Sociedad
de Ornitología
Neotropical

TRANSIENT SWAINSON'S THRUSH (*CATHARUS USTULATUS*) WINTERING IN THE ANDEAN FOOTHILLS OF ECUADOR ARE ALMOST EXCLUSIVELY YOUNG MALES

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Abstract · We know relatively little about the non-breeding period of most migratory birds. Decades of research on Swainson's Thrush (*Catharus ustulatus*) have focused on their breeding ecology, whereas their non-breeding ecology is limited to broad patterns of distribution and migratory stop-over ecology. For nearly 50 years, the US Breeding Bird Survey recorded declines of 0.7% per year for the Russet-backed Swainson's Thrush (*C. u. swainsonii*) subspecies, which spends the non-breeding period in South America. However, there is an insufficient understanding of the constraints across their annual cycle to determine the reasons for the sustained decline. In 2013 and 2014, we examined their little studied non-breeding period on the Andean slopes of Ecuador, where prior experience showed that they were seasonally abundant. Here, rapid deforestation threatens primary forests. We used point counts and radio telemetry to evaluate whether the primary forests were preferentially used in relation to recently regenerated second-growth forests. From point counts, 76% of detections and almost all captured individuals occurred in secondary forests. Of 86 birds captured in mist nets, 85 were males and 83 were young, indicating a highly skewed ratio in favor of young males. Radio telemetry demonstrated a preference for the secondary forest, especially for fruiting *Cecropia* spp. trees, with no apparent territorial behavior by those tracked and with short residency times. A marked decrease in density over the course of the field season suggests an itinerant population possibly tracking ephemeral fruit resources. Alternatively, these temporal and spatial patterns could suggest that this population undergoes a mid-winter intra-tropical migration, or at least landscape-level movements. However, we observed thrushes throughout our extended sampling period, suggesting transiency with high turnover. This study documents demographic separation during the non-breeding period with preference for secondary forests and high transiency, important findings in informing management across the annual cycle.

Resumen · Individuos transeúntes del zorzal de Swainson (*Catharus ustulatus*) invernando en las estribaciones andinas de Ecuador
Conocemos relativamente poco del periodo no reproductivo de la mayoría de las aves migratorias. Décadas de investigación sobre el zorzal de Swainson (*C. ustulatus*) se han enfocado en su ecología reproductiva, mientras que la ecología en periodos no reproductivos está limitada a patrones generales de distribución y de paraderos migratorios. Por casi 50 años, el Censo de Aves Reproductoras de Estados Unidos ha detectado reducciones poblacionales de 0,7% para la subespecie *C. u. swainsonii*, que permanece en Sudamérica durante el periodo no reproductivo. Sin embargo, hay una comprensión insuficiente de las limitaciones en su ciclo anual que determinen las razones de esta reducción sostenida. En 2013 y 2014, examinamos el poco estudiado periodo no reproductivo en las laderas de los Andes del Ecuador, donde experiencias previas mostraron que eran estacionalmente abundantes. Aquí, la rápida deforestación amenaza el bosque primario. Usamos censos de puntos fijos y radiotelemetría para identificar si el bosque primario se usaba preferencialmente sobre el bosque secundario recientemente regenerado. En los censos, el 76% de las detecciones y casi todos los individuos capturados ocurrieron en bosque secundario. De los 86 individuos capturados con redes de niebla, 85 fueron machos y 83 juveniles, lo que indica un alto sesgo a favor de machos juveniles. La radiotelemetría demostró preferencias por el bosque secundario, especialmente por árboles en fruto de *Cecropia* spp., sin aparente comportamiento territorial por parte de las aves rastreadas y con tiempos cortos de residencia. Una marcada disminución de la densidad en el transcurso de la investigación en campo sugiere una población itinerante, que posiblemente rastrea los recursos frutales efímeros. Alternativamente, estos patrones temporales y espaciales podrían sugerir que esta población sufre una migración intratropical, o al menos movimientos de amplio espectro, a mediados del invierno. Sin embargo, observamos zorzales durante el periodo extendido de muestreo, lo que sugiere transitoriedad con un alto intercambio. Este estudio documenta la separación demográfica durante el periodo no reproductivo con un uso intensivo de bosque secundario y alta transitoriedad, hallazgos importantes para informar el manejo a lo largo del ciclo anual.

Key words: Demographic habitat segregation · Floaters · Migratory bird · Non-breeding ecology · Non-breeding season

INTRODUCTION

Documenting the population demographics, movement dynamics and habitat use of local populations of migratory birds during the non-breeding period of the annual cycle is essential to understand the constraints on fitness (Sherry and Holmes 1996, Webster et al. 2002). Furthermore, understanding temporal and spatial patterns of winter habitat use helps identify critical habitats and periods of use, both essential for conservation management (Ramos and Warner 1980, Martin and Finch 1996, Marra et al. 2006). The breeding ecology of migratory birds has been studied extensively and long-distance tracking technologies have recently provided new insights into the migratory behavior of birds (Webster et al. 2002, Boulet and Norris 2006, Moore et al. 2003). Despite the increased attention to the nonbreeding ecology of Nearctic-Neotropical migrants in the last half century, comparatively less research has focused on this phase of their annual cycles (Johnson and Geupel 1996, Webster and Marra 2005, Marra et al. 2015).

Studies of non-breeding migrant songbirds often focus on species and populations that hold territories, where older males outcompete younger individuals and females for the best habitat (Marra and Holmes 2001, Moore et al. 2003). Young males and females are typically subordinate to older males, and in such cases they occupy less optimal territories, or "float" opportunistically through the landscape (Moore et al. 2003). The spatial extent of non-breeding habitat use is thus correlated with age and sex for many populations. Within the genus *Catharus*, territorial Hermit Thrushes (*C. guttatus*) wintering in pine plantations of Louisiana occupied relatively small patches (mean = 0.55 ± 0.03 ha) that minimally overlapped over three wintering seasons (Brown et al. 2000, Brown and Long 2007); here, several birds were non-territorial (14%) and used larger areas, moving among occupied territories. Wintering Wood Thrushes (*Hylocichla mustelina*) in Veracruz, Mexico, also used an assortment of survival strategies, including a sedentary and floating behavior (Rappole et al. 1989). Rappole et al. (1989) found from 61 radio-tracked birds that sedentary ones were more likely to survive during this period, suggesting that the floating strategy was suboptimal. All age and sex classes were represented among territorial and non-territorial birds, implying no socially dominant classes during the non-breeding period (Rappole et al. 1989).

Longer intra-tropical movements of non-breeding migrants, in contrast to floating, are well documented among *Catharus* and other species (Morton 1977, Loiselle & Blake 1991, Lefebvre & Poulin 1996, Kristensen et al. 2013). Recent results from light-level geolocators on Swainson's Thrush and veeries (*C. fuscescens*) have revealed previously undocumented patterns of large-scale mid-season movements by some individuals (Delmore et al. 2012, Cormier et al. 2013, Heckscher et al. 2015). However, geolocation accuracy (McKinnon et al. 2013) does not reveal patterns of habitat selection and finer-spatial-scale movements. Their collective results do suggest that some populations undertake non-breeding seasonal movements outside of migration.

Swainson's Thrush is a long-distance Nearctic-Neotropical migrant that breeds across North America and spends the non-breeding period in Central and South America (Mack & Yong 2000, Delmore et al. 2012, Cormier et al. 2013), where

little is known about their non-breeding ecology. There are two recognized subspecies: the coastal (*C. u. ustulatus*) and the boreal (*C. u. swainsoni*) (Mack & Yong 2000, Ruegg 2007). Tracking studies of the coastal subspecies identified Mexico and Central America as their non-breeding grounds, while the boreal subspecies occurs primarily along the eastern slope of the Andean foothills and in lower numbers in lowlands of Venezuela, Colombia, Ecuador, Peru, Bolivia, and into northern Argentina (Delmore et al. 2012). Despite these advances, there is currently little known about the temporal and spatial use of local habitats and resources by Swainson's Thrush during this period.

It is not clear how space use varies by age and sex class, and the causes or consequences of such mid-season movements. Here, we examined the fine-scale space use and habitat occupancy patterns of Swainson's Thrush at a mid-elevation site on the eastern slope of the Andes. We assessed the use of primary and secondary forest, identified the degree of territoriality, and documented the demographic make-up and resource use. We predicted Swainson's Thrush would show similar demographic habitat use patterns to some other studied migrant thrushes (Brown et al. 2000, but excluding Wood Thrushes in Veracruz, Rappole et al. 1989), with younger individuals occupying the secondary forest as transients or floaters, whereas older birds would hold territories in higher quality primary forest habitats.

METHODS

Study area. We conducted this research at the Wildsumaco Wildlife Sanctuary (0°40'18"S, 77°35'57"W), in the eastern foothills of the Ecuadorian Andes (approx. 1500 m), along a network of trails. This area, located in the Gran Sumaco region, is adjacent to Parque Nacional Sumaco and is under threat due to conversion of primary forest for agriculture. Expansion of roads in recent years allowed international oil companies and opportunistic farmers to gain access and clear the forest. Wildsumaco Wildlife Sanctuary has primary forests intermixed with pastures and former agricultural plots in various seral stages.

Vegetation surveys. We assessed vegetation using relevés. Vegetation surveys were conducted at each of 24 point-count locations along the trail network at Wildsumaco, with 12 stations each in both primary and secondary habitats. A 25 m plot was established, with the point-count location as the center, and vegetation was divided into four categorical layers. The tree layers were: (1) woody plants > 5 m in height, (2) shrub-layered woody plants with a range of 0.5–5 m in height, (3) a herb layer of 0.1–0.5 m in height, and (4) a moss layer less than 0.1 m in height. The percentage covered by each of these four layers was visually estimated using a 0–5 scale. A score of five for any of the layers represented >75% cover in the plot, four indicated 50–75%, three indicated 25–50%, two indicated 5–25%, one indicated <5%, and zero indicated 0%.

We estimated the average upper and lower heights (bounds) for both tree (to the nearest meter) and shrub (to the nearest decimeter) layers within the plot. We recorded the diameter at breast height (DBH) to the nearest centimeter for both the smallest and largest tree within each plot.
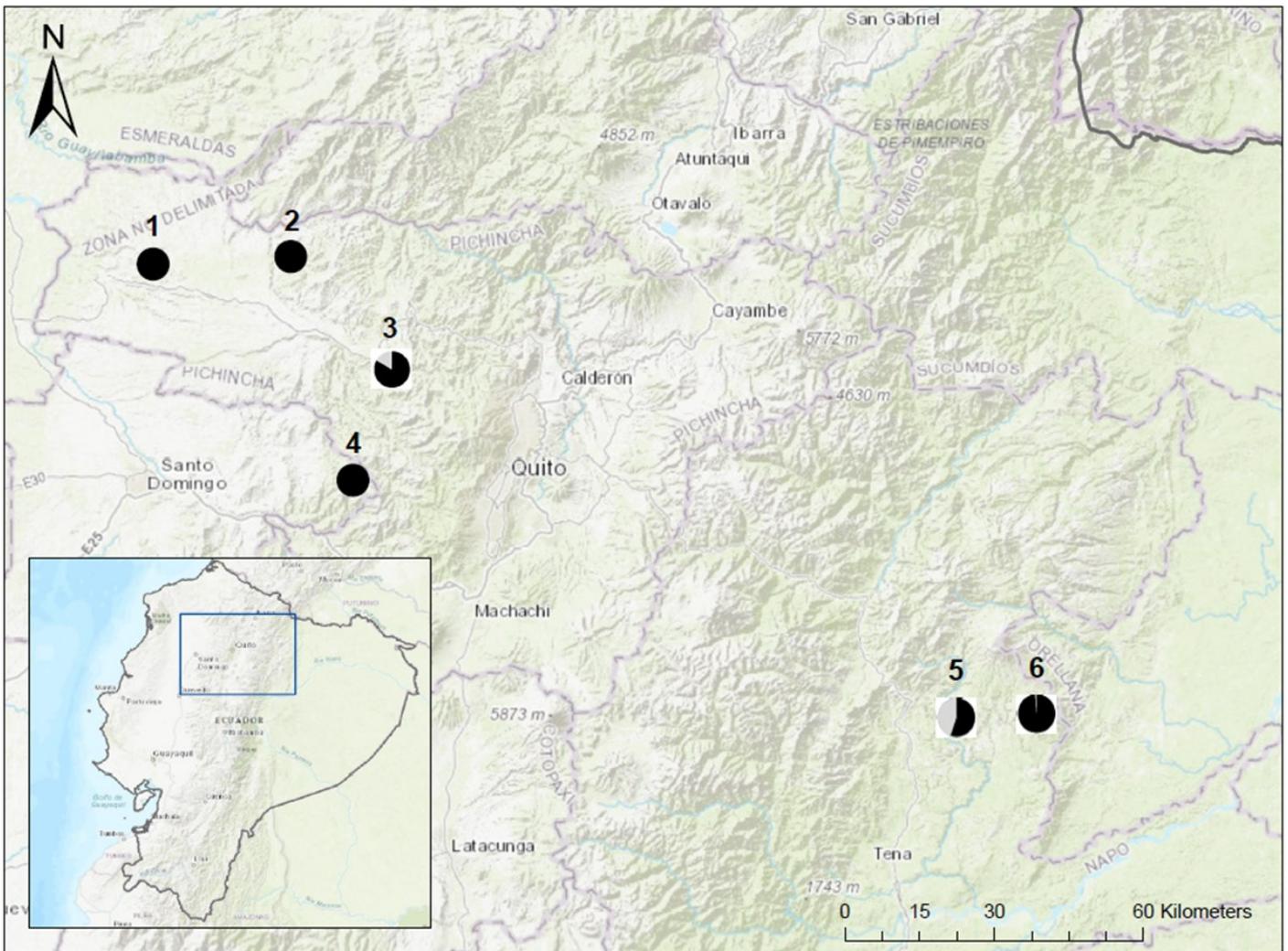
Figure 1. Site locations of five sampling points used by UCLA in relation to Wildsumaco (6). The ratio of male:female (black:gray, respectively) is given for each location. 1) Pedro Vicente Maldonado 1 M:0 F. 2) Reserva Forestal La Magusa 3 M: 0 F. 3) Mindo 10 M: 2 F. 4) Guajalito 1 M: 0 F. 5) Hollín 5 M: 4 F. 6) Wildsumaco 85 M: 1 F.

The species was recorded if identification was possible. We recorded the number of obvious sublayers in order to provide information regarding the structure and succession properties of that forest. A spherical densitometer reading in each cardinal direction was taken and averaged to determine the canopy cover at the center point of the plot. Lastly, the number of snags within the plot was recorded according to the following size classes: <14.9, 15–27.9, 28–63.9, 64–101.9, and >102 cm DBH.

Because of the high plant diversity in this forest, most species or genera in the survey were left unidentified with the exception of *Cecropia* spp., an early successional plant that is easily identified and whose fruit is an important resource for many residential and migrating bird species at our site, including Swainson's Thrush (Inserillo pers. observ.).

Point counts. We conducted point-count surveys to compare the relative abundances of Swainson's Thrush between primary and secondary forest habitat types at 24 stations. We classified the primary forest assessing the overall structure of the forest, characterized by larger, more mature trees, higher canopy, and less understory growth. The secondary/ disturbed habitats consisted of smaller pioneer species of trees (e.g., high *Cecropia* spp. density), a lower overall canopy, and a denser understory. Each survey point was at least 200 m away from the others to limit the possibility of double

-counting individuals when conducting surveys.

We completed each survey point twice a week on consecutive days and all surveying took place in fair weather—no rain or wind—between 0:700 h and 10:30 h (ECT). These were 5-min point counts in which we noted all detections of Swainson's Thrush. We recorded the minute of detection, type of detection (i.e., visual or aural), and estimated distance from the survey point, which allowed us to estimate population density. Distance accuracy was increased through repeated practice sessions, in which distance was estimated and then verified by visual confirmation (not part of the analyzed data). We excluded any bird from the analyses suspected of being double-counted, as well as detected birds outside the survey area.

Habitat association measures. In January 2013 and January-March 2014, we captured Swainson's Thrushes in mist nets in both primary and secondary forest using playbacks of various recordings of calls and songs (source: www.xeno-canto.org). We opened mist nets just before daylight on capturing days (~ 06:00 h), checked every 30 min and kept them open until 12:00 h. Only birds caught in the 2014 field season received radio transmitters (N = 24). We recorded molt patterns for aging and scored subcutaneous fat and weight to assess whether individuals were suitable for carrying a radio tag. All individuals were reliably aged by plumage char-
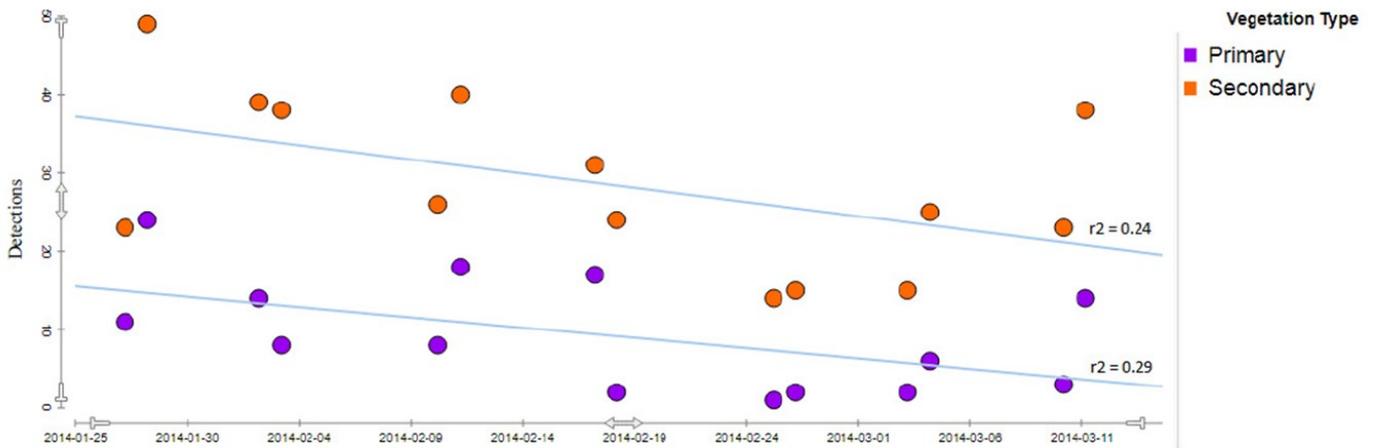
Figure 2. Total number of Swainson's Thrush detections at both primary and secondary stations over the course of the seven-week surveying period, showing the higher densities in secondary stations during the 2014 non-breeding period. The combined density of Swainson's Thrushes in both primary and secondary forests at Wildsumaco declined significantly with time (F = 6.54, df = 1, P = 0.027).

acteristics (Pyle 1997). We obtained blood samples from each bird through the brachial vein and used them for molecular sexing. Replicate blood and feather samples were deposited in the Ornithology Collection at the Sección de Ornitología, Museo de Zoología de la Pontificia Universidad Católica del Ecuador.

24 birds received radio transmitters (3 caught in primary and 21 caught in secondary habitats). We put transmitters only on birds assessed to be in good condition, i.e., no obvious ectoparasites, robust pectoral muscles (indicating that individuals were in good health), and no active molt that would interfere with the transmitter antenna. We used scissors to trim the feathers above the scapulars and lower neck, applied a small dab of epoxy to the transmitter and held it onto the bird, making sure the antenna was in line with the spine, consistent with published methods that meet ethical guidelines. Once the transmitter was adhered (approx. 4 min), the bird was released within 10 m of the capture site. This deployment method was used to ensure the transmitter would fall off pre-migration in the spring (Reitsma pers. observ.).

We waited 24 hours to begin radio telemetry tracking with a 16-channel ATS receiver. Telemetry operations occurred between 07:00–12:00 h and 13:00–17:00 h daily. We tracked individuals until the birds were no longer detected, the battery of the transmitter died (approx. 28 days), or the transmitter was determined to have fallen off and was immobile for at least one week. We determined the locations for individual birds by synchronized telemetry rounds done from fixed points located by GPS units. Two personnel simultaneously covered different areas of fixed-points during the search periods. At each fixed-point, we recorded the name of the point and time of initiation, the strength, and compass bearing for each signal. We recorded the strength of each signal based on a qualitative scale practiced by both technicians to ensure consistency (nine rankings, from weakest to strongest), and signal strength was a corroborative datapoint used in determining bird locations.

The fixed-point position, time of initiation, and compass bearing were then used later to generate locations of each bird over the duration of their stay. Birds and their corresponding spatial coordinates were formatted using ArcMap

10.2. We generated shape files in ArcMap 9.0 (ESRI) from the points and then used QGIS 2.2.0 to triangulate locations. We generated home ranges from the total locations for each bird and assessed the degree of overlap among individuals. Only data with strong signal strengths during telemetry surveys was used in these triangulation simulations. Weaker signals created significant variability in the detectability, whether it was from topography, dense vegetation, or distance, and therefore were excluded from the analysis.

The sex of each bird captured in both 2013 and 2014 (N = 86) was determined using the Qiagen DNeasy Blood & Tissue Kit. This same sexing technique was also used for an additional 27 Swainson's Thrush's blood samples that were obtained by other researchers at five different locations in Ecuador, four of which were on the western side of the Andean Mountain range (K. Ruegg, unpubl.data) (Figure 1).

Statistical Analysis. We used a t-test (two-sample assuming unequal variances) to compare primary and secondary forest measurements. We used chi-square analyses to compare all sex and age class ratios, contrasting our observed results against the null 1:1 ratio. We used a Wilcoxon rank sum test to compare the total number of Swainson's Thrushes detected in both primary and secondary forests and an ANOVA to test for differences in point count detections throughout the sample period (R version 3.1.0).

RESULTS

Vegetation surveys. The maximum DBH was greater at primary (N = 12) compared to secondary (N = 12) point count stations (means: primary = 133.08 cm, secondary = 67.08 cm) (t = −2.78, df = 22, P = 0.013). Primary forest stations had significantly higher cover for woody plants >5 m in height (t = −4.56, df = 22, P < 0.001). The lower bound in the canopy of the primary stations was significantly higher than the secondary stations (t = −3.76, df = 22, P = 0.001).

Point counts. We recorded a total of 527 Swainson's Thrush detections during 336 point counts at 24 survey stations during the 2014 winter field season. There were 127 detections (24.1%) at 12 stations located in the primary forest and 400
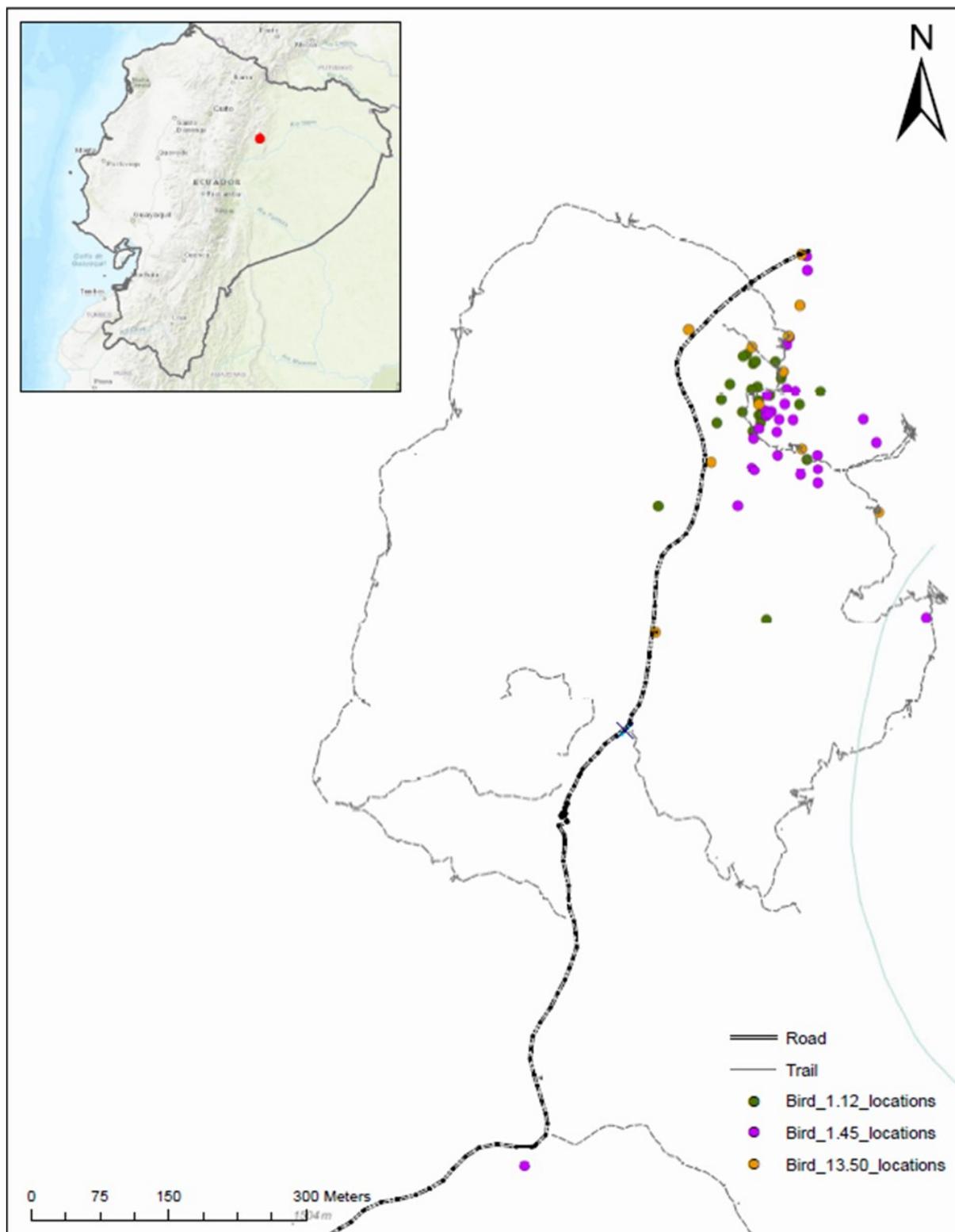
Figure 3. Radio-tracking locations of three Swainson's thrushes at Wildsumaco Wildlife Sanctuary showing the degree of overlap in the area used by each. All three of these individuals were released with transmitters within 24 hr of each other.

(75.9%) at the 12 stations located in the secondary forest; thus, the total number detected was significantly greater in secondary compared to primary forests (W = 534, df = 22, $P <$ 0.001). The combined density of Swainson's Thrush in both primary and secondary forests at Wildsumaco declined significantly with time (F = 6.54, df = 1, P = 0.027; Figure 2).

Demographics. We captured 86 individuals during the sample periods in 2013 and 2014. 85 of them were molecularly sexed as males (98.8%, χ^2 = 82.05, df = 1, $P <$ 0.0001) (Figure

1). Of the 26 molecularly sexed samples obtained from UCLA from sites 15–160 km away, 20 were male and six were female (χ^2 = 7.54, df = 1, P = 0.003). Of the 86 birds caught at Wildsumaco, all but three were aged as second-year or within their first calendar year of life (χ^2 = 7.54, df = 1, P = 0.003).

Telemetry. Of the 24 radio transmitters deployed throughout the wintering period between 10 January and 13 February 2014, 15 of them yielded at least one location point after the triangulation calculations were run (mean = 11.3 loca-

tions/bird). The other nine birds left a detectable range soon after the transmitter's deployment and two birds lost their transmitters, the transmitters malfunctioned, or died. Birds that remained in the detectable area stayed an average of 17.1 (± 2.68) days. The continually detected birds had high overlap (Figure 3), with each bird occupying an average area of 2.36 ha (± 0.92 ha). We frequently detected thrushes in close proximity to conspecifics marked with transmitters and showing no signs of intraspecific aggression. There were no later detections of birds once detection had initially ceased) (i.e., they left the area entirely). Individual birds did not disperse from the release site incrementally after the transmitter's deployment, but rather covered large areas until they made a longer distance flight out of the detection range.

DISCUSSION

Our results demonstrate the importance of secondary forests for male Swainson's Thrushes hatched the previous summer. Furthermore, the disproportionate representation of young males across an area within Ecuador beyond our study site suggests a specific use pattern and behavior or strategy of tracking seasonally available fruit (e.g., *Cecropia* spp., which we observed them eating regularly) in secondary forests. The scarcity of females and older individuals at ours and nearby sites suggests demographic segregation of Swainson's Thrush during the non-breeding season. However, we have not found any habitats occupied by females and older males. All secondary habitats used by Swainson's Thrush occurred close to either a road or pasture. Telemetry data and frequent observations indicate these young males were not territorial and many often used a single *Cecropia* spp*.,* suggesting they track ephemeral fruiting trees. The 15 birds with comparatively robust telemetry data did not exclude conspecifics, but rather exhibited significant overlap (Figure 3). We commonly saw up to eight Swainson's Thrushes in the same tree foraging together with little or no apparent aggressive conspecific interaction. Similarly, non-territorial Northern Waterthrushes in Puerto Rico did not consistently display territorial behaviors during the wintering period (Smith et al. 2011), and wintering Chestnut-sided (*Setophaga pensylvanica*) and Bay-breasted Warblers (*S. castanea*) lacked territorial behavior in Panama (Greenberg 1984). This contrasts with some Neotropical migrant passerines in which both sexes aggressively defend territories (Marra 2000, Marra and Holmes 2001).

Swainson's Thrush was documented primarily in secondary forests in Costa Rica (Blake and Loiselle 2001) and Ecuador (Becker and Ágreda 2005), but age and sex ratios were not reported in either of these studies. The five additional sites near ours (shown in Figure 1) were within 160 km, four of which were located on the western side of the Andean ridge and one on the eastern side, like ours. More work is needed to learn where older males and females reside during the non-breeding season, and whether they occupy other habitats or occur farther north for earlier departure to the breeding grounds. Uneven migratory passerine sex ratios during the non-breeding period have been documented: for example, Hooded Warbler (*S. citrina*) males and females on the Yucatan Peninsula, Mexico, occupied different habitats (Lynch et al. 1985). Sexual habitat segregation was docu-

mented in Jamaica in American Redstarts (*S. ruticilla*) (Marra and Holmes 2001) and Black-throated Blue Warblers (*S. caerulesces*) in Puerto Rico (Wunderle 1995). Ornat and Greenberg (1990) found the same in eight out of nine wintering warblers in Mexico, including the American Redstart, the Common Yellowthroat (*Geothlypis trichas*), the Magnolia Warbler (*S. magnolia*), the Northern Parula (*S. americana*), the Black-and-white Warbler (*Mniotilta varia*), the Prothonotary Warbler (*Protonotaria citrea*), and the Black-throated Green Warbler (*S. virens*). European Robins (*Erithacus rubecula*) also exhibit demographic segregation: younger and smaller individuals were found in areas of greater shrub development, whereas older birds in better condition were found in woodlands during the wintering period in southern Iberia (Catry et al. 2004).

The young males in this population occupied relatively large areas compared to territorial non-breeding Hermit Thrushes in Louisiana (Brown and Long 2007) and some Northern Waterthrushes in Puerto Rico (Smith et al. 2011). Transiency among non-breeding birds observed tracking food resources include *Turdus* species in Spain (Tellería et al. 2014), Yellow-rumped Warblers (*S. coronata*) in South Carolina (Borgmann et al. 2004), two migrant warblers in Panama (Greenberg 1984) and some tropical residents (Morton 1977, Loiselle and Blake 1991). Tracking studies of Palearctic-Afrotropical species document several species' resource tracking correlated with landscape greenness (Kristensen et al. 2013, Thorup et al. 2017). The lack of recaptures of these young males in our study and virtually no older birds or females suggest that they were not floaters passing through territories of social dominants (Rappole et al. 1989).

The fact that transient populations might locally track abundant fruit is consistent with individuals occupying large areas, showing extreme overlap with conspecifics and only remaining in the area for about two and a half weeks on average. Alternatively, individuals may be exhibiting a larger-scale intra-tropical migration. An intra-tropical migration was reported in a congener, the Veery, wintering in Brazil (Heckscher et al. 2015), with individuals moving on average >1300 km from their original non-breeding site towards the northeast over multiple years, coinciding with the annual Amazonian flood pulse (Heckscher et al. 2011). Northern Waterthrushes, Prothonotary Warblers and American Redstarts in the black mangroves (*Avicennia germinans*) of Panama showed local changes in abundance of birds at sites on the Pacific and Caribbean coasts that correlated with changes in food abundance during the dry season (Lefebvre and Poulin 1996). We do not provide direct evidence for an intra-tropical migration of Swainson's Thrush but as with tracking patchy food supplies, it is a possible explanation for the transience of the population, or perhaps predictable pulses in patchy food have induced an intra-tropical migration.

Our study demonstrates the significant use of secondary forests (and the lesser importance of primary forest) on the non-breeding grounds for young male Swainson's Thrushes. It also demonstrates the value of species like *Cecropia* spp. in providing seasonally significant fruit resources to migrants. The use of non-breeding habitats appears to be highly segregated by age and sex, having potential impacts on managing landscapes for the conservation of migratory species such as this one. These demographic patterns of habitat use in space and time are critical to the development of future conserva-

tion strategies in areas of the Neotropics undergoing rapid land use change. Is this demographic in our study pushed to marginal habitats and forced to use a transient strategy, or are young forests of many types and food sources viable alternatives to survive the first non-breeding season? The extraordinary bias toward young males at this site may have implications for present or future population trends of this and perhaps other species. These findings demonstrate the clear need for an enhanced research focus on the non-breeding grounds, where a wide range of demographically important patterns of space and habitat use likely still remain to be discovered. Such information is a fundamental element of effective conservation planning and action.

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