



RESEARCH ARTICLE

## Fall stopover strategies of three species of thrush (*Catharus*) in northern South America

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### ABSTRACT

Northern South America is a geographic bottleneck that may be limiting the survival of Nearctic–Neotropical migrants. However, very little is known about the migration ecology of transcontinental migrants wintering in South America. We studied the fall migratory strategies of three species of thrush (*Catharus ustulatus*, *C. fuscescens*, and *C. minimus*) at 2 major migrant gateways into South America: the Darién and the Sierra Nevada de Santa Marta (SNSM) of northern Colombia. Assuming that migration route shapes the stopover strategy of birds and that our sites receive birds from 2 different routes, we predicted that (1) migrants traveling over land through Central America (Darién) would make short and frequent stopovers followed by short flights and (2) migrants crossing the Caribbean (SNSM) would make few and long stopovers to acquire fuel for longer flights. To test these predictions, we estimated condition on arrival, stopover duration, fuel deposition rates, and potential flight ranges after stopover, using 3 yr of capture–recapture data. Each species adopted a different stopover strategy, with Swainson’s Thrush arriving in South America through the Darién, making the shortest stopovers and achieving the shortest flight ranges (800 km); Gray-cheeked Thrush arriving primarily through the Darién, making short stopovers but achieving longer flight ranges (1,200 km); and Veery arriving in both the Darién and the SNSM, making the longest stopovers and achieving the longest flight ranges (1,900 km). Our results suggest that stopover strategies are shaped by both migratory route (over land vs. over water) and distance to final destination in South America. Unraveling the breeding origins and wintering destinations of individuals passing through northern Colombia would greatly improve our understanding of hemispheric migration systems and will be critical if we are to protect the most important stopover sites and habitats.

**Keywords:** fuel deposition rate, Gray-cheeked Thrush, migration, Neotropics, stopover, Swainson’s Thrush, Veery

### Estrategias migratorias otoñales de tres especies de *Catharus* en el norte de Sur América

#### RESUMEN

El norte de Sur América es un cuello de botella geográfico que puede limitar la sobrevivencia de las aves migratorias Neárticas Neotropicales. Sin embargo, aún conocemos poco sobre la ecología migratoria de especies que pasan el invierno en Sur América. Estudiamos las estrategias migratorias otoñales de tres especies de *Catharus* (*C. ustulatus*, *C. fuscescens* y *C. minimus*) en dos sitios de entrada a Sur América: el Darién y la Sierra Nevada de Santa Marta (SNSM) en el norte de Colombia. Asumiendo que la ruta determina la estrategia migratoria, y que nuestros sitios reciben aves de dos rutas diferentes, predecimos que (1) aves volando sobre Centro América (Darién) harán escalas cortas y frecuentes seguidas por vuelos cortos, y (2) aves volando sobre el Caribe (SNSM) harán pocas escalas largas adquiriendo combustible para vuelos largos. Estimamos la condición física al llegar, la duración de la escala, la tasa de acumulación de combustible y la distancia potencial de vuelo, usando tres años de datos de captura y recaptura. Cada especie adoptó una estrategia diferente: *C. ustulatus* llegó a Sur América por el Darién e hizo las paradas y vuelos más cortos (800 km), *C. minimus* llegó por el Darién e hizo escalas cortas pero logrando vuelos largos (1200 km), y *C. fuscescens* llegó tanto por el Darién como por la SNSM e hizo las escalas y vuelos más largos (1900 km). Nuestros resultados sugieren que la estrategia migratoria depende tanto de la ruta (sobre continente o sobre mar) como de la distancia hasta el sitio de invierno en Sur América. Conocer los sitios de reproducción y los destinos de invierno de las aves que pasan por el norte de Colombia contribuirá a mejorar nuestro conocimiento sobre los sistemas migratorios y será crítico para la protección de los sitios de parada y los hábitats más importantes.

**Palabras clave:** tasa de acumulación de combustible, escalas migratorias, migración, Neotropicales, *Catharus ustulatus*, *Catharus fuscescens*, *Catharus minimus*

## INTRODUCTION

Reversing population declines of many Nearctic–Neotropical migratory birds will require conservation strategies that address their needs at all stages of their annual cycle (Robbins et al. 1989, Sauer et al. 2008, Faaborg et al. 2010). The majority of studies of migratory birds are still focused on the breeding grounds, however, even though there is growing evidence that limiting factors act during the nonbreeding period (Sillett et al. 2000, Sillett and Holmes 2002, Norris et al. 2004, Faaborg et al. 2010). In particular, very little is known about the biology of migrants that winter in South America and, especially, about their migration ecology as they travel to and from their wintering grounds (Faaborg et al. 2010, 2013). A rapidly growing body of research, using remote tracking techniques, has started to unveil many aspects of the geographic origins, destinations, and routes of various species (Bowlin et al. 2005, González-Prieto et al. 2011, Heckscher et al. 2011, Delmore et al. 2012, Cormier et al. 2013, McKinnon et al. 2013). Therefore, it is now timely to complement this exciting information with detailed field research that documents the behavior of birds on the ground and in important stopover areas (Robinson et al. 2010, Bridge et al. 2011, Taylor et al. 2011, Fudickar et al. 2012). Northern Colombia is one of these important regions, recently identified as a gateway for migrants entering and leaving South America (Heckscher et al. 2011, Bayly et al. 2012, 2013, Gómez et al. 2013).

Thrushes in the genus *Catharus* have been widely used as a model system in the study of migratory bird behavior (Bowlin et al. 2005, Cochran and Wikelski 2005). These birds provide a particularly useful model because, aside from performing some of the longest migrations of all Nearctic–Neotropical landbirds, they are relatively common, easy to capture due to their understory habits, and large enough to carry tracking devices (Mack et al. 2000, Lowther et al. 2001, Remsen 2001, Ruegg and Smith 2002, Bowlin et al. 2005, Heckscher et al. 2011, Taylor et al. 2011, Delmore et al. 2012). Furthermore, the existing body of information on these species allows us to construct hypotheses about their stopover ecology that can be tested in the field.

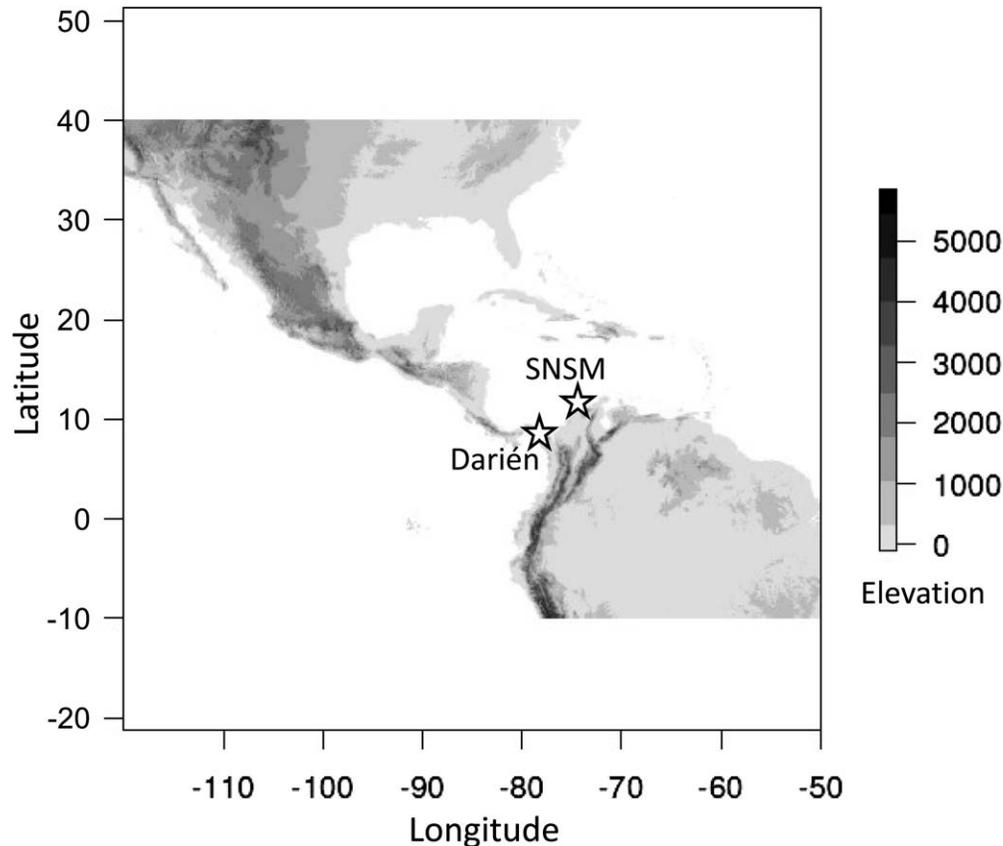
Three *Catharus* species migrate through northern Colombia during the fall: Swainson's Thrush (*C. ustulatus*), Veery (*C. fuscescens*), and Gray-cheeked Thrush (*C. minimus*). Despite having largely separate wintering areas, and potentially different migration routes from North America to South America, all 3 species pass through the narrow area of northern Colombia during the fall. This region is therefore a potential geographic bottleneck for these long-distance migrants, and understanding how they are using this area during stopover could be important for their conservation.

Swainson's Thrushes of the eastern or olive-backed subspecies (*C. u. swainsoni*; Ruegg 2007) migrate primarily through the Caribbean lowlands of Central America in both spring and fall and are often abundant during fall migration from the Yucatán through Costa Rica and Panama (Galindo et al. 1963, Mack et al. 2000, eBird 2014). They winter along the base of the eastern Andes, from western Venezuela through Colombia, Ecuador, Peru, and Bolivia, and can reach northern Argentina (Mack et al. 2000, Cormier et al. 2013). Some birds probably make overwater crossings from Florida and the eastern U.S. Gulf Coast to the Yucatán and northern South America, but the vast majority probably enter South America via Panama (Galindo et al. 1963, Loftin 1977, Gómez et al. 2013).

By contrast, most Veery arrive on the northern coast of Colombia after crossing the Caribbean from the southeastern United States (González-Prieto et al. 2011, Heckscher et al. 2011, Bayly et al. 2012, Gómez et al. 2013). They are uncommon fall migrants in Central America but sometimes appear in large numbers along the Caribbean coast from Belize to Panama (Rogers and Odum 1966, Remsen 2001, Bayly and Gómez 2011, eBird 2014). The species winters in southern Amazonia and as far south as the Pantanal and southeastern Brazil and apparently makes long intrawinter movements (Remsen 2001, Heckscher et al. 2011, eBird 2014).

Information about the fall migration of Gray-cheeked Thrush is scarcer. The few fall records from the Sierra Nevada de Santa Marta, Venezuela, and the Guyanas (Gómez et al. 2013, eBird 2014), and reports of relatively large numbers of birds during the fall in Panama (Galindo et al. 1963, Rogers and Odum 1966), suggest that this species has a prevailing Central American route into South America. Wintering grounds are believed to be primarily in the northwestern Amazon basin, extending to the base of the Colombian and Venezuelan Andes (Hilty and Brown 1987, Hilty 2003, N. J. Bayly and C. Gómez personal observation).

Here, we test whether migratory bird species with different winter destinations and migration routes show differences in migration stopover strategy. We use 3 yr of field data from 2 sites in northern Colombia: the Sierra Nevada de Santa Marta (SNSM) and the forests of the Darién close to the border between Colombia and Panama (Figure 1). By comparing arrival condition, stopover durations, fuel deposition rates, and potential flight range of *Catharus* from these 2 sites, we test the following predictions. (1) Given that Swainson's Thrush follows a predominantly continental route into South America with few large ecological barriers, we predict that it will be more abundant at the Darién site than at the SNSM and that its migratory strategy will consist of relatively short stopovers and short consecutive flights. (2) Given that Veery migrate primarily over the Caribbean (Heckscher et al. 2011, Bayly



**FIGURE 1.** Map showing the 2 study areas in northern Colombia (the Darién and the Sierra Nevada de Santa Marta [SNSM]) where southward migration of 3 species in the genus *Catharus* was monitored from 2009 to 2012.

et al. 2012), we predict that its strategy will consist of long flights interspersed by long stopovers during which birds refuel substantially. (3) For Gray-cheeked Thrush, historical records lead us to predict that the species has a predominantly Central American route and, therefore, is expected to be more common in the Darién and to make short and frequent stopovers resulting in short flight distances, as in Swainson's Thrush. (4) We further predict that individuals of all 3 species arriving through the Darién into South America (i.e. those potentially taking a Central American route) will adopt a stopover strategy similar to that predicted for Swainson's Thrush.

## METHODS

### Study Sites and Field Methods

Two of the largest expanses of tropical forest in northern Colombia, separated by 450 km of largely agricultural land, are located in the isolated mountains of the SNSM near the Caribbean coast, and at the meeting point between Central America and South America commonly referred to as “the Darién” or “the Darién gap” (IDEAM 2010).

We worked in 2 areas of the SNSM. The first, Hacienda La Victoria, is situated in the northwest corner of the SNSM (11.1197750°N, -74.0819510°W) and consisted of a matrix of shade coffee plantations with large remnants of premontane tropical forest 1,200 m above sea level (Bayly et al. 2013). The second area, the Quebrada Valencia reserve, is located in the foothills of the northern slope of the SNSM (11.23624°N, -73.79921°W) and consisted of lowland tropical rainforest 175 m above sea level (Bayly et al. 2012). Although forests at 175 m and 1,200 m are different in structure and composition, we pooled the data from the 2 sites, because our main objective was to compare 2 geographically distinct areas (the SNSM and the Darién) and we considered the 2 SNSM sites to be representative of the wider SNSM region. Although our study species show differences in abundance along the elevation gradient of the SNSM during migration, with Gray-cheeked Thrush present in greater numbers in premontane forest and Veery in lowland forest (Gómez et al. 2013), defining fine-scale habitat quality for each species was not in the scope of our study.

In the Darién, we worked in the Tacarcuna Nature Reserve (8.1561470°N, -77.2506470°W) near the village of

Sapzurro on the Caribbean coast, close to the border between Colombia and Panama (Figure 1). Habitat at the Darién site consisted of tropical rainforest 100 m above sea level.

We monitored the southward migration of birds from mid-September to mid-November during 2009, 2010, and 2011 in the SNSM and during 2011 and 2012 at the Darién site. At each site, we set up a constant-effort banding station consisting of 10 to 15 twelve-meter mist nets (we used 32-mm-mesh Japanese and North Ronaldsay nylon nets) covering an area of forest  $\approx 1$  km<sup>2</sup>. Mist nets were positioned strategically to maximize capture rates, and positions were maintained virtually constant at the sites during each year and between years. Mist nets were opened daily from dawn (0545–0600 hours) for an average of 4.5 hr and were checked every 30 min. All birds captured were transported in individual cloth bags to a banding station where they were marked using numbered Porzana-made metal bands (band reporting website: <http://www.aselva.co>). For all captured and recaptured birds, we recorded band number, date and time of capture, age according to plumage (Pyle 1997), visible subcutaneous fat score (Kaiser 1993), pectoral muscle score (Redfern and Clark 2001), wing chord ( $\pm 1$  mm), and body mass ( $\pm 0.1$  g) using an electronic balance (Fast Weigh digital pocket scale, model M-500). *Catharus* cannot be reliably sexed using external characters during the nonbreeding period (Pyle 1997), so we did not include sex as a factor in our data. All birds were released immediately after processing.

### Phenology of Migration

To determine the migration phenology of the 3 study species, we analyzed captures from the Darién in 2011 and 2012, and from the SNSM from 2009 to 2011. We present the mean capture total summed every 2 days across years to represent the phenology of migration. Mist-net effort was largely constant, and although weather conditions occasionally led to a reduced mist-net effort, we have not corrected for mist-net effort because the variation in effort is expected to have had limited impact on phenologies.

### Correction of Raw Capture Totals

To correct raw capture totals for variation in capture probability between sites, we estimated the expected number of captures by species, year, and site, using recapture probabilities estimated from mark–recapture models (see below; Hochachka and Fiedler 2008). To do this, we ran POPAN models in MARK version 5.1 (White and Burnham 1999) using a logit link function to estimate survival ( $\Phi$ ) and recapture probability ( $p$ ), a multinomial logit function to estimate the PENT probability (i.e. probability of an individual from the “superpopulation” entering our local population), and a log function for the

corrected estimate of the size of the super population ( $N$ ; Hochachka and Fiedler 2008). In all cases, we assumed constant survival and recapture probability throughout our sampling period.

### Models of Body Mass Change

Changes in the body mass of migrating birds largely reflect changes in the energy reserves available to individuals, and these reserves are primarily due to fat deposition (Piersma 1990, McWilliams and Whitman 2013). For example, body mass and fat score have been shown to be positively and strongly correlated in both Veery and Gray-cheeked Thrush (Bayly et al. 2012, 2013). We modeled change in body mass as a function of the number of days since a bird was first captured, following Bayly et al. (2012, 2013). Change in body mass for all recaptured individuals was calculated as the difference between mass at first capture and mass at any successive capture event. To correct for variation in size between individuals and species, we expressed mass change as a percentage of lean body mass (LBM, the estimated mass of a bird without visible fat reserves; McWilliams and Whitman 2013). We estimated LBM using the regression equation for body mass against wing length for all captured individuals with fat score zero. We used the equations reported in Bayly et al. (2012) for Veery ( $LBM = 6.47 + 0.212 \cdot \text{wing length}$ ,  $n = 124$ ) and in Bayly et al. (2013) for Gray-Cheeked Thrush ( $LBM = 3.60 + 0.227 \cdot \text{wing length}$ ,  $n = 43$ ). For Swainson’s Thrush, we estimated the equation using the subset of birds with fat score zero captured during fall migration in the Darién ( $LBM = -7.137 + 0.339 \cdot \text{wing length}$ ,  $n = 55$ ).

Modeling was carried out with the statistical package R, using general linear models with normal errors (R Development Core Team 2013) and forcing the intercept through zero, given that change in body mass at the point of first capture is zero. We tested a set of 6 models (Table 1) with the following variables: interval of days between captures (I), date at first capture (D), starting body mass (CI), expressed as a condition index where  $CI = (\text{mass at first capture} / \text{wing length}) \cdot 100$ , and the difference in hour of capture between captures (H). We included H as an additive term in all models to correct for body-mass increase with time of day (Schaub and Jenni 2000, Thomas 2000). Age is known to affect body mass change in *Catharus* (e.g., Bayly et al. 2013); however, because we did not have enough recaptures of adults to allow robust modeling of this parameter, we decided to exclude it as a variable in our analyses. Similarly, a lack of sufficient recaptures in some years made it unfeasible to model years separately, so data were pooled across years (2009–2012). For Gray-cheeked Thrush and Veery, we carried out an additional analysis to explore whether models of body mass change supported an effect of site (S) (Table 1; also see Table 4 in the Appendix).

**TABLE 1.** Model set designed to examine how body mass varies in 3 species in the genus *Catharus* during stopovers in northern Colombia as a function of the number of days since first capture. Variables: I = interval in days between captures, D = date of first capture, CI = initial body mass (CI = [mass/wing length]\*100), S = site (the Sierra Nevada de Santa Marta or the Darién). Difference in hour of capture between captures (H) was included as an additive term in all models to correct for increases in body mass with time of day.

| Model (Change in body mass =)                                  | Interpretation   |
|--|--|
| I + H  | Mass varies as a linear function of days since first capture   |
| I + I <sup>2</sup> + H   | Mass varies as a quadratic function of days since first capture  |
| I + I <sup>2</sup> + I <sup>3</sup> + H                        | Mass varies as a polynomial function of days since first capture   |
| I:D + I <sup>2</sup> :D + I <sup>3</sup> :D + H                | Interaction of days since first capture and date   |
| I:CI + I <sup>2</sup> :CI + I <sup>3</sup> :CI + H             | Interaction of days since first capture and initial body mass  |
| I:D:CI + I <sup>2</sup> :D:CI + I <sup>3</sup> :D:CI + H       | Interaction of days since first capture, first capture date, and initial body mass                                   |
| I:S + I <sup>2</sup> :S + I <sup>3</sup> :S + H                | Models including site as an additional factor and interacting with changes in body mass, date, and initial body mass |
| I:D:S + I <sup>2</sup> :D:S + I <sup>3</sup> :D:S + H          |  |
| I:D:CI:S + I <sup>2</sup> :D:CI:S + I <sup>3</sup> :D:CI:S + H |  |

Our model set aimed to determine whether linear, quadratic, or polynomial functions best described the variation of body mass with time and included plausible interactions of the individual variables with days since first capture. Model selection was carried out using Akaike's Information Criterion (AIC), comparing  $\Delta_i$  values, where  $\Delta_i$  is the difference between each model and the model with the lowest AIC; and Akaike model weights ( $w_i$ ), where  $w_i$  reflects the relative support that model  $i$  receives over other models (Burnham and Anderson 2002, Johnson and Omland 2004). Where  $\Delta_i < 2$  and  $w_i \leq 10\%$ , we carried out model averaging using a multimodel inference package in R (MuMIn) to get weighted averages for all the parameters in the top models (Johnson and Omland 2004).

### Stopover Duration and Percentage of Transients

We estimated the fall stopover duration of *Catharus* in the Darién and the SNSM using mark-recapture analysis, except for Veery in the SNSM, for which we used the stopover durations presented by Bayly et al. (2012). For the other species, we estimated "stopover after" and "total stopover" (Schaub et al. 2001, Efford 2005, Morris et al. 2005) for years in which >40 individuals were captured per species and site. For those species and years with smaller sample sizes, we present "minimum stopover duration" only, which was calculated as the average time interval between first and last capture. To estimate "stopover after" and "total stopover," we analyzed capture histories in MARK using 2 models, 1 with constant survival and recapture probability ( $\Phi(\cdot)$  p(.)) and another evaluating the effect of transient individuals (those stopping for only 1 day) on survival probability ( $\Phi(\text{trans})$  p(.)). When models supported the presence of transients, we estimated the percentage of the population assumed to be transient using the equation  $T = [1 - (\Phi_1/\Phi_2)] * 100$  (Pradel et al. 1997). Age is potentially an important variable that can influence stopover duration, but we were unable to model its effect because samples sizes were

insufficient. Our results therefore represent the average stopover duration for the population as a whole.

We used AIC to infer model suitability and calculated  $\hat{c}$ , which is a measure of the overdispersion of the data (Lebreton et al. 1992), to assess model fit. All subsequent estimates were corrected for the resulting value of  $\hat{c}$ . In general, a model is considered to have relatively good fit if  $\hat{c} \leq 2$ . Where  $\Delta_i$  and  $w_i$  were not supportive of a single model, we carried out model averaging. The resulting estimates of survival ( $\phi$ ) were used to estimate "stopover after" using the equation for life expectancy:  $LE = -1/\ln(\phi)$ . "Total stopover" was calculated by estimating  $\phi$  and the seniority probability ( $\gamma$ ) using this equation: total stopover =  $[-1/\ln(\phi)] + [-1/\ln(\gamma)]$ .

### Arrival Fuel Load

Fuel load on arrival is a measure of how much stored energy a bird has available on arrival at a stopover site. It can also serve as a measure of the probability that a bird will make a multiday stopover, given that "fatter" birds are less likely to need to refuel than lean birds (Bayly 2006, Hedenström 2008, McLaren et al. 2013). We calculated fuel load on arrival by subtracting LBM from the mass of birds at first capture and expressing the difference as a percentage of LBM. This calculation assumes that most birds were first captured on or within 1 day of arrival at the stopover site. Violation of this assumption will result in overestimates of arrival fuel loads. We carried out chi-square and paired Student's  $t$ -tests with 95% confidence intervals to compare fuel loads between sites and species.

### Departure Fuel Load and Potential Flight Range

Departure fuel load, expressed as a percentage of LBM, is an estimate of the energy reserves with which birds leave a site after stopover (Bayly et al. 2013). We calculated departure fuel load by entering total stopover duration into the model of body mass change that received the greatest support from AIC. Our body-mass-change models predict

**TABLE 2.** Raw capture and recapture totals, and expected totals (EXP ± SE), corrected for capture probability using POPAN models in MARK, for 3 species in the genus *Catharus* during fall migration at 2 sites in northern Colombia between 2009 and 2012. Totals are separated by age class (HY = hatch year, AHY = after hatch year, U = unknown), and capture effort is expressed in net hours (1 net hour = one 12-m net open for 1 hr). Abbreviations: SWTH = Swainson's Thrush, VEER = Veery, GCTH = Gray-cheeked Thrush, SNSM = Sierra Nevada de Santa Marta.

|        | 2009                         |          |   |         |         | 2010   |       |         |         |        | 2011  |           |          |         |       | 2012     |          |     |         |       | Total effort   |           |   |
|--------|------------------------------|----------|---|---------|---------|--------|-------|---------|---------|--------|-------|-----------|----------|---------|-------|----------|----------|-----|---------|-------|----------------|-----------|---|
|        | HY                           | AHY      | U | EXP     | HY      | AHY    | U     | EXP     | HY      | AHY    | U     | EXP       | HY       | AHY     | U     | EXP      | HY       | AHY | U       | EXP   | Total captures | Total EXP |   |
| Effort | -                            | -        | - | -       | -       | -      | -     | -       | -       | -      | -     | -         | -        | -       | -     | -        | -        | -   | -       | -     | -              | -         | - |
| SWTH   | 7 (0)                        | 2 (0)    | 0 | -       | 63 (1)  | 50 (1) | 0     | -       | 232 (9) | 63 (4) | 0     | 543 ± 120 | 366 (33) | 163 (4) | 4 (0) | 645 ± 13 | 1,600.1  | -   | -       | -     | 828 (50)       | 1,188     |   |
| VEER   | 206 (38)                     | 113 (19) | 0 | 388 ± 6 | 71 (10) | 47 (6) | 0     | 141 ± 7 | 98 (5)  | 34 (0) | 0     | 135 ± 2   | 104 (10) | 76 (2)  | 0     | 216 ± 6  | 76 (2)   | 0   | 78 (10) | 1 (0) | 312 (17)       | 351       |   |
| GCTH   | 22 (9)                       | 9 (1)    | 0 | 88 ± 15 | 20 (5)  | 14 (1) | 1 (0) | 44 ± 3  | 88 (4)  | 31 (2) | 0     | 128 ± 3   | 119 (3)  | 78 (10) | 1 (0) | 263 ± 10 | 317 (32) | -   | -       | -     | 317 (32)       | 391       |   |
|        | Sierra Nevada de Santa Marta |          |   |         |         |        |       |         |         |        |       |           |          |         |       |          |          |     |         |       |                |           |   |
| Effort | 3,997                        |          |   |         |         |        |       |         |         |        |       |           |          |         |       |          |          |     |         |       |                |           |   |
| SWTH   | 7 (0)                        | 2 (0)    | 0 | -       | 63 (1)  | 50 (1) | 0     | -       | 7 (0)   | 3 (0)  | 1 (0) | -         | -        | -       | -     | -        | -        | -   | -       | -     | 134 (2)        | 9,165.3   |   |
| VEER   | 206 (38)                     | 113 (19) | 0 | 388 ± 6 | 71 (10) | 47 (6) | 0     | 141 ± 7 | 45 (4)  | 14 (1) | 2 (0) | -         | -        | -       | -     | -        | -        | -   | -       | -     | 498 (78)       | 529       |   |
| GCTH   | 22 (9)                       | 9 (1)    | 0 | 88 ± 15 | 20 (5)  | 14 (1) | 1 (0) | 44 ± 3  | 21 (3)  | 8 (0)  | 0     | 81 ± 14   | -        | -       | -     | -        | -        | -   | -       | -     | 95 (19)        | 213       |   |

**TABLE 3.** Estimates of stopover duration (minimum, "stopover after," and total), departure fuel load (LBM = lean body mass), and potential flight range for 3 species of thrush in the genus *Catharus*. In parentheses are minimum and maximum stopover durations (95% confidence intervals), rounded to the nearest day. Blank spaces indicate species with insufficient sample sizes. The flight range gained on site reflects the distance that a bird could fly using the fuel accumulated during stopover only. "Total distance" takes into account both the mean fuel load that birds carried on arrival and the fuel load accumulated during stopover.

|                     | Site   | Year | Stopover duration |          |          |                |       | Departure fuel load (%LBM) | Mean LBM (g) | Departure mass (arrival mass + fuel load) (g) | Flight range gained on site | Total distance |
|---------------------|--------|------|-------------------|----------|----------|----------------|-------|----------------------------|--------------|---|-----------------------------|----------------|
|                     |        |      | Minimum           | After    | Total    | Departure mass |       |                            |              |   |                             |                |
| Swainson's Thrush   | Darién | 2011 | 3 (1-5)           | 3 (1-8)  | 4 (1-8)  | 10.0%          | 25.58 | 29.07                      | 540 km       | 750 km  |                             |                |
|                     | SNSM   | 2012 | 3 (1-8)           | 3 (2-5)  | 5 (2-7)  | 12.6%          | 25.58 | 29.73                      | 680 km       | 880 km  |                             |                |
|                     | SNSM   | 2009 | 0                 | -        | -        | -              | -     | -                          | -            | -   | -                           |                |
| Veery               | Darién | 2010 | 5 (1-9)           | -        | -        | -              | -     | -                          | -            | -   | -                           |                |
|                     | Darién | 2011 | 0                 | -        | -        | -              | -     | -                          | -            | -   | -                           |                |
|                     | Darién | 2012 | 3 (1-8)           | 3 (1-6)  | 6 (2-7)  | 16.0%          | 26.71 | 34.55                      | 800 km       | 1,440 km                                      |                             |                |
| Gray-cheeked Thrush | SNSM   | 2009 | 5 (4-6)           | 4 (3-6)  | 9 (6-12) | 32.7%          | 26.71 | 37.58                      | 1,570 km     | 1,930 km                                      |                             |                |
|                     | Darién | 2010 | 4 (2-5)           | 4 (2-10) | 8 (2-17) | 28.6%          | 26.71 | 36.49                      | 1,390 km     | 1,780 km                                      |                             |                |
|                     | SNSM   | 2011 | 1 (1-4)           | 1 (1-6)  | 3 (1-10) | 10.8%          | 26.53 | 32.31                      | 590 km       | 1,170 km                                      |                             |                |
| Gray-cheeked Thrush | SNSM   | 2012 | 2 (1-5)           | 2 (1-3)  | 3 (2-5)  | 10.8%          | 26.53 | 32.31                      | 590 km       | 1,170 km                                      |                             |                |
|                     | SNSM   | 2009 | 4 (1-10)          | 5 (2-11) | 8 (2-13) | 18.3%          | 26.53 | 32.68                      | 980 km       | 1,230 km                                      |                             |                |
|                     | SNSM   | 2010 | 2 (1-5)           | 2 (1-4)  | 4 (1-5)  | 9.8%           | 26.53 | 30.43                      | 530 km       | 790 km  |                             |                |
|                     |        | 2011 | 7 (3-10)          | -        | -        | -              | -     | -                          | -            | -   | -                           |                |

daily mass gain minus overnight weight loss, which is the energy birds consume every night at the basal metabolic rate (Dunn 2001). Because *Catharus* are expected to depart shortly after sunset on their last day of stopover, we include an additive term for overnight weight loss ( $O$ ) to the equation for mass gain when calculating departure fuel load ( $O = 2.6\%$  LBM, following Bayly et al. 2013).

To estimate potential flight range after stopover, we entered values for departure fuel load, wingspan, and wing area into the program Flight (Pennycuick 2008). We calculated 2 flight ranges: (1) the range considering only the fuel gained at each site (e.g., the increase in range as a result of the stopover, LBM + mass gain); and (2) total flight range, taking into consideration mean mass on arrival and adding the total fuel attained during stopover (arrival mass + mass gain). The values used for wingspan (WS) and wing area (WA) were as follows: Veery, WS = 0.285 m, WA = 0.0156 m<sup>2</sup> (Bayly et al. 2012); Gray-cheeked Thrush, WS = 0.307 m, WA = 0.0168 m<sup>2</sup> (Bayly et al. 2013); and Swainson's Thrush, WS = 0.297 m, WA = 0.0142 m<sup>2</sup> (Yong and Moore 1997). Starting altitude was set at 100 m, cruising altitude at 1,000 m, and muscle fraction at 0.17 (Bayly et al. 2012). Body-drag coefficient was set at 0.1, which is the default value recommended for small passerines in the program Flight. For European passerines similar in size to *Catharus* species, body-drag coefficient values between 0.2 and 0.4 have been reported (Hedenström and Liechti 2001). It should therefore be borne in mind that flight ranges may be slightly overestimated if body-drag coefficients are >0.1 in *Catharus*.

## RESULTS

### Phenology of Migration

Timing of migration varied between species and sites, but most birds passed in October (Figure 2A, 2B). Veery was the earliest species to pass through the Darién, primarily between September 30 and October 8, whereas in the SNSM its passage was concentrated from October 5 to 15. Swainson's Thrush and Gray-cheeked Thrush passed through the Darién simultaneously, with a first peak around October 8 and a second main passage period from October 14 to 30. In the SNSM, Swainson's Thrush passed earlier than in the Darién and in much lower numbers. Gray-cheeked Thrush passed through the SNSM in low and relatively constant numbers throughout October.

On the basis of raw capture totals and taking into account mist-net effort, both Swainson's Thrush and Gray-cheeked Thrush were markedly more abundant in the Darién, whereas Veery showed similar abundances at both sites (Table 2). Capture totals corrected for encounter probability (EXP in Table 2) were slightly higher than raw totals but remained within the same order of magnitude

and showed a similar overall pattern. The total number of captures by year also varied within species, particularly in Swainson's Thrush (Table 2); however, a large portion of this variation can be attributed to mist-net effort.

Recapture rates varied between 1.5% and 20% at both sites, indicating the variation in the relative number of individuals of all species that made multiday stopovers at the study sites. Immature individuals were more abundant than adults at both sites during all years, but the ratio was not constant between years (Table 2). The year with the highest ratio of immature to adult birds for all species was 2011 (Table 2). Estimates of daily survival ( $\Phi$ ) and recapture probability ( $p$ ) are presented in Figure 3.

### Arrival Fuel Load

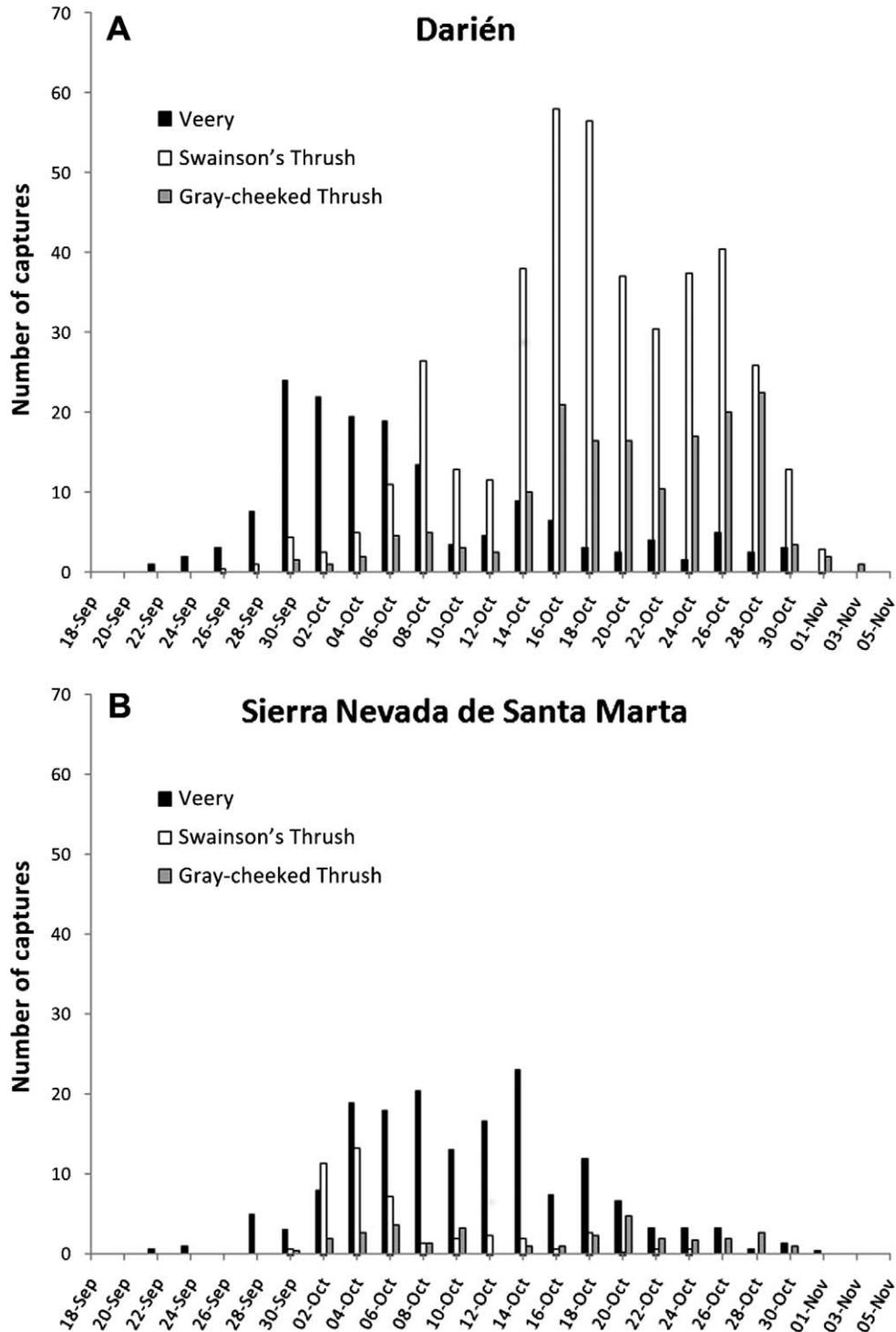
For all species, fuel loads on first capture showed considerable variation (from -25% up to 60% LBM) at both sites (Figure 4). However, all species arrived with significantly lower fuel loads in the SNSM than they did in the Darién (Swainson's Thrush:  $t_{132} = -2.32$ ,  $P = 0.02$ ; Veery:  $t_{306} = 29.02$ ,  $P < 0.001$ ; Gray-cheeked Thrush:  $t_{94} = -12.94$ ,  $P < 0.001$ ). More than 50% of the first captures in the SNSM had fuel loads  $\leq -5\%$  LBM, whereas most individuals in the Darién had fuel loads  $\geq 5\%$  LBM (Figure 4).

### Change in Body Mass

Most recaptured individuals gained mass between captures (Figure 5), and a polynomial model best described body mass change for all species and sites, with just 1 exception (Figure 6). For both Veery and Gray-cheeked Thrush, polynomial models including the factor "site" received the highest support from AIC (Veery: AIC = 472.28,  $w_i = 0.960$ ; Gray-cheeked Thrush: AIC = 279.01,  $w_i = 0.987$ ); this is evidence for a higher rate of mass change in the SNSM than in the Darién in Veery but supports the opposite pattern for Gray-cheeked Thrush. Because of a lack of recaptures of Swainson's Thrush in the SNSM ( $n = 2$ ), we could not test for site differences in this species.

### Stopover Duration and Percentage of Transients

"Total stopover" durations varied between 3 and 9 days for all species, with a tendency to be longer in the SNSM regardless of species (Table 3). The shortest durations were those of Gray-cheeked Thrush in the Darién, whereas Veery in the SNSM made the longest stopovers. Models for Swainson's Thrush and Veery in the Darién supported the presence of transients in the population, whereas there was no evidence of transients of either species in the SNSM (Tables 4, 5, and 6 in the Appendix). For Swainson's Thrush, the estimated percentage of transients in the Darién was 96% and 79% in 2011 and 2012, respectively, whereas for Veery it was 96% in both 2011 and 2012.

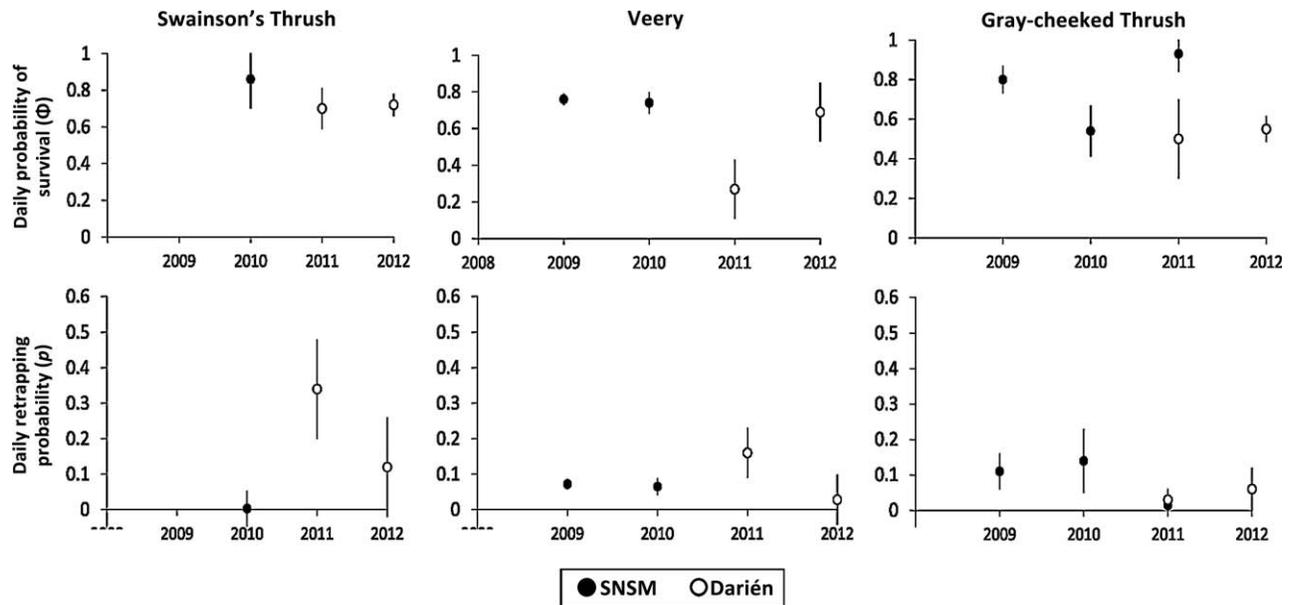


**FIGURE 2.** Phenology of the southward migration of 3 species in the genus *Catharus* through (A) the Darién in 2011 and 2012 and (B) the Sierra Nevada de Santa Marta, Colombia, 2009–2011, based on new captures averaged over 2-day periods.

**Departure Fuel Load and Potential Flight Range**

The gain in fuel load during a stopover at either site generally varied between 10% and 20% of LBM (Table 3). However, gains in Veery in the SNSM were larger, being

closer to 30% of LBM (Table 3). These gains increased flight range by about 500–700 km, but for Veery in the SNSM, flight range increased by >1,400 km. Considering the reserves that birds had on arrival, total departure flight



**FIGURE 3.** Daily survival and recapture probabilities estimated from capture–recapture models (see Table 6 in the Appendix) for 3 species in the genus *Catharus* on migration in northern Colombia (SNSM = Sierra Nevada de Santa Marta). Estimates are presented separately for each year and study site. Error bars show the standard errors of the estimates.

ranges were typically between 800 and 1,200 km (>1,700 km for Veery in the SNSM), with birds in the Darién benefiting from the larger reserves carried on arrival (Table 3).

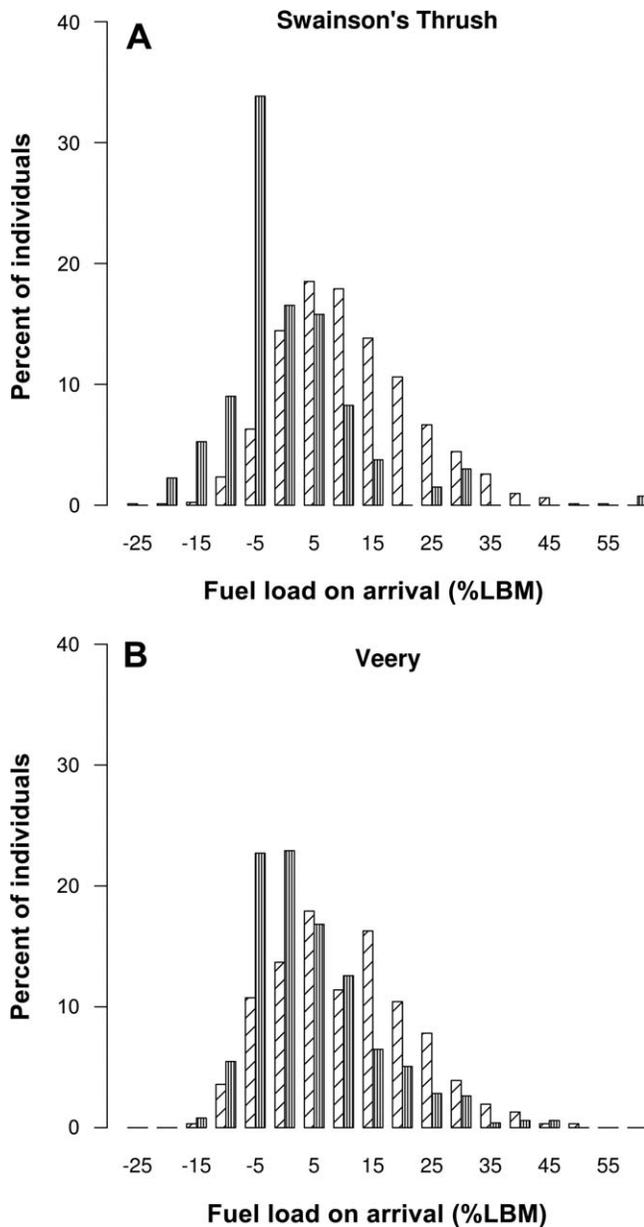
## DISCUSSION

Our results suggest that these three *Catharus* species adopt markedly different stopover strategies at 2 sites in northern Colombia during their southward migration. In agreement with our predictions, Swainson's Thrush seem to take a primarily Central American route into South America, given that birds arrived mostly through the Darién and in relatively good body condition. Most individuals were either transient or made short stopovers that resulted in the shortest potential flight ranges of the 3 species (800 km). On the whole, this species seems to have a “frequent-short-stopover-short-flight” strategy. The results for Veery partially supported our prediction, in that birds that arrived through the Darién did so in better body condition than those from the SNSM (which suggests an overland route) and, hence, made shorter stopovers than the latter (Bayly et al. 2012). However, Veery from both sites attained equivalent potential flight distances, which were the longest of the 3 species (2,000 km); this suggests that Veery has a “few-stopover-long-flights” strategy, regardless of the route taken. Gray-cheeked Thrush was much more abundant in the Darién, suggesting a primarily Central American route, as predicted. However, potential

flight ranges after stopover were generally long (1,200 km), contradicting our prediction and supporting a few-stopover-long-flights strategy more similar to that of the Veery.

Although we do not yet have quantitative data to describe the diet of *Catharus* during migration at our sites, our field observations and superficial examination of fecal samples from bird bags indicate that they eat large quantities of fruit during their fall stopover. This is not surprising, given that fruit has been shown to be metabolized more efficiently into fat by birds and has also been shown to contain a high antioxidant content, which makes it more appealing to fueling migrants (Blake and Loiselle 1992, Suthers et al. 2000, Smith et al. 2007, Bolser et al. 2013). We frequently saw birds eating fruit from native forest trees of the families Melastomataceae, Rubiaceae, and Moraceae, as well as eating the fruit of *Carludovica palmata*. More study is needed to properly quantify the diets of these migrants, but fruit resources from these forests are doubtlessly playing a crucial role in providing an important part of the fuel for migrating *Catharus* in northern Colombia.

Our predictions about stopover strategies were based primarily on birds taking 1 of 2 routes (Alerstam 2011), either an overland route through Central America or an oversea route across the Caribbean. However, our observed flight ranges for each species, regardless of site, condition on arrival, or stopover duration, suggest that the distance remaining to each species' wintering grounds may be the



**FIGURE 4.** Histograms of fuel loads at first capture (surrogate for arrival fuel load) of individuals of 3 species in the genus *Catharus* captured during southward migration in northern Colombia. A value of zero means that birds were first captured at lean body mass (LBM), which is equivalent to having no visible fat reserves. Data are shown separately for each study site but are combined across years (Darién: 2011 and 2012; Sierra Nevada de Santa Marta: 2009 to 2011).

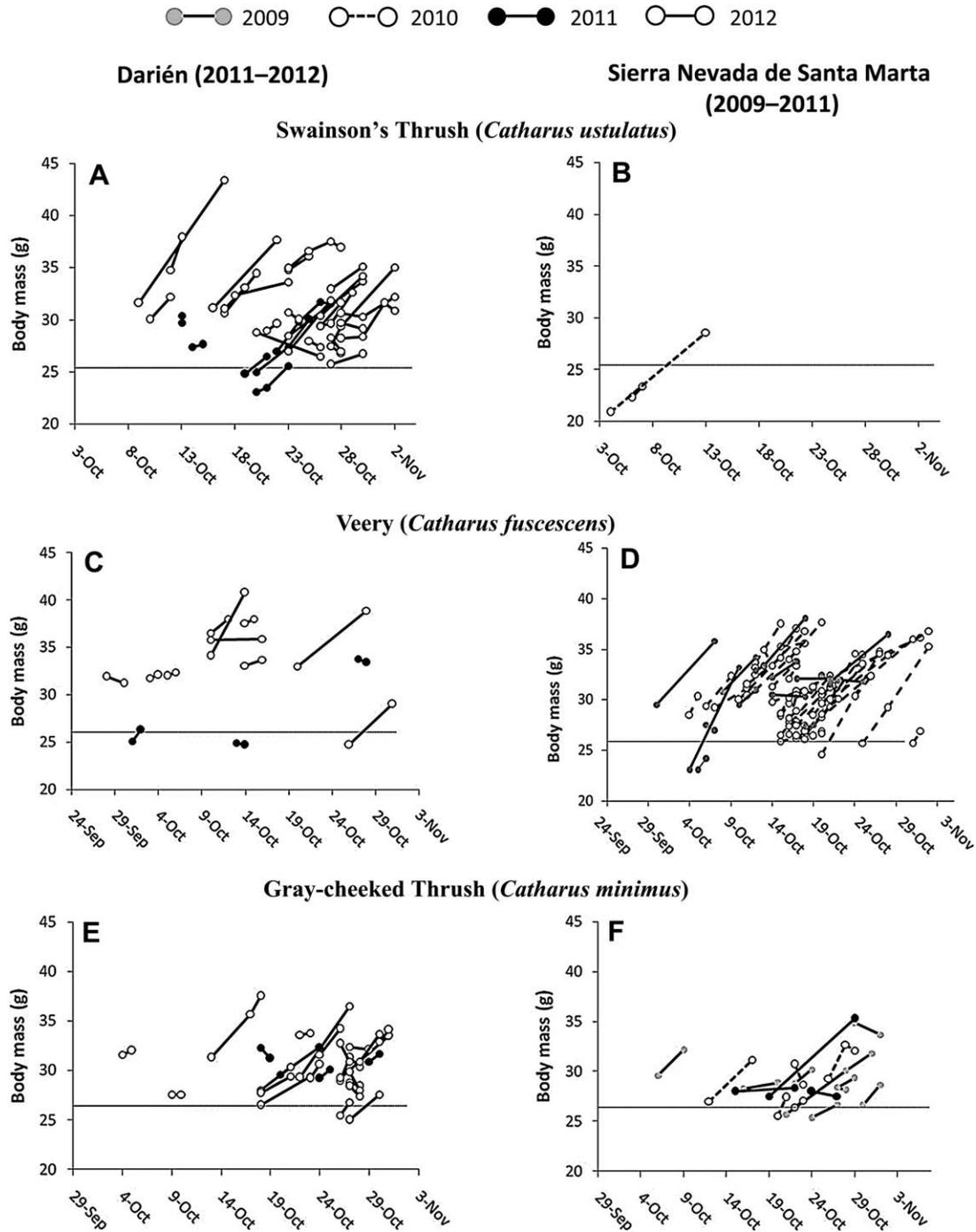
strongest determinant of stopover strategy, with Veery traveling the farthest from northern Colombian stopovers sites and Swainson's Thrush the shortest distance (Ruegg and Smith 2002, Heckscher et al. 2011, Cormier et al. 2013). Distance to final destination could therefore be a critical factor shaping migratory strategies, and future research on the wintering grounds, linking populations to

breeding and migration routes, will be essential to fully understand these hemispheric systems.

Although we cannot be sure whether individual birds arrived at our sites via different routes, differences in body condition on arrival supported this assumption. In the SNSM, all *Catharus*, primarily Veery and Gray-cheeked Thrush, arrived in poor body condition and in need of extensive refueling. On the other hand, birds in the Darién, primarily Swainson's Thrush and Gray-cheeked Thrush, arrived in better body condition and generally continued their migration the following evening (as reflected by a high percentage of transients) or only stopped for short periods. In both cases, our results confirm the importance of these 2 areas for migrants heading to their wintering grounds in South America.

Another explanation for the variation in body condition is that birds take similar routes into South America but originate from different populations in North America, thus arriving with different fuel loads at our sites (Delmore et al. 2012). Indeed, differences in the timing of passage between sites, within the same species, could be an indication that birds originated from different populations. Whether *Catharus* entering South America through the Darién or through the SNSM come by different routes (i.e. through Central America or by crossing the Caribbean) or are from different populations is still unknown and may be the key to understanding what determines the differences in arrival condition (Heckscher et al. 2011, Delmore et al. 2012). Weather patterns—in particular, wind direction and storms—could also have an important effect on the condition of birds on arrival, and on the composition and abundance of species at each site in different years (Marra et al. 2005, Bonter et al. 2009, Chilson et al. 2012). For example, a large arrival of Swainson's Thrush in the SNSM in 2010 was associated with a change in the prevailing wind direction, which pushed birds east of their normal trajectory (Gómez et al. 2013). Understanding how weather affects the abundance and composition of migrants at different stopover sites in the Neotropics is a topic for future research.

Although our data show clear differences in stopover strategy between species and sites, our study has limitations that need to be accounted for when interpreting the results. For example, small sample sizes for some species, sites, and years, and different recapture rates of adult and immature birds, limited the power of our models to estimate rates of body mass change and stopover durations. This also meant that we could not test for age differences in stopover strategy, although we know that individual *Catharus* of different ages can behave differently (Bowlin et al. 2005, González-Prieto et al. 2011, Bayly et al. 2012, 2013). Another limitation is that our localized capture areas and field-data-collection design did not

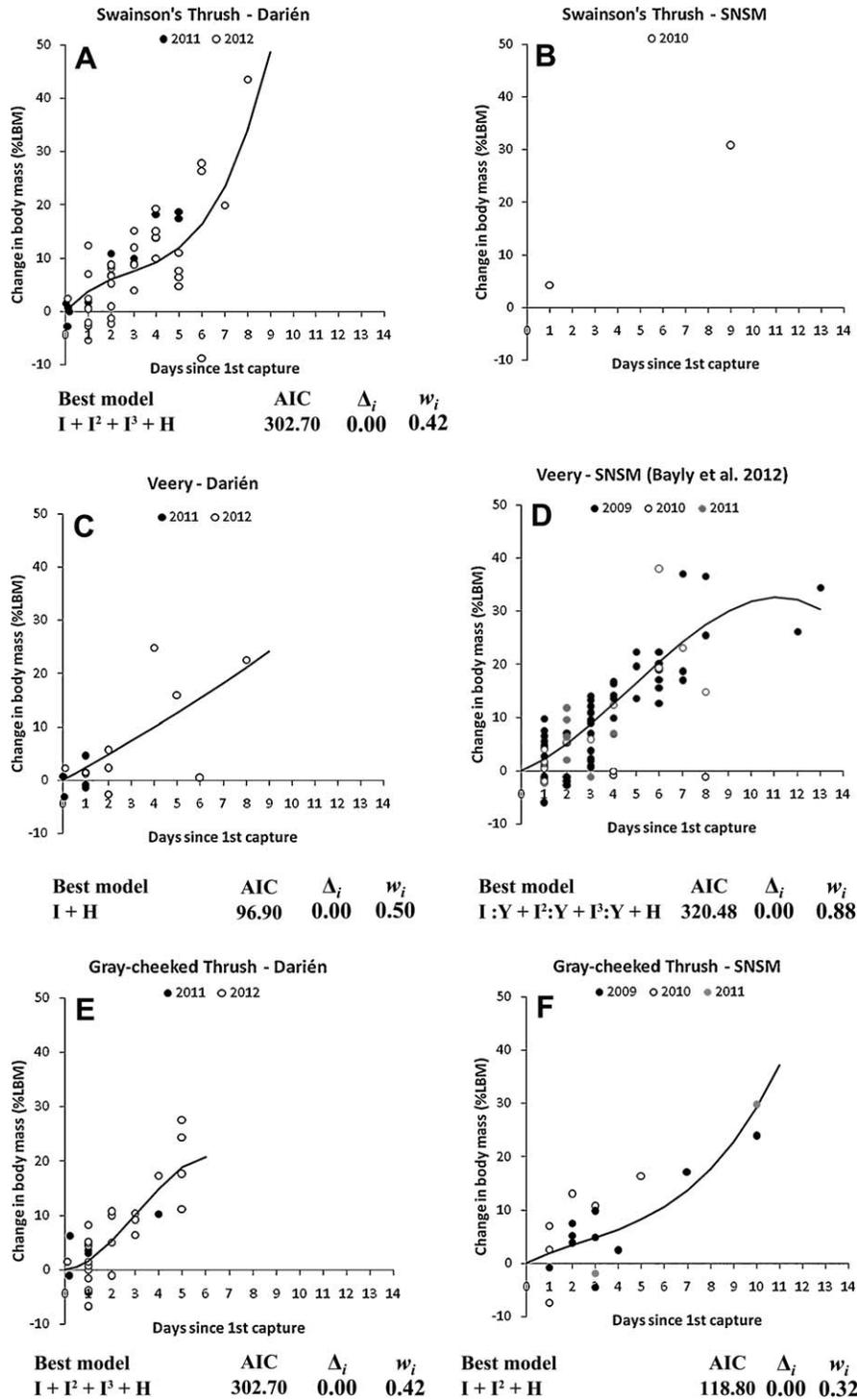


**FIGURE 5.** Change in body mass between successive captures of individuals of Swainson's Thrush (**A, B**), Veery (**C, D**) and Gray-cheeked Thrush (**E, F**) during southward migration in the Darién (left) and the Sierra Nevada de Santa Marta (right), Colombia. Variation in the shading of symbols reflects different years (2009–2012), and lines connect capture events of the same individual. The horizontal line is the mean lean body mass for each species. (**D**) was adapted from Bayly et al. (2012).

allow us to account for birds that moved beyond the trapping areas but remained within the stopover region. Recent work has shown that *Catharus* can move large distances within stopover sites and regions (Taylor et al.

2011, Cormier et al. 2013), which means that stopover duration may be underestimated in designs such as ours.

Despite these limitations, our study is one of the first to provide information about the differences in stopover site



**FIGURE 6.** Change in body mass (expressed as percent lean body mass [%LBM]) in individuals of three species of thrush as a function of the number of days since first capture in the Darién and the Sierra Nevada de Santa Marta (SNSM). Symbols represent birds from multiple years (2009–2012), and lines represent the predicted mass-change trajectory for each species based on model-averaged parameters from models that received the greatest support from AIC values. The model with most support from AIC is shown in the table under each graph with the respective AIC,  $\Delta_i$ , and  $w_i$  values. (A, B) Swainson’s Thrush. (C, D) Veery, adapted from Bayly et al. (2012). (E, F) Gray-cheeked Thrush. Table 5 in the Appendix shows the AIC,  $\Delta_i$ , and  $w_i$  values for all the models that were evaluated.

use by Nearctic–Neotropical migrants within South America, while simultaneously highlighting the energetic importance of stopover sites in northern Colombia for *Catharus*. These data collected through field studies are essential to complement the information produced by remote tracking techniques, which still have some limitations despite a significant and continuous process of improvement (Fudickar et al. 2012, Hobson et al. 2012a, 2012b). Only a combination of population-level field studies at a network of sites and a larger sample of remotely tracked individuals will reveal a complete picture of migration and stopover use throughout the Neotropical region. Our field studies in northern Colombia have also demonstrated the critical importance of this region to Nearctic–Neotropical migrants during spring migration (Bayly et al. 2013, Gómez et al. 2013).

To more fully put the results presented here into a hemispheric context, we must determine the geographic origin and wintering destination of individual birds stopping over in northern Colombia during the fall. We also need to understand how birds select the sites and habitats where they stop to refuel in South America and the implications that this selection may have on the success of their migration (Bayly et al. 2012, Gómez et al. 2013). Similar studies should be carried out in other areas of northern South America and in Central America, targeting those sites that have been highlighted as potentially important through geolocator data (Jahn et al. 2013, Laughlin et al. 2013, McKinnon et al. 2013). Most importantly, there is a need to analyze how all of these events connect to other stages in the annual cycle and how these connections affect individual fitness and survival (Boulet and Norris 2006, Faaborg et al. 2010). Knowing where, when, and how species use stopover sites and whether they have preferential migratory routes will allow us to increase the efficacy of conservation efforts during one of the most critical stages in the annual cycle of migrants.

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## APPENDIX

**TABLE 4.** Model set and associated AIC,  $\Delta_i$ , and  $w_i$  values for models of body mass change as a function of site (S), days since first capture (I), date (D), initial body mass (CI), and hour of capture (H) for Veery and Gray-cheeked Thrush captured on >1 occasion during southward migration in northern Colombia. The models that included site (in bold) received high support for both species.

| Model  | Veery         |             |             | Gray-cheeked Thrush |             |             |
|--|---------------|-------------|-------------|---------------------|-------------|-------------|
|  | AIC           | $\Delta_i$  | $w_i$       | AIC                 | $\Delta_i$  | $w_i$       |
| I + H  | 502.36        | 30.07       | 0.00        | 286.79              | 7.78        | 0.01        |
| I + I <sup>2</sup> + H   | 499.33        | 27.04       | 0.00        | 288.38              | 9.37        | 0.00        |
| I + I <sup>2</sup> + I <sup>3</sup> + H                        | 499.09        | 26.80       | 0.00        | 290.27              | 11.26       | 0.00        |
| I:D + I <sup>2</sup> :D + I <sup>3</sup> :D + H                | 497.38        | 25.10       | 0.00        | 290.64              | 11.63       | 0.00        |
| I:CI + I <sup>2</sup> :CI + I <sup>3</sup> :CI + H             | 501.05        | 28.76       | 0.00        | 288.23              | 9.22        | 0.01        |
| I:D:CI + I <sup>2</sup> :D:CI + I <sup>3</sup> :D:CI + H       | 499.03        | 26.74       | 0.00        | 288.85              | 9.84        | 0.00        |
| I:S + I <sup>2</sup> :S + I <sup>3</sup> :S + H                | <b>472.29</b> | <b>0.00</b> | <b>0.96</b> | 280.09              | 1.08        | 0.30        |
| I:D:S + I <sup>2</sup> :D:S + I <sup>3</sup> :D:S + H          | 484.91        | 12.62       | 0.00        | <b>279.01</b>       | <b>0.00</b> | <b>0.52</b> |
| I:D:CI:S + I <sup>2</sup> :D:CI:S + I <sup>3</sup> :D:CI:S + H | 478.71        | 6.42        | 0.04        | 281.49              | 2.48        | 0.15        |

**TABLE 5.** Model set and associated AIC,  $\Delta_i$ , and  $w_i$  values for models of body mass change in 3 species of thrush in the genus *Catharus* on stopover at 2 sites in northern Colombia during southward migration. Variables include days since first capture (I), date (D), initial body mass (CI), and hour of capture (H). Models that received the best support from AIC are highlighted in bold for each species and site.

| Model  | Swainson's Thrush            |             |             | Veery         |             |             | Gray-cheeked Thrush |             |             |
|--|------------------------------|-------------|-------------|---------------|-------------|-------------|---------------------|-------------|-------------|
|  | AIC                          | $\Delta_i$  | $w_i$       | AIC           | $\Delta_i$  | $w_i$       | AIC                 | $\Delta_i$  | $w_i$       |
|  | Darién                       |             |             |               |             |             |                     |             |             |
| I + H  | 303.79                       | 1.09        | 0.25        | <b>96.90</b>  | <b>0.00</b> | <b>0.50</b> | 303.79              | 1.09        | 0.25        |
| I + I <sup>2</sup> + H                                   | 304.30                       | 1.60        | 0.19        | 98.84         | 1.95        | 0.19        | 304.30              | 1.60        | 0.19        |
| I + I <sup>2</sup> + I <sup>3</sup> + H                  | <b>302.70</b>                | <b>0.00</b> | <b>0.42</b> | 100.82        | 3.92        | 0.07        | <b>302.70</b>       | <b>0.00</b> | <b>0.42</b> |
| I:D + I <sup>2</sup> :D + I <sup>3</sup> :D + H          | 307.77                       | 5.07        | 0.03        | 99.24         | 2.34        | 0.15        | 307.77              | 5.07        | 0.03        |
| I:CI + I <sup>2</sup> :CI + I <sup>3</sup> :CI + H       | 305.72                       | 3.02        | 0.09        | 102.65        | 5.75        | 0.03        | 305.72              | 3.02        | 0.09        |
| I:D:CI + I <sup>2</sup> :D:CI + I <sup>3</sup> :D:CI + H | 310.05                       | 7.34        | 0.01        | 100.89        | 4.00        | 0.07        | 310.05              | 7.34        | 0.01        |
|  | Sierra Nevada de Santa Marta |             |             |               |             |             |                     |             |             |
| I + H  | -                            | -           | -           | 329.81        | 9.33        | 0.01        | 121.80              | 3.00        | 0.07        |
| I + I <sup>2</sup> + H                                   | -                            | -           | -           | 323.17        | 2.68        | 0.23        | <b>118.80</b>       | <b>0.00</b> | <b>0.32</b> |
| I + I <sup>2</sup> + I <sup>3</sup> + H                  | -                            | -           | -           | <b>320.48</b> | <b>0.00</b> | <b>0.88</b> | 119.94              | 1.14        | 0.18        |
| I:D + I <sup>2</sup> :D + I <sup>3</sup> :D + H          | -                            | -           | -           | 324.95        | 4.47        | 0.09        | 119.77              | 0.97        | 0.20        |
| I:CI + I <sup>2</sup> :CI + I <sup>3</sup> :CI + H       | -                            | -           | -           | 331.66        | 11.18       | 0.00        | 120.89              | 2.09        | 0.11        |
| I:D:CI + I <sup>2</sup> :D:CI + I <sup>3</sup> :D:CI + H | -                            | -           | -           | 334.96        | 14.47       | 0.00        | 120.71              | 1.91        | 0.12        |

**TABLE 6.** Capture–recapture models evaluated in order to estimate stopover duration for 3 *Catharus* species on migration at 2 sites in northern Colombia. Models that received the greatest support from AIC are highlighted in bold.

| Year | Model                        | Swainson's Thrush |             |             | Veery            |             |             | Gray-cheeked Thrush |             |             |
|------|------------------------------|-------------------|-------------|-------------|------------------|-------------|-------------|---------------------|-------------|-------------|
|      |                              | AIC <sub>c</sub>  | $\Delta_i$  | $w_i$       | AIC <sub>c</sub> | $\Delta_i$  | $w_i$       | AIC <sub>c</sub>    | $\Delta_i$  | $w_i$       |
|      | Sierra Nevada de Santa Marta |                   |             |             |                  |             |             |                     |             |             |
| 2009 | $\Phi(\cdot)$ p(.)           | -                 | -           | -           | <b>499.51</b>    | <b>0.00</b> | <b>1.00</b> | <b>81.79</b>        | <b>0.00</b> | <b>0.87</b> |
|      | $\Phi(\text{trans})$ p(.)    | -                 | -           | -           | 579.60           | 80.08       | 0.00        | 85.59               | 3.80        | 0.12        |
| 2010 | $\Phi(\cdot)$ p(.)           | <b>33.82</b>      | <b>0.00</b> | <b>0.77</b> | <b>155.02</b>    | <b>0.00</b> | <b>0.60</b> | <b>53.14</b>        | <b>0.00</b> | <b>0.91</b> |
|      | $\Phi(\text{trans})$ p(.)    | 36.20             | 2.38        | 0.23        | 155.78           | 0.76        | 0.40        | 57.79               | 4.65        | 0.09        |
| 2011 | $\Phi(\cdot)$ p(.)           | -                 | -           | -           | -                | -           | -           | <b>38.83</b>        | <b>0.00</b> | <b>0.89</b> |
|      | $\Phi(\text{trans})$ p(.)    | -                 | -           | -           | -                | -           | -           | 43.12               | 4.28        | 0.10        |
|      | Darién                       |                   |             |             |                  |             |             |                     |             |             |
| 2011 | $\Phi(\cdot)$ p(.)           | 105.80            | 15.52       | 0.00        | 32.77            | 0.14        | 0.48        | <b>48.24</b>        | <b>0.00</b> | <b>0.79</b> |
|      | $\Phi(\text{trans})$ p(.)    | <b>90.28</b>      | <b>0.00</b> | <b>1.00</b> | <b>32.64</b>     | <b>0.00</b> | <b>0.52</b> | 50.95               | 2.71        | 0.21        |
| 2012 | $\Phi(\cdot)$ p(.)           | 369.37            | 6.88        | 0.03        | <b>128.50</b>    | <b>0.00</b> | <b>0.61</b> | <b>226.50</b>       | <b>0.00</b> | <b>0.86</b> |
|      | $\Phi(\text{trans})$ p(.)    | <b>362.48</b>     | <b>0.00</b> | <b>0.97</b> | 129.41           | 0.91        | 0.39        | 230.20              | 3.69        | 0.13        |