Age and year effects could not be determined due to small sample size. For more details regarding data processing and mapping methods, see Heckscher et al. (2011).

All of our study subjects initially settled south of the Amazon River. All but one bird settled on the western Brazilian Shield geological formation (Figure 1). Subsequently, most veeries moved north to second sites in lowland Amazonia and the Guiana Shield; however, three birds (12%) moved south of which two settled in Bolivia (Figure 2). A negative relationship between the date of arrival at first sites and the duration at those sites (N = 19; y = −0.8x + 34702; R² = 0.41, P = 0.003) indicates that the initiation of movement to second sites was not dependent on the duration at first sites. The farther south a bird initially settled, the longer its distance to second sites (N = 20; y = −0.006x – 6.5; R² = 0.25, P = 0.02), suggesting that the location of second sites were not influenced by the location of first sites. The date of initiation of northward migration
Intratropical migration of the veery

Figure 1. Mean locations of 25 first South American non-breeding sites (a) and 21 second sites (b) of veeries (Catharus fuscescens) tracked via light-archival geolocator units from a Delaware, USA, breeding population from 2009 to 2013. The approximate western boundary of the Brazilian Shield is indicated as a thin curved line. The intratropical migration of veeries from the Brazilian Shield physiographic region is evident.

Figure 2. Southward movement of two male (a, c) and one female (b) veeries (Catharus fuscescens) from first non-breeding sites (solid circle) to second sites (open circle) in South America. The distance (km) of the intratropical movement is to the left of each corresponding second site. Dates of departure from first sites: 7 January 2010 (a), 28 February 2010 (b), February 2013 (precise day unknown) (c).

(i.e. sustained movement north; Heckscher et al. 2011) was not dependent on the duration at second sites ($N = 9$; $y = -0.8x + 33982$; $R^2 = 0.78$, $P = 0.001$) nor was it influenced by the latitude of second sites ($N = 12$; $y = 0.03x - 1372$; $R^2 = 0.001$, $P = 0.9$). Taken cumulatively, these data show no interdependency of the intratropical movement and subsequent settlement with Nearctic–Neotropical migration. Discontinuity among the three migratory events is corroborated by the southward movement of three birds opposite from a northbound trajectory expected if intratropical migration marked the onset of migration back to North America as migratory stopover sites or staging areas are expected to be geographically positioned en route to breeding regions (Heckscher et al. 2011, Moore & Simons 1989, Moore et al. 1995). Finally, the maximum duration spent at first and second sites (first site: 121 d. second site: 97 d; Table 1) both exceeded 50% of the South American non-breeding season (minimum range of 8 December–6 April; Table 1), far longer than expected for temporary stopover or staging areas. Given these data, we argue the veery’s intratropical movement must continue to be viewed as a separate migratory event, as suggested by Heckscher et al. (2011), independent from Nearctic–Neotropical migration with probable distinct ecological consequences.

Outlaw et al. (2003) and Voelker et al. (2013) hypothesized that the genus Catharus originated in Central or North America, respectively, with recent expansion into South America. As time progresses, migration systems may become increasingly complex (Ruegg & Smith 2002). The veery’s non-breeding season encompasses two separate regions, consists of a series of spatially and temporally distinct events, and incorporates an annual, predictable, independent, large-scale intratropical migration averaging >1300 km, farther than many documented migratory events in the northern hemisphere. Therefore, it seems probable to us that this system has relatively ancient South American ancestral roots rather than a system recently derived. Further, the ability to isolate the mid-season movement from other migratory events is significant in that it lends
support to the possibility that intratropical migration preceded and perhaps facilitated Nearctic–Neotropical migration in this lineage (Levey–Stiles model of the origins of Nearctic–Neotropical migration; Levey & Stiles 1992). Notably, that scenario was considered yet ultimately rejected by Outlaw et al. (2003) with the caveat that their decision was based largely on equivocal data.

Departure from the Brazilian Shield was initiated from west to east as evidenced by an inverse relationship between the longitude of first sites and the corresponding date of departure (N = 19; y = −0.12x + 5073; R² = 0.2, P = 0.05). Therefore, movement to second sites remained consistent with the Amazonian flood pulse (Hecksher et al. 2011), which increases in magnitude in a west to east pattern (Junk 1997). However, the proximate cue prompting movement may well be indirect considering that the Brazilian Shield is a topographically diverse region. Thus, if veeries are settling outside of lowland forest (i.e. terra firme) they nevertheless could be indirectly affected by its rising waters (e.g. via a corresponding shift in resource availability or interspecific competition). Precipitation or fruit availability unrelated to the Amazonian flood pulse could also prompt movement. However, latitudinal and longitudinal precipitation patterns are quite variable and unpredictable in this region (Liebmann & Marengo 2001) and a marked seasonal change in precipitation (i.e. the cessation of the rainy season) occurs long after veeries have moved. Presently, there is not an obvious synchrony between veery departure date and seasonal fruit availability (Haugaasen & Peres 2007).

The settlement and subsequent migration of, plausibly, tens of thousands of veeries from the Brazilian Shield has heretofore gone unrecognized. The contribution to tropical forest structure and function may be significant. Herein, we have refined considerably our knowledge of this system. This migration is an intriguing tropical phenomenon with potentially important ecological and theoretical consequences that warrants further investigation.

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LITERATURE CITED


Intratropical migration of the veery


