FALL MIGRATION OF THE VEERY (CATHARUS FUSCECSENS) IN NORTHERN COLOMBIA: DETERMINING THE ENERGETIC IMPORTANCE OF A STOPOVER SITE

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Abstract.—Migration is a highly energy-demanding process, and migratory birds store energy at stopover sites along their migration routes to meet these demands. The Veery (Catharus fuscescens) performs one of the longest migrations of all Neotropical migratory landbirds, yet the stopover sites that it uses and their relative importance to migratory success are poorly known. We studied the Veery during two fall migrations (2009 and 2010) in northern Colombia, where we hypothesized that birds would replenish energy reserves after crossing the Caribbean Sea to fuel flights toward their wintering grounds. To determine the relative energetic importance of our study site, we combined estimates of fuel deposition rates, stopover durations, and flight ranges to estimate the percentage of the total migratory distance that could be covered following a stopover. Veeries arrived at our study site with low energy reserves, and recaptured birds increased their body mass at a mean rate of 3.6% of lean body mass day–1 over an average of 9 days. At departure, birds carried energy reserves equivalent to 34.5% of lean body mass, giving rise to a maximum potential flight range of 2,200 km, thereby allowing them to cover ≤30% of the total fall migration distance, depending on how reserves are used. By showing how a stopover site is used in energetic terms, we highlight the importance of a site in northern Colombia to long-distance Neartic–Neotropic migrants and also introduce a method that contributes to the prioritization of stopover sites across regions and species. Received 29 August 2011, accepted 17 April 2012.

Key words: departure fuel load, flight range, fuel deposition rate, migration, Neotropical migratory birds, South America, stopover duration, stopover site prioritization.

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Migration is a highly energy-demanding process, and the ability of organisms to meet these energy requirements is expected to be a key determinant of the success of migration (Alerstam and Lindström 1990, Baker et al. 2004, Newton 2006). Migratory birds perform the longest migrations of all animals, and they meet the energetic demands through multiple physiological and behavioral adaptations (Piersma 1998, Hedenström 2008). One such adaptation is the storage of energy at stopover sites to power migratory flights. The relative contribution of stopover sites to the energy requirements for migratory flights and their distribution in space are expected to vary among species according to the spatial and temporal distribution of resources (Weber et al. 1998), distance to final destination (Weber and Houston 1997), location of ecological barriers (Schaub and Jenni 2000a, Delingat et al. 2008), and rates of energy deposition experienced between sites (Weber et al. 1998, Erni et al. 2002), among other factors.

The Veery (Catharus fuscescens) performs one of the longest migrations known for a Nearctic–Neotropical migratory landbird (Remsen 2001). Between their North American breeding grounds and wintering grounds in South America (Fig. 1), Veeries can cover >6,500 km (Hecksher et al. 2011). Although the location of stopover regions along this route is beginning to be understood (Hecksher et al. 2011), the relative importance of individual stopover sites or habitats for energy storage in each region is unknown. The distribution of specimens from South America (Remsen 2001), the occurrence of the Veery in Central America (Ridgely and Gwynne 1989, Stiles and Skutch 1989, Bayly and Gómez 2011), and five geolocator tracks from a breeding population in the northeastern United States (Hecksher et al. 2011) indicate that many individuals depart in the fall from the southeastern United States to make a >1,500 km flight across the Caribbean Sea. Consequently, birds arriving in northern South America may have exhausted their energy reserves and would need to replenish them at coastal stopover sites.

Between the Caribbean coast of South America and wintering areas 3,000 km to the south, extensive areas of presumably suitable stopover habitat exist in the Amazon basin. Birds stopping over in northern South America might, therefore, store limited energy reserves and make numerous multiday stops en route to wintering areas. Evidence from birds tracked with geolocators suggests that strategies are flexible, with birds making between zero and two additional multiday stopovers between northern South America and their first wintering site (Hecksher et al. 2011). Movement rates imply that birds typically make daytime stops between flights (Hecksher et al. 2011), as would be expected of a nocturnal migrant (Cochran and Wikelski 2005). It therefore appears that although large areas of suitable habitat exist, the storage of moderate energy reserves and subsequent use of one or two stopover sites en route is favored; however, the exact onward strategy may depend on the quality of stopover sites encountered in northern South America. To determine how a stopover site in northern South America is used, we studied the fall migration of the Veery in northern Colombia.

The implicit importance of stopover sites to overall migratory success has caused many authors to attempt to categorize their value for migratory birds, to facilitate the prioritization of sites for protection (Petit 2000, Mehlman et al. 2005, Bonter et al. 2009, Faaborg et al. 2010). These exercises have largely been based on subjective assessments, although Dunn (2000, 2002) proposed that rates of energy deposition could serve as empirical indicators of habitat quality; however, rates treated in isolation function only at local scales when comparing the importance of individual stopover sites. The ideal measure would consider ultimate survival or reproductive success of individuals using a site (Hedenström 2008). However, neither is a practical measure, given the difficulties of linking stopover locations to individual fitness. We therefore propose an empirical indicator of site importance based on the energy stored at a site, expressed as a percentage of the total energy required to migrate from breeding to wintering grounds (or vice versa). Because energy requirements vary with the strategy adopted, our approach equates stored energy with distance, allowing a site’s value to be expressed as an increase in potential flight range. Potential ranges are expected to be translated into actual flight ranges through multiple shorter flights in the case of the Veery, although it is important to note that energy stores may have other functions (e.g., emergency reserves). This indicator applies primarily to sites where birds store energy, and not to sites used as “fire escapes” during an emergency (e.g., islands during
adverse weather) or those used only as takeoff points prior to ecological barriers (Mehlman et al. 2005).

We introduce this approach using data on the stopover behavior of the Veery during two fall migrations in the Sierra Nevada de Santa Marta, northern Colombia. We combine estimates of stopover duration using mark–recapture analysis with models of body-mass change to estimate the total energy stored during stopover. By then converting this estimate to a potential flight range, we evaluate the contribution of a stopover site in northern South America to the entire fall migration of the Veery.

**Methods**

**Study site.**—Our study took place in the Sierra Nevada de Santa Marta (SNSM), an isolated coastal mountain range on the northern coast of Colombia that rises from sea level to 5,795 m (Fig. 1). We collected data at the Quebrada Valencia reserve (11°14′10.48″N, 73°47′57.15″W), located 2 km from the Caribbean coast in the northern foothills of the SNSM. The main vegetation type in the steep-sided valley formed by the Valencia River was humid tropical lowland forest with an average altitude of 175 m above sea level.

**Data collection.**—We carried out constant-effort mist netting during the fall migration of 2009 and 2010 at a fixed banding station, using two types of mist net (12 m long, either 32-mm or 36-mm mesh). Placement of mist nets was determined by topography and to maximize capture rates, which often resulted in placement of nets along ridgelines rising up from a valley bottom, rather than on steep slopes. We operated 12 to 16 mist nets on 37 days between 20 September and 3 November 2009 and on 33 days between 29 September and 1 November 2010, resulting in 2,105 mist-net hours (1 mist-net hour = one 12-m net open for 1 h) in 2009 and 2,127 mist-net hours in 2010. Mist nets were operated for an average (± SD) of 4.3 ± 0.6 h (n = 69) after sunrise. All Veeries captured were fitted with a uniquely numbered Porzana-made metal band. Prior to release, we recorded age (Pyle 1997), fat score (visible fat deposits scored on a nine-point scale, following Kaiser 1993), muscle score (scale of 0 to 3 following Redfern and Clark 2001), wing chord (± 1 mm), and body mass (± 0.1 g, using an electronic balance).

**Modeling changes in body mass.**—The objective of modeling changes in body mass was to predict the average increase in energy reserves (consisting of both fat and protein) for a given stopover duration. To ensure that mass gain was an appropriate measure of increasing energy reserves, we first carried out a regression analysis of change in mass against change in fat score (Fig. 2) and also determined whether muscle score changed between captures. We then modeled change in body mass as a function of the number of days since a bird was first captured, using a modified version of the method presented by Atkinson et al. (2007). The dependant variable, change in body mass, was calculated as the change in mass between first capture and each successive capture for all birds captured on more than one occasion. By including each successive capture of an individual bird, this method makes maximum use of often limited recapture data and increases the power of models to describe nonlinear patterns. We expressed changes in mass as a percentage of each bird’s estimated lean body mass (LBM) to account for differences in structural size between birds and to facilitate interspecific comparisons. We estimated LBM, or the mass of a bird with no visible fat deposits, by regressing body mass against wing length for a subset of birds with fat score zero (LBM = 6.47 + 0.212 * wing length; F = 32.9, df = 123, R² adj = 0.21, P < 0.001). We acknowledge that the precision of our LBM estimates will be affected by variations in gut content and flight muscle size, and possibly other factors, but we do not expect this potential variation to affect our conclusions.

We modeled changes in body mass in relation to day of first capture in a two-stage process. The first step was to determine whether mass changes were linear or nonlinear over time. We ran a linear model (I), a quadratic model (I+I²), and a polynomial model (I+I²+I³), where I is the interval in days between captures. We compared models by calculating the relative support that each received from Akaike’s information criterion corrected for small sample sizes (AICc) and from ΔAIC, where ΔAIC was the difference between models and the model with the lowest AIC, (ΔAIC = AIC_w - minimum AIC). Models with ΔAIC < 2 are considered equally plausible (Burnham and Anderson 1998) and were therefore included in stage 2.

In the second stage, when there was support for a nonlinear model, we included initial body mass as a variable in subsequent models because the rate of mass change may depend on the day of capture in relation to stopover initiation. Under a typical stopover scenario, body mass increases over time; therefore, body mass at first capture is an appropriate substitute for time present at the site. Because body mass is related to structural size, we modeled starting body mass as a condition index (CI), where CI = mass/wing length (simple indices such as these have been criticized [e.g.,
Laborcha and Hayes 2012], and it may be preferable to enter body mass without correction. We also included the following factors in a hierarchical model set at the second stage: year (2009 and 2010), age (hatch-year [HY] and after-hatch-year [AHY]), and date at first capture (days counted continuously from 30 September [= day 1]). All factors were entered into our models as an interaction with the interval between captures (I). We excluded additive terms, to ensure that we modeled the effect of factors on the rate of mass change and not their additive effect on body mass (e.g., mass change = 1 + I:year and not mass change = 1 + I:year + year). Further, in all models, we forced the intercept through zero, because body-mass change at the point of capture is zero. Model selection was subsequently carried out using AICc and Akaike weights (w) (Burnham and Anderson 1998), where w reflects the relative support that model i receives over other models.

We carried out the above two stages first with a data set combining years, and then by separating years. Models of body-mass change for 2010 did not contain the factor age because of insufficient captures of AHY birds. All modeling was carried out in the program R using general linear models with normal errors (R Development Core Team 2008).

The method used to model body-mass changes was dependent on certain assumptions. First, we assumed that all birds had initiated migration and that no individuals were in either a wintering or a postbreeding state. The Veery neither breeds nor winters in northern Colombia, so this assumption holds at our study site. Second, when temporal changes in mass are nonlinear, the accurate modeling of such patterns depends on the assumption that birds are caught on or near their day of arrival. This assumption appears to hold at our site, given the low body masses of birds on first capture. However, the body mass of some birds suggested that they were captured toward the end of their stopover—if more birds were actually captured later in their stopover, our modeled rates may be overestimated.

Finally, despite the fact that body mass typically shows a diurnal increase in birds (Thomas 2000), we did not include time of capture in our analyses. This is equivalent to assuming that mass did not change with time of capture. Estimates of rates of mass change can be estimated and corrected for by regressing body mass or a condition index (e.g., mass/wing length) against hour of capture, but this correction also depends on the assumption that the probability of capture of “lean” and “fat” birds does not vary with time of day. This assumption may be violated if lean birds are more motivated to feed and, therefore, have a higher probability of being captured earlier in the day than fat birds. To determine whether this was true for the Veery, we classified birds with fat scores ≤1 as “lean” (n = 258) and birds with scores ≥2 as “fat” (n = 165) and carried out a chi-square analysis to compare the total number of captures per 30 min in relation to sunrise, with expected capture totals based on the frequency of captures of fat birds. We found that more lean birds were captured in the first 1.5 h after sunrise, and fewer 4 h after sunrise (χ2 = 26.4, df = 9, P = 0.002). This significant difference in capture probability would result in overestimates of hourly mass increases, so we chose to not correct for hour of capture. Moreover, given the limited variation in capture times of recaptured birds (96% of captures occurred before 1100 hours CST), any correction would likely have little effect on our results, which we confirmed by including hour of capture in our final model; hour of capture added just a 0.2% increase in predicted body-mass change over 9 days.

Stopover duration.—Several methods for estimating stopover duration have been proposed, but each has its deficiencies and potential sources of bias and error (Schaub et al. 2001, Efford 2005, Morris et al. 2006). Consequently, we present three commonly used methods and discuss their relative merits in relation to our study. (1) We used minimum stopover duration, defined as the number of days elapsed between the first and last capture of individual birds, recaptured at least once, and inclusive of the first and last day. (2) We used “stopover after” (Schaub et al. 2001), estimated by analyzing mark–recapture data in Program MARK, version 5.1 (White and Burnham 1999), following the methods outlined by Schaub et al. (2001) and Efford (2005) and with a variation introduced by Morris et al. (2005). We first created separate capture histories for each year of the study and for each bird, in which each day that mist netting took place was defined as a capture occasion. On each capture occasion, a bird was assigned a score of 1 (captured) or zero (not captured). We used the multiple-day constancy method proposed by Morris et al. (2005) to avoid pooling capture histories across days. This method divides capture histories into periods of equal length, across which survival and capture probability are kept constant, thereby reducing the number of parameters to be estimated. To define our starting model, we varied the constancy period incrementally from 2 to 6 days until we obtained a model in which all parameters were estimable. We calculated ĉ for this starting model to check for model fit using the method implemented in MARK (White and Burnham 1999). All subsequent estimates were corrected for the resulting value of ĉ. Once a starting model was selected, we fitted models with and without time-dependence and with an age structure to reflect the presence of transients in the population (Pradel et al. 1997). We used AICc to infer model suitability and used the estimate of survival (Φ) from the model receiving the greatest support from AICc to estimate stopover duration using the formula for life expectancy: LE = –1/lnΦ. When a transient model was supported, we used the estimate for Φp. In our study, models that received the greatest support from AICc did not include time-dependence in Φ, so we did not need to account for time-dependence when calculating life expectancy (see Efford 2005, Morris et al. 2006). (3) We used total stopover, calculated by combining the estimate of stopover after (as measured above) with an estimate of the time that a bird was present at the site prior to capture, following Schaub et al. (2001). To determine the time present prior to capture, we estimated the seniority probability (γ) in MARK. Total stopover was subsequently estimated as follows: total stopover = (–1/lnΦ) + (–1/lnγ).

Contribution to migration.—We defined the contribution of a stopover to migration as equal to the percentage of the total migratory journey that can be completed using the energy accumulated during a stopover. To calculate this contribution, we first estimated departure body mass from our stopover site by entering stopover duration estimates into our final models for body-mass change for each year or when combining years as in the following equation:
Mass increase = \( b_1 \text{MSD} + b_2 \text{MSD}^2 + b_3 \text{MSD}^3 + b_4 \text{Cl}_{m} \text{MSD} + O \)  

where \( \text{MSD} = \) mean stopover duration, \( \text{Cl}_{m} = \) modal condition index and \( b_1, b_2, b_3, b_4 \) are the model coefficients. Our equations of mass increase predict daily mass increase minus overnight mass loss between the day of first capture and any successive day. On the day of departure, Veeries, like other nocturnal migratory birds, are expected to initiate migratory flights shortly after sunset and, therefore, do not experience overnight mass loss. We therefore included the term \( O \) (overnight mass loss; 2.6% LBM) to adjust expected mass increase to reflect the total increase prior to sunset. We estimated \( O \) using the stopover calculator in the program FLIGHT, version 1.12 (Pennycuick 2008), assuming that overnight mass loss is equivalent to the existence metabolic rate (Dunn 2001), that LBM = 26.8 g, and that nights were 12 h in length. Because the mass increase predicted by Equation 1 is expressed as a percentage of LBM, we converted it to a mass in grams based on the estimated LBM of a bird of mean wing length (26.8 g, mean wing length = 96 mm).

Taking our estimate of mass increase from Equation 1, we estimated two values of departure body mass: (1) LBM + mass increase, and (2) mean body mass on first capture + mass increase. Departure body masses were then converted to an estimated flight range so that they could be expressed as a percentage of the total migratory distance—our measure of the contribution to migration. We calculated total migratory distance as the distance between population centers in the northeastern United States (González-Prieto et al. 2011) and wintering areas in Brazil occupied after completing fall migration (Bent 1949, Remsen 2001; Heckscher et al. [2011] showed that birds can make an intratropical migration in January–February to occupy a second wintering region to the north of the Amazon), when following a route via the Florida peninsula (Heckscher et al. 2011) and the SNSM (Fig. 1). This gave rise to an estimated total straight-line distance of 7,200 km (between populations, total distance may vary between 6,000 km and >10,000 km). To calculate flight ranges based on departure body masses, we used FLIGHT, which assumes that fuel stores consist of both fat and protein. We used a wingspan of 0.285 m (mean of 6 measurements taken in 2009 at the study site), a wing area of 0.0156 m² (mean of 6 measurements), and the default setting of 0.17 (17% of total body mass) for the flight muscle fraction. Although a flight-muscle-fraction value was unavailable for Veeries, the default value would seem reasonable on the basis of values from individuals in the genera Parkesia and Turdus (Pennycuick 2008). The fat fraction for any given departure body mass was calculated following the “Find fat fraction” guidelines provided in the FLIGHT manual, in which the fraction is the value that gives rise to a “total body mass” equivalent to \( m_{\text{min}} \) (the mass of a bird that has used all consumable fat) after a migration simulation has been run. We estimated \( m_{\text{min}} \) as 26.0 g, based on the body mass of Veeries with a fat and muscle score of zero. We set flight altitude as 1,000 m (varying altitude had a minimal effect on estimates) and departure altitude as the altitude of the study site. After departing from the stopover site, birds would be expected to make daytime stops between nocturnal flights, and we assume that birds were able to maintain their body mass during these stops. The contribution of stopovers to migration was calculated as (estimated flight range)/(total migration distance).
The AIC\textsubscript{c} and ΔAIC values suggested a difference in rates of body-mass change between years (Table 1), so years were analyzed separately (Table 2). In 2009, a polynomial relationship between mass gain and the number of days since capture received the greatest support. There was also support for age and date having a weak effect (Table 3); support for the latter may reflect the tendency for AHY birds to arrive before HY birds (González-Prieto et al. 2011). In 2010, linear and polynomial models of mass change received similar support. We selected the linear model as the final model because it was more biologically plausible than the polynomial model, the latter predicting a rapid decrease in mass after 8 days. Models containing date also received support from AIC with Δ values <2; however, with the 95% confidence interval of the coefficient for date containing zero (–0.17 to 0.05), the support for these models was weak and they were excluded from the final model set (Table 3).

Stopover duration.—Stopover durations were calculated from the capture histories of 263 individuals in 2009 and from 101 individuals in 2010. Of the individuals analyzed, 41 (15.6%) and 13 (12.9%) were recaptured within the same year in 2009 and 2010, respectively. In both years, a “stopover after” model with no time-dependence in either survival or recapture probability received the greatest support from AIC\textsubscript{c} [Φ (.) p (.)], with all other models having Δ\textsubscript{AIC} > 2. In 2009, there was support for an age structure in survival probability to account for

![Fig. 4. Body-mass changes in Veeries captured on more than one occasion in relation to the number of days since first capture at a stopover site in northern Colombia during fall migration in 2009 (black squares) and 2010 (white squares). Changes in body mass are expressed as a percentage of a bird’s estimated lean body mass (LBM) using the regression equation: LBM = 6.47 + 0.212*wing length. The solid line is the predicted trajectory of mass gain from the following model: body-mass change = (9.56*I) + (0.53*I\textsuperscript{2}) + (–0.03*I\textsuperscript{3}) + (–27.03*I*CI), where I is the number of days since first capture and CI = 0.3 (modal value). Coefficient estimates were derived from the model combining years in Table 3.](image-url)
Both models had adequate model fit based on $\hat{c}$ values, 1.09 and 1.37, respectively. These models and minimum stopover durations predict stopovers between 4 and 5 days in duration (Table 3). "Total stopover" estimates were 8.1 or 8.5 days long, or 9 days if one considers that a bird will not depart during the day. Although the precision of estimates was lower in 2010, stopover estimates were very similar between years (Table 3).

Contribution to migration.—Entering minimum stopover durations or "stopover after" estimates into the final models for body-mass change (Table 3), the average Veery would increase its mass by 4.1–5.1 g during a stopover in the SNSM, which is equivalent to a gain of 15.3–19.2% of LBM (Table 4). These gains correspond to potential flight range of 934 km to 1,142 km, respectively, which is equivalent to a contribution of 13.0% and 15.9% of the total energy required to undertake fall migration. Considering the reserves that Veeries had on first capture, the potential contribution to migration increases to between 19.1% and 21.6%, respectively.

"Total stopover" duration estimates were longer and gave rise to expected mass gains of 7.7–8.8 g, which are equivalent to 28.6–32.7% of LBM, respectively (Table 4). Predicted departure masses based on total stopover durations (36.4–38.2 g) were in good agreement with observed masses (Fig. 3) and gave rise to potential flight ranges of up to 2,200 km (Fig. 5). The contribution to migration varied little between years, and, when entering a stopover duration of 9 days into the model based on the analyses that combined years, a flight range of 2,205 km and a contribution to migration of 30.6% were predicted. When considering only the remaining distance to wintering areas and not the total distance, the energy stored in the SNSM represents more than two-thirds of the energy required to reach wintering areas.

### Discussion

Our study site on the northeastern Caribbean coast of Colombia is >1,000 km from Central America (Nicaragua), 950 km from Cuba, and >1,500 km from Florida. Therefore, Veeries arriving in the

### Table 3

Model coefficients and their 95% confidence intervals (in parentheses) for the final models used for predicting body-mass change (see Table 4). The model that received the greatest support from AICc values was chosen in all cases, except for 2010, for which model predictions from a linear model were more biologically plausible than those from a polynomial model, which predicted large decreases in mass after 8 days.

<table>
<thead>
<tr>
<th>Year</th>
<th>2009 and 2010</th>
<th>2009</th>
<th>2010</th>
</tr>
</thead>
<tbody>
<tr>
<td>Model</td>
<td>$I + I^2 + I^3 + I:CL$</td>
<td>$I + I^2 + I^3 + I:CL$</td>
<td>$I + I^3$</td>
</tr>
<tr>
<td>Coefficients</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$I$</td>
<td>9.46 (5.79 to 13.12)</td>
<td>5.70 (10.0 to 1.39)</td>
<td>18.3 (11.2 to 25.4)</td>
</tr>
<tr>
<td>$I^2$</td>
<td>0.53 (0.13 to 0.92)</td>
<td>0.45 (0.04 to 0.86)</td>
<td>—</td>
</tr>
<tr>
<td>$I^3$</td>
<td>–0.03 (–0.06 to –0.01)</td>
<td>–0.03 (–0.06 to –0.01)</td>
<td>—</td>
</tr>
<tr>
<td>$I:CL$</td>
<td>–27.0 (–38.0 to –16.1)</td>
<td>–16.2 (–3.61 to –28.8)</td>
<td>–50.2 (–73.2 to –27.2)</td>
</tr>
<tr>
<td>$I:D$</td>
<td>—</td>
<td>0.05 (–0.01 to 0.11)</td>
<td>—</td>
</tr>
</tbody>
</table>

### Table 4

Stopover duration estimates, predicted departure fuel loads, and estimated flight ranges for Veeries stopping over in northern Colombia during fall migration. Estimated flight ranges are expressed as a contribution to the total fall migration distance, where total distance = 7,200 km. Flight ranges were calculated assuming that (A) birds use only energy reserves accumulated during stopover or (B) birds use energy reserves accumulated during stopover and reserves carried on arrival at the stopover site.

<table>
<thead>
<tr>
<th>Method of stopover estimation</th>
<th>Model</th>
<th>Stopover duration (days)</th>
<th>Expected departure fuel load (A)</th>
<th>Expected departure fuel load (B)</th>
<th>Flight range (km) (A)</th>
<th>Flight range (km) (B)</th>
<th>Contribution to migratory journey (A)</th>
<th>Contribution to migratory journey (B)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2009</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Minimum</td>
<td>—</td>
<td>5.2 days (4.3–6.0)</td>
<td>19.2% LBM</td>
<td>1,142</td>
<td>1,558</td>
<td>15.9%</td>
<td>21.6%</td>
<td></td>
</tr>
<tr>
<td>After $\phi$ (tr) $p$ (.)</td>
<td></td>
<td>4.4 days (3.1–6.4)</td>
<td>15.3% LBM</td>
<td>934</td>
<td>1,374</td>
<td>13.0%</td>
<td>19.1%</td>
<td></td>
</tr>
<tr>
<td>Total $\phi$ (tr) $\gamma$ (.) $p$ (.)</td>
<td></td>
<td>8.5 days (6.0–12.2)</td>
<td>32.7% LBM</td>
<td>1,780</td>
<td>2,171</td>
<td>24.7%</td>
<td>30.2%</td>
<td></td>
</tr>
<tr>
<td>2010</td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Minimum</td>
<td>—</td>
<td>4.0 days (2.6–5.4)</td>
<td>15.6% LBM</td>
<td>965</td>
<td>1,298</td>
<td>13.4%</td>
<td>18.0%</td>
<td></td>
</tr>
<tr>
<td>After $\phi$ (tr) $p$ (tr)</td>
<td></td>
<td>4.1 days (1.9–10.0)</td>
<td>15.6% LBM</td>
<td>965</td>
<td>1,298</td>
<td>13.4%</td>
<td>18.0%</td>
<td></td>
</tr>
<tr>
<td>Total $\phi$ (tr) $\gamma$ ( .) $p$ (tr)</td>
<td></td>
<td>8.1 days (2.2–17.6)</td>
<td>28.6% LBM</td>
<td>1,579</td>
<td>1,915</td>
<td>21.9%</td>
<td>26.6%</td>
<td></td>
</tr>
<tr>
<td>2009 and 2010 Combined</td>
<td></td>
<td>9 days</td>
<td>34.5% LBM</td>
<td>1,897</td>
<td>2,205</td>
<td>26.3%</td>
<td>30.6%</td>
<td></td>
</tr>
</tbody>
</table>

Notes: $\phi$ = survival probability; $\gamma$ = seniority probability; $p$ = capture probability; "tr" indicates that an age structure was used to reflect the presence of transients.

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transients [$\Phi$ (trans) $p$ (.)]. Both models had adequate model fit based on $\hat{c}$ values, 1.09 and 1.37, respectively. These models and minimum stopover durations predict stopovers between 4 and 5 days in duration (Table 3). "Total stopover" estimates were 8.1 or 8.5 days long, or 9 days if one considers that a bird will not depart during the day. Although the precision of estimates was lower in 2010, stopover estimates were very similar between years (Table 3).

Contribution to migration.—Entering minimum stopover durations or "stopover after" estimates into the final models for body-mass change (Table 3), the average Veery would increase its mass by 4.1–5.1 g during a stopover in the SNSM, which is equivalent to a gain of 15.3–19.2% of LBM (Table 4). These gains correspond to potential flight range of 934 km to 1,142 km, respectively, which is equivalent to a contribution of 13.0% and 15.9% of the total energy required to undertake fall migration. Considering the reserves that Veeries had on first capture, the potential contribution to migration increases to between 19.1% and 21.6%, respectively.

"Total stopover" duration estimates were longer and gave rise to expected mass gains of 7.7–8.8 g, which are equivalent to 28.6–32.7% of LBM, respectively (Table 4). Predicted departure masses based on total stopover durations (36.4–38.2 g) were in good agreement with observed masses (Fig. 3) and gave rise to potential flight ranges of up to 2,200 km (Fig. 5). The contribution to migration varied little between years, and, when entering a stopover duration of 9 days into the model based on the analyses that combined years, a flight range of 2,205 km and a contribution to migration of 30.6% were predicted. When considering only the remaining distance to wintering areas and not the total distance, the energy stored in the SNSM represents more than two-thirds of the energy required to reach wintering areas.
study region during fall migration have, presumably, completed a long oversea crossing, as suggested by geolocator evidence (Hecksher et al. 2011). In the present study, the body mass of birds on first capture was generally at or near LBM (Fig. 3), which implies that birds had largely exhausted their energy reserves on arrival. The majority of birds (87%) recaptured at the site gained mass rapidly, and—on the basis of actual body masses (Fig. 3), predicted departure loads, and potential flight ranges (Table 4)—these gains involved more than just recovery after the overwater crossing. Indeed, for a bird with stopover duration of 9 days, the estimated gain was up to 34.5% of LBM, equivalent to an increase in potential flight range of 1,900 km.

The region occupied by the Veery in Brazil at the start of the “winter” (Remsen 2001, Hecksher et al. 2011; Fig. 1) is 3,000–4,500 km from the SNSM. The reserves accumulated at our study site could therefore be used to cover up to two-thirds of the journey during a series of nocturnal flights, whereas the remaining energy could potentially be accumulated during daytime stops en route, or by making one or more multiday stopovers. Geolocator evidence supports the latter hypothesis, demonstrating that Veeries generally make one or two additional stops in the Amazon basin (Hecksher et al. 2011). Some geolocator-tracked birds made shorter movements than predicted from our study site (expected ≈ 2,000 km; actual mean = 1,360 km; range: 600–1,820 km; n = 4), but one bird made a rapid movement of 1,750 km, close to our predicted flight ranges. Shorter movements are likely if birds stop before completely exhausting their reserves, especially when migrating over suitable stopover habitat or if additional reserves function as insurance against unfavorable conditions rather than to extend flight range.

Two lines of evidence suggest that our study site represents high-quality stopover habitat and could potentially support longer movements than those observed by Hecksher et al. (2011). First, our study area on the northern flank of the SNSM represents a humid enclave in a region largely dominated by dry habitats and agricultural land. Moister habitats are considered higher-quality for migrants (Marra and Holmes 2001, Sapir et al. 2004), and they can positively affect the outcome of migration (Norris et al. 2004). Secondly, the mean rate of energy deposition (3.6% LBM day−1) at our study site was high compared with other studies. For example, Yong and Moore (1997) recorded rates of approximately 0.8% LBM day−1 in Veeries, 1.8% in Gray-cheeked Thrushes (C. minimus), and 2.6% in Swainson’s Thrushes (C. ustulatus) on the Gulf Coast of North America. Bonter et al. (2007) recorded mean rates of <1% in recaptured Swainson’s and Gray-cheeked thrushes in Canada, whereas Schaub and Jenni (2000b) recorded rates between 0.1% LBM day−1 and 3.2% LBM day−1 in migrating warblers at several sites in Europe. Birds were regularly observed consuming fruit in our study area (N. Bayly pers. obs.), and abundant fruit resources may explain the rates achieved.

Geolocator-tracked Veeries showed considerable variation among individuals (Hecksher et al. 2011). Considered alongside our findings, this suggests that further work at a variety of stopover sites is required to determine to what extent differing habitat quality can affect the magnitude of energy stores and subsequent migratory strategies.

Assessing the energetic contribution of a stopover site to migration.—Our understanding of stopover-site use and our ability to quantify parameters associated with stopovers have improved considerably in the past 20 years, especially with the application of mark–recapture methods to the estimation of stopover durations (Schaub et al. 2001, Morris et al. 2005). Several different measures of stopover behavior have been used to compare stopover sites (Dunn 2000, 2002; Mehlman et al. 2005), but an overriding scheme allowing for an objective assessment of stopover-site use in terms of energy deposition remains elusive.

The method that we have described for modeling changes in body mass has advantages over widely used alternatives such as calculating fuel-deposition rates (FDR = change in body mass day−1; Yong and Moore 1997, Fransson 1998, Schaub and Jenni 2000b), which are appropriate when body-mass changes are linear in time but can result in errors when they are not—especially if recaptures are not evenly distributed in relation to the start of a stopover. By modeling mass change as a function of the number of days since first capture, we can describe mass-gain curves with greater precision and derive more reliable estimates of overall rates of change (Atkinson et al. 2007).

Another commonly used method is the estimation of hourly rates of mass gain based on the body-mass distribution of all individuals in relation to time of capture (Winker 1995, Dunn 2002, Johnson and Winker 2008). An advantage of this method is that it does not require recaptures, but its underlying assumptions may not always be met (Dunn 2002, Delingat et al. 2009). For example, in our study the temporal capture probability of “lean” versus “fat” birds was not the same and could bias hourly mass-gain estimates upward. When we applied this method to all first captures of Veeries, the estimated rate of change (9.4% LBM day−1) was 3× higher than our model rate for recaptured birds (3.6% LBM day−1) and was not supported by rates recorded in individual birds (Fig. 4). Other studies have reported overestimates (Delingat et al. 2009), as well as biologically infeasible rates (see rates >15% LBM day−1 in Bonter et al. 2007; see maximum rates for passerines in Lindström 2003). Overestimations may arise if changes in gut content are

![Figure 5. Relationship between departure body mass and potential flight range for Veeries as predicted by the program FLIGHT, version 1.22 (Pennycook 2008).](image-url)

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**Fig. 5.** Relationship between departure body mass and potential flight range for Veeries as predicted by the program FLIGHT, version 1.22 (Pennycook 2008).
interpreted as changes in energy stores; a bird’s gut will be empty after the overnight fast, and food intake at the initiation of foraging will increase mass. By only considering birds captured >2 h after sunrise, this method could still provide insights into fueling, particularly when recaptures are lacking.

We have presented three different estimates of stopover duration (Morris et al. 2005, Bayly and Rumsy 2007) because of the lack of consensus as to which is most appropriate (Efford 2005, Pradel et al. 2005). Here we favor our “total stopover” estimates, which receive strong support from the durations recorded in birds tracked with geolocators (Hecksher et al. 2011; mean stopover = 9.5 days, n = 4) and from the distribution of recaptures in time (Figs. 3 and 4). Although mark–recapture models have greatly improved our ability to estimate stopover durations, some assumptions that underlie them are not necessarily met by data sets of mist-net captures (Efford 2005, Pradel et al. 2005). For example, capture probability is unlikely to be constant during a stopover and most likely declines after each capture because birds learn the position of mist nets within a study area. Second, birds may move in and out of the capture area on release and, therefore, are not always available for sampling, despite being present at the study site (Calvert et al. 2010). If these issues could be resolved, “stopover after” estimates may be more appropriate because they have greater theoretical support according to Efford (2005).

We believe that the method introduced here for determining the importance of a site provides an important advance in our ability to directly compare and generate an objective prioritization of stopover sites used during midday stopovers. This method relies heavily on advances made by others in the modeling of body-mass changes (Atkinson et al. 2007), estimation of stopover durations (Schaub et al. 2001, Morris et al. 2005), and determination of flight ranges (Pennycuick 2008) and is essentially a suggestion of how these advances can be combined to create a framework for assessing the energetic contribution of a stopover site. At this stage it is important to apply the method to other sites and species, and we encourage others to test its utility.

An important advantage of this method is that it can be applied to standard data generated at mist-netting stations and to historical data sets that arise from the same. Further, it allows for direct comparison among regions and species. One disadvantage is that recapture rates in many species may not support the minimum sample-size requirements of the analyses presented here (Mehlman et al. 2005). We also accept that combining rate of mass-gain estimates with stopover estimates will generate cumulative errors that will be further augmented by errors in flight-range estimates. It is also important to note that energy reserves may have additional functions, such as generating water (Gerson and Guggielmo 2011). Finally, this method considers only how individuals use a stopover site, yet population-level estimates of use will be essential for a rigorous prioritization of stopover sites or regions.

In addition to introducing a method for prioritizing stopover sites according to their energetic importance, our results and other recent advances (González-Prieto et al. 2011, Hecksher et al. 2011) highlight the importance of northern Colombia as a stopover region for the Veery and demonstrate, for the first time, how stopover sites within South America may be used by Neotropical migrants to fuel southward movements exceeding 1,000 km. The energetic importance of our study site has conservation implications, especially considering that humid tropical lowland forest in the SNSM has been reduced by as much as 95% from its original extent (390,000 ha; FPSNSM 1998). Many other distinct habitat types exist within the SNSM and northern Colombia, ranging from tropical dry forest to humid montane forest, and it is important to determine their relative quality for the Veery and other Neotropical migrants in order to generate an effective prioritization of stopover sites in the region.

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