SPRING MIGRATORY STOPOVER OF SWAINSON'S THRUSH ALONG THE PACIFIC COAST OF SOUTHWEST COSTA RICA

SCOTT WILSON,[1,4] KEITH A. HOBSON,[2] DOUGLAS M. COLLISTER,[3] AND AMY G. WILSON[1]

ABSTRACT.—Stopover behavior and migratory pathways of neotropical migrant birds in Central and South America have received little study. We examined stopover ecology of Swainson's Thrush (*Catharus ustulatus*) on the Osa Peninsula, Costa Rica, during spring migration, 2002–2005. Capture rates per net hour were high ($\bar{x}$ = 21.8 individuals/100 net hrs) suggesting large numbers pass through lowland coastal areas in spring. Mean passage date of males was ~6 days earlier than females. Timing of passage by age class was variable; after-second year (ASY) birds preceded second-year (SY) birds in 2 years, SYs preceded ASYs in 1 year, and both had the same mean passage date in 1 year. We also observed annual variation in relative abundance of the two age groups. Only 1.7% of marked Swainson's Thrushes were recaptured on subsequent days suggesting most individuals left the immediate area soon after initial capture. Stopover lengths ranged from 1 to 9 days, although most were <4 days. Many individuals had some energy stores on arrival (fat score ≥ 1) but reserves varied between years and tended to be lower in SYs compared to ASYs. Regression of body mass against time of day indicated that individuals tended to gain mass throughout the morning (0.67% of lean body mass/hr on average). Our findings for stopover lengths, rates of mass gain, and recapture rates are within the range observed at North American stopover sites in spring. However, our capture rates were relatively higher, perhaps because the small land mass of southern Central America concentrates individuals at stopover sites in these regions. *Received 26 September 2006. Accepted 31 March 2007.*

Annual movements between breeding and wintering areas allow neotropical migrant songbirds to benefit from the seasonal flush of food in temperate breeding areas, while enhancing survival by wintering in the tropics (Greenberg 1980). However, long-distance migration is energetically expensive and reserves required to traverse these distances may exceed the amount individuals can store (Alerstam and Lindström 1990, Schaub and Jenni 2000a). Thus, migrants need to stopover *en route* where they must forage quickly in unfamiliar habitats (Moore and Aborn 2000, Petit 2000) while coping with weather (Rappole and Warner 1976, Richardson 1978), predators (Lindström 1990), and other individuals competing for the same resources (Moore and Wang 1991). Failure to meet these demands may be costly. Most annual mortality for migrant songbirds may occur during migration even though these periods only rep-

resent ~25% of the annual cycle (Sillett and Holmes 2002). An individual's inability to refuel quickly at stopover sites can also lower fitness through delayed arrival in breeding areas and a subsequent reduction in breeding success (Marra et al. 1998, Smith and Moore 2005).

Nearly all studies of spring stopover of neotropical migrants have been conducted in North America, representing the latter half of the migration for most species. Little is known about migratory behavior and stopover ecology during the early stages of spring migration in tropical areas of Central and South America. Central America has a small landmass relative to North America and, for some species that breed across the boreal forest and winter in South America, the entire breeding population may pass through a narrow geographic corridor during migration. Even minor disturbances to stopover sites in these areas could have implications for population dynamics (Newton 2006). Deforestation and habitat disturbance have been extensive throughout much of Central America and are expected to continue (Achard et al. 2002). Thus, it is important to further our understanding of migratory routes and stopover areas used by neotropical migrants throughout sites in the tropics.

[1] Center for Applied Conservation Research, 2424 Main Mall, University of British Columbia, Vancouver, BC, V6T 1Z4, Canada.

[2] Environment Canada, 11 Innovation Boulevard, Saskatoon, SK, S7N 3H5, Canada.

[3] Calgary Bird Banding Society, 247 Parkside Crescent SE, Calgary, AB, T2J 4J3, Canada.

[4] Corresponding author; e-mail: wilsonwa@interchange.ubc.ca

We examined migratory timing and stopover behavior of Swainson's Thrush (*Catharus ustulatus*) at a site on the Osa Peninsula, Costa Rica. The Swainson's Thrush is a neotropical migrant that breeds across the boreal forest, western mountain regions, and Pacific coast of North America. Coastal breeding populations winter in southern Mexico and northern Central America, while continental breeding populations primarily winter in western South America (Mack and Wang 2000, Ruegg and Smith 2002). Swainson's Thrush is a common migrant in Pacific coast regions of southwestern Costa Rica in spring (Stiles and Skutch 1995), and we previously showed that individuals passing through these regions likely breed in areas of the west-central boreal forest and interior western mountains of North America (Wilson et al. 2008). Our specific objectives in the present study were to examine: (1) capture rates over time, (2) differences in migratory timing between age and gender classes, and (3) stopover length, recapture rates, and rates of mass gain.

METHODS

Study Area.—The study was conducted on the northwest tip of the Osa Peninsula, Costa Rica, during spring migration 2002–2005. Our study area (08° 41′ N, 83° 38′ W) was 3 ha in size ~10 km north of Corcovado National Park. Annual mean temperatures on the Osa Peninsula are 27° C and precipitation is 550 cm with dry and wet seasons occurring in December–April and May–November, respectively (Holdridge 1967). Habitat in the region consists of tropical wet and premontane forest (Sanchez-Azofeifa et al. 2002). The immediate study area was mostly secondary forest, 15–25 years of age, with larger stands of primary forest along the eastern and southern edges. There were two small open areas (~30 by 30 m) within the 3-ha plot. This is typical of habitat structure along coastal areas outside Corcovado National Park, where settlement has led to fragmentation and patches of younger-age forests. Much of the habitat adjacent to our site was secondary forest, particularly along the coast in both directions. The habitat beyond our site towards the interior of the peninsula was a mixture of primary and secondary forest with some cleared areas for agriculture (Sanchez-Azofeifa et al. 2002). Common tree species included *Spondias monbin*, *Hyeronima alchorneoides*, *Elaeis oleifera*, *Socratera exorrhiza*, and *Ochroma pyramidale*; common understory shrubs, vines, and small trees included *Apebia tiboubou*, *Heliconia* spp., *Vosychia* spp., *Philodendron* spp., and *Piper* spp.

Capture Methods.—The site was operated from late March through April annually. We captured individuals using 12–15 mist nets (3-tier, 12-m length, 30-mm mesh) that were opened at dawn and operated for ~6 hrs. Nets were evenly spaced throughout the study area and mostly within or on the edge of secondary forest habitats. A few were just inside primary forest at the edge of the study area. We made minor adjustments to the location of some net lanes between years because of slight changes in land use. These changes did not influence our survey effort and we do not believe they influenced our results. Individuals captured were banded with a numbered USGS aluminum band and classified to age where possible as second year (SY) or after-second year (ASY) based on plumage, feather shape and wear, and wing morphology (Pyle 1997). We also recorded date and time of capture, wing chord, body mass, and fat score (Helms and Drury 1960). We measured all individuals recaptured on subsequent days but only recorded time of capture for those recaptured on the same day. Plumage examination indicated that Swainson's Thrushes captured were from continental populations (olive-backed group) that breed across the boreal forest and interior western mountains (Mack and Wang 2000, Ruegg and Smith 2002). The Swainson's Thrush is sexually monomorpic and individuals were genetically assigned to gender following Griffiths et al. (1998) and Wilson et al. (2008). The Swainson's Thrush is a rare winter resident in the area (Stiles and Skutch 1995) and a separate study failed to capture any individuals during three 8-day periods from early December to early March 2005–2006 (D. M. Collister, unpubl. data). Thus, nearly all individuals captured were likely passage migrants.

Statistical Analyses.—Swainson's Thrushes primarily migrated through the site between late March and late April (Wilson et al. 2008). We used only 2004 and 2005 data for some analyses because data from 2002 and 2003

TABLE 1.   Timing of study, effort, and capture data for Swainson's Thrushes on the Osa Peninsula, Costa Rica.

Year	Dates	Net hrs	Individuals captured	Individuals recaptured (subsequent days)
2002	17 Mar–12 Apr[a]	2,041	439	
2003	15 Apr–10 May	2,123	404	10 (2.5%)
2004	28 Mar–29 Apr	2,468	546	9 (1.6%)
2005	30 Mar–29 Apr	2,213	540	7 (1.3%)

[a] We did not band all Swainson's Thrushes in 2002 and did not estimate recapture rates for that year. A small number of the 439 captures in 2002 were likely recaptures.

were outside the late March–late April period. We used general linear models (GLM) to compare timing of migration by age and gender, and we present means with standard error for most measures. Energetic condition was compared using fat scores (Helms and Drury 1960) and residuals from a regression of mass against wing length. We used mass-wing residuals rather than deviation from the average mass because an individual's size will affect mass, and wing length is a useful way to standardize for size (Schulte-Hostedde et al. 2005). Examination of mass-wing length residuals indicated a linear relationship and no tendency for body size to influence energetic condition (Schulte-Hostedde et al. 2005). We also report fat scores for comparison with other studies but did not conduct analyses using these scores because they are a subjective measure.

We estimated stopover length by calculating minimum stopover duration where the individual's date of first capture was subtracted from the last date recaptured (Cherry 1982). This method is conservative because it does not incorporate time the bird spent at the site before first capture or after last capture. We also used open population capture-recapture models (Schaub et al. 2001). This approach uses Cormack-Jolly-Seber models to estimate the likelihood of capture for an individual present at the site and recruitment analyses to estimate probability of arrival in the study area prior to capture. Parameter estimation using this method is limited when recapture sample sizes are small, as was the case in our study. We used the multiple day constancy method of Morris et al. (2005) which holds parameters fixed across days reducing the number of parameters that need to be estimated without pooling data.

We calculated change in mass of recaptured individuals by subtracting the mass at first capture from mass at final capture. This value was divided by the stopover duration to calculate change in mass per day. We also estimated rates of mass gain by regressing mass against time of capture for all individuals because recaptured individuals may not be a random sample of the entire population (Winker et al. 1992, Dunn 2001). We included wing length in the model to control for effects of size on mass gain. The regression coefficient for time of capture represents the average change in mass per minute. We used the mass versus time of capture regression equation to estimate the expected rate of mass gain for an individual of average wing length over the 6-hr period since sunrise. Statistical analyses were conducted using the R Statistical Language and Environment package (R Development Core Team 2006).

RESULTS

Capture Rates and Migration Timing.—We captured 1,931 Swainson's Thrushes over the 4-year study. These numbers equated to 19.1, 22.1, and 24.4 Swainson's Thrushes/100 net hrs for each year, 2003–2005, respectively (Table 1). We did not band all individuals in 2002 and could not estimate recaptures. However, based on recapture rates from the other 3 years, we likely captured ~21 individuals/100 net hrs in 2002. The lower numbers in 2002 and 2003 are likely because banding did not encompass the full migratory period of Swainson's Thrushes. Data from 2002 and 2003 indicated most individuals passed through the site between late March and late April. In 2002, banding extended from 17 March to 12 April, but only 7 and 17% of individuals were caught prior to 28 March and
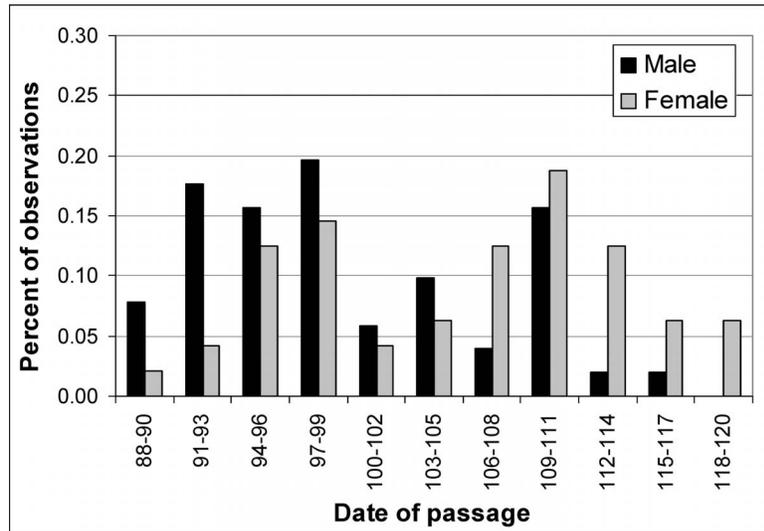
FIG. 1.   Timing of spring migration of male and female Swainson's Thrushes through the Osa Peninsula, Costa Rica, in 2004 (males = 51, females = 48). Date of passage refers to Julian day with 1 Apr = 92.

30 March (start dates for 2004 and 2005), respectively. In 2003, banding was conducted from 15 April to 10 May but only 4% of individuals were caught after 29 April (end date for 2004 and 2005). We may have missed some birds, especially early in migration but our data for 2004 (28 Mar–29 Apr) and 2005 (30 Mar–29 Apr) likely represent ~80–90% of the individuals passing through the site (Fig. 1). Recapture rates during 2003–2005 were low with 10 (2.5%), 9 (1.65%), and 7 (1.3%) individuals caught on subsequent days in each year, respectively. There were no year to year recaptures.

The mean passage date of males in 2004 was ~6 days earlier than for females (males: 98 ± 1.0 (mean Julian day $\pm$ SE), $n = 51$; females: 104 ± 1.2, $n = 48$). We also examined passage date through the site with all known-age birds in 2004 and 2005. In 2004, 46% of birds captured were SY, 27% were ASY, and 27% were of unknown age. The mean passage date of ASYs (103 ± 0.6, $n = 149$) was ~3 days earlier than SYs (106 ± 0.5, $n = 249$) in 2004. Passage dates were earliest for ASY males, intermediate for SY males and ASY females, and latest for SY females for birds of known age and gender (Fig. 1). More individuals captured in 2005 were SY (84%) versus ASY (11%) but there was little difference in timing of passage between

the two groups (ASY: 103 ± 0.9, $n = 59$; SY: 103 ± 0.4, $n = 459$). We only attempted to classify age of 167 of 439 individuals captured in 2002. Of these, 49% were SYs, 31% were ASYs, and 20% could not be classified to age. SY's within the shortened 2002 period passed through on average 1 day earlier than ASYs (SY: 92 ± 0.6, $n = 82$; ASY: 93 ± 0.9, $n = 51$). Of 404 individuals in 2003, 73% were SYs, 13% were ASYs, and 14% could not be classified to age. ASY's preceded SYs by 2 days on average in 2003 (SY: 111 ± 0.3, $n = 295$; ASY: 109 ± 0.6, $n = 54$). Estimates should only be compared within years because the data do not cover the same periods each year.

Stopover Length and Mass Gain.—Mean minimum stopover lengths ranged from 1 to 9 days with a mean of 3.2 days ($n = 9$) in 2004 and 2.3 days ($n = 7$) in 2005. The distribution tended to be skewed as 14 of 16 individuals had stopover lengths of 1–4 days while two stayed for 6 and 9 days. The median minimum stopover length was 2 days in both years. Stopover lengths estimated by the multiple day constancy (MDC) method were 4.0 ± 3.9 days (mean $\pm$ SD) in 2004 and 1.2 ± 0.7 days in 2005. The minimum stopover duration and MDC capture-recapture methods produced similar results with the capture-recapture method estimating slightly longer

TABLE 2. Regression coefficients for equation of mass against wing chord and time of capture for Swainson's Thrushes on the Osa Peninsula, Costa Rica. Standard errors are in parentheses. Time represents average change in mass (grams) per minute.

Class	n	Intercept	Wing chord	Time
All birds	1,042	1.096 (2.10)	0.278 (0.022)	0.003 (0.0007)
ASY	201	0.924 (4.72)	0.283 (0.048)	0.0018 (0.0017)
SY	675	−1.153 (2.73)	0.302 (0.029)	0.0036 (0.0009)

stopovers in 2004 and shorter stopovers in 2005. We did not compare stopover length by age and gender because of the low number of recaptures.

Regression equations for body mass against wing chord and time of capture indicated a significant influence of both wing and time since sunrise on body mass ($R^2 = 0.15$, $F_{2,1039} = 92.65$, $t_{wing} = 12.89$, $P_{wing} < 0.001$, $t_{time} = 4.79$, $P_{time} < 0.001$, Table 2). We predicted from the regression equation that an average-sized individual (mean wing = 95.7 mm) would add about 1.08 grams over the 6-hr period from sunrise equating to 0.18 g/hr. This estimate would be ~0.67% of lean body mass/hr using the average mass for individuals with a fat score of 0. We examined age effects on rates of body mass gain by regressing mass against time of capture for SYs and ASYs separately. The equation for SYs revealed a significant effect of wing length and time since sunrise on mass ($R^2 = 0.16$, $\beta_{wing} = 0.30$ (SE = 0.03), $P_{wing} < 0.001$, $\beta_{time} = 0.004$ (SE = 0.001), $P_{time} < 0.001$). We predict an average-sized SY individual with a mean wing length of 95.3 mm would add 1.3 g over the 6-hr morning period. Wing chord for ASYs had a significant effect but time since sunrise did not although the coefficient was positive ($R^2 = 0.15$, $\beta_{wing} = 0.28$ (SE = 0.05), $P_{wing} < 0.001$, $\beta_{time} = 0.002$ (SE = 0.002), $P_{time} = 0.284$).

Analysis of fat reserves at time of banding revealed that most individuals had some fat (72.5% of individuals had a fat score ≥1, Fig. 2). There was a tendency for ASYs to have higher fat scores than SYs and higher fat scores in 2004 than 2005 for both groups. Measures of energetic condition from residuals of a mass-wing regression did not reveal distinct differences by age or gender and there was variability within classes. Residual estimates for each group were [mean ± SE (n)]

ASY male: 0.43 ± 0.51 g (14), SY male: 0.44 ± 0.44 g (21), ASY female: −0.06 ± 0.49 g (14), SY: female −0.10 ± 0.32 g (25). Recaptured and non-recaptured individuals had similar fat scores (mean ± SE) (recapture = 1.4 ± 0.35, non-recapture = 1.5 ± 0.05). Analyses of mass change from recaptured birds revealed variability among individuals. Seven of 15 individuals in 2004 and 2005 lost mass during the stopover (average loss = 0.6 g/day) while 8 gained mass (average gain = 0.3 g/day). The average mass change based on these individuals was lower than predicted by regressing mass against time of capture using all birds.

DISCUSSION

Captures.—Swainson's Thrushes were common spring migrants at a stopover site along the Osa Peninsula, Costa Rica. This species is a rare winter resident in the region and all individuals captured were likely passage migrants. Individuals from South American wintering areas likely reached the study site by following the Panama isthmus or via an ocean crossing from Colombia making landfall between the Azuero Peninsula of Panama and the Osa Peninsula of Costa Rica (Wilson et al. 2008). Swainson's Thrushes are also common spring migrants along the Caribbean coast of Central America (Galindo et al. 1963, Ridgely and Gwynne 1989, Ralph et al. 2005). Most continental birds enter North America along the Gulf coast (Rappole and Warner 1976; Wang and Moore 1993, 1997) before moving to breeding locations across the boreal forest and mountainous areas from Alaska to eastern Canada and the northeastern United States (Mack and Wang 2000, Ruegg and Smith 2002).

Swainson's Thrush capture rates averaged 20–25 individuals/100 net hrs and are among the highest reported for this species in spring.
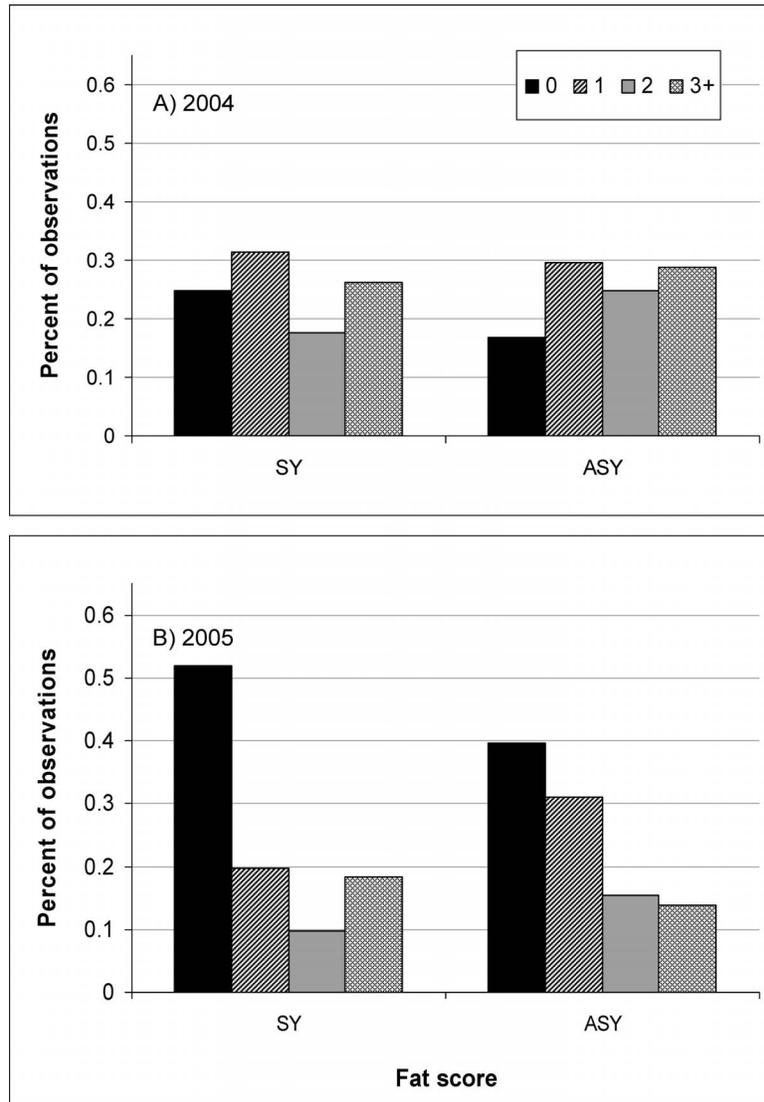
FIG. 2. Fat scores for second year (SY) and after-second year (ASY) Swainson's Thrushes on the Osa Peninsula, Costa Rica, in (A) 2004 (SY = 249, ASY = 149) and (B) 2005 (SY = 450, ASY = 58).

Spring capture rates along the northern Gulf coast of Mexico for four thrush species combined were ~8–10 individuals/100 net hrs; Swainson's Thrushes accounted for about 36% of those captures (Wang and Moore 1997). Elsewhere, spring capture rates of Swainson's Thrushes (individuals/100 net hrs) were 0.49 in Minnesota (Winker et al. 1989), 1.5 in southern Alberta (Collister et al. 2005), and 2.35 in South Dakota (Swanson et al. 2003). At Almirante on the Caribbean coast

of Panama, 365 Swainson's Thrushes were captured during netting in April 1963 (net hrs not available, Galindo et al. 1963), slightly lower than numbers caught in April at our site. Caution is required when inferring abundance from capture rates of mist-net studies because of differences in methodology, effort, dates of study, and habitat (Remsen and Good 1996). Mist-netting studies may also be biased against larger species and those that primarily inhabit the canopy and subcanopy layers

(Blake and Loiselle 2001). Swainson's Thrushes primarily forage in lower forest levels (Mack and Wang 2000) and were usually observed in the understory at our site. Thus, mist-net captures likely provide an accurate index of abundance for this species. The high number of captures in our study relative to North American sites may have been due to the small landmass of southern Central America, which likely concentrates individuals during migration.

Migration Timing.—Males passed through the site ~6 days earlier than females in 2004 with mean passage dates of 6 April and 12 April, respectively. Few studies have examined gender differences in migratory timing of *Catharus* thrushes because they are sexually monomorphic and require genetic techniques to accurately ascertain gender. Wing lengths of migrating thrushes along the Gulf coast in spring declined over time, suggesting earlier passage of larger males (Wang and Moore 1997). A similar pattern was noted among Swainson's Thrushes at a spring stopover site in Minnesota (Winker et al. 1989). Gender-specific spring migration patterns are frequently reported in sexually dimorphic species (Francis and Cooke 1986, Wang et al. 1998, Swanson et al. 1999). Mean passage date of male Northern Wheatears (*Oenanthe oenanthe leucorhoa*) in Scandinavia was 5 days earlier than females (Dierschke et al. 2005) while on Appledore Island, Maine, male American Redstarts (*Setophaga ruticilla*) and Common Yellowthroats (*Geothlypis trichas*) preceded females by 2 and 5 days, respectively (Morris and Glasgow 2001, Morris et al. 2003).

Earlier spring passage of males is likely related to male-male competition in breeding areas and the need for males to establish territories prior to arrival of females (Lack 1954). Earlier passage of males through stopover sites could be due to: (1) earlier departure from wintering areas (Marra et al. 1998), (2) faster migration rates (Swanson et al. 1999), or (3) more northerly wintering areas and a shorter distance to stopover sites (Chandler and Mulvihill 1990). Although our site was relatively close to wintering areas, differences between males and females were similar to patterns from other species at North American stopover sites. This might suggest that earlier passage of males was due to earlier departure

and/or more northern wintering areas, although it is still possible that males travel more quickly than females in spring.

We found mixed results for age-specific timing of migration. Using all known-age individuals, ASYs preceded SYs by about 3 days in 2004 but the two groups had similar mean passage dates in 2005. Within the shortened study periods in the first 2 years, SYs preceded ASYs by 1 day in 2002 and ASYs preceded SYs by 2 days in 2003. However, these data were based on all known-age birds and, given gender-specific differences in passage date, it is difficult to interpret timing by age group when males and females are pooled. Furthermore, there tended to be more unknown age individuals at the start of the season, which may not have been equally representative of both age groups. Although the sample size was smaller, our data for individuals of known age and gender in 2004 may be most informative and indicated that ASY males passed through earliest, SY males and ASY females were intermediate, and SY females were the latest to arrive. This is consistent with earlier migration by males and a tendency for older birds to precede first-year birds (Francis and Cooke 1986, Stewart et al. 2002). We are uncertain why there was annual variation in age ratios. There was a relatively higher proportion of ASYs in 2002 and 2004 than in 2003 and 2005. Annual variation in the abundance of age groups at stopover sites may be due to greater productivity the previous spring, age-specific differences in survival, or variability in the routes or stopovers sites used by different age groups (Ralph 1981, Wang et al. 1998, Dean et al. 2004). Changes in study design or survey effort may also influence age ratios at stopover sites (Kelly and Finch 2000). Our data from 2002 and 2004 included a higher number of individuals from the early migratory period which, if there was a tendency for older birds to move earlier, may explain the higher proportion of ASYs captured in those years. Further research on variation in the abundance and timing of passage by age class at other tropical stopover sites would be useful.

Stopover Ecology.—Only 26 of 1,490 individuals (1.7%) captured in 2003 to 2005 were recaptured on subsequent days suggesting the majority of individuals moved from

the study area soon after capture. Spring recapture rates were similar to those from the St. Croix River Valley, Minnesota (1.2%, Winker et al. 1989) but were lower than rates observed elsewhere. Recapture rates were 9 and 7% from two separate studies along the northern Gulf coast (Kuenzi et al. 1991, Wang and Moore 1997), 5.7% along coastal regions of south Texas (Rappole and Warner 1976), and 5.2% along the Caribbean coast of Panama (Galindo et al. 1963).

One reason for the low recapture rate at our study site may have been that it was small (3 ha) with extensive areas of similar nearby habitat. Thus, individuals may continue to move through these habitats without returning to the study site. Recapture rates may be higher at sites that are spread over a wider region increasing the likelihood of capturing individuals that wander but remain within the general area. Galindo et al. (1963), on the Caribbean coast of Panama, surveyed four plots over a 25.9 km² area and recorded higher recapture rates. Cochran and Wikelski (2005), using radio-telemetry, found that Swainson's Thrushes at stopover sites in Illinois established small foraging areas of ~100 m in diameter and remained in that area until the next flight. However, the large number of individuals at our site may have influenced how many remained in the area (Moore and Wang 1991, Wang et al. 1998). Differences in food abundance between locations may also lead to variation in stopover behavior and recapture rates (e.g., Petit 2000).

Individuals may also be less likely to remain at stopover sites if they have sufficient reserves to continue on migration. Stopover length is often negatively related to energetic condition (Moore and Kerlinger 1987, Cochran and Wikelski 2005). Experimental studies have found that, following a trans-Gulf crossing, individuals with greater energetic reserves have higher migratory restlessness than those in poor condition (Wang and Moore 1993, but see Smith and Norment 2005). Multi-day stopovers may be necessary if all fat reserves are depleted, as is often the case along the gulf coast (e.g., Kuenzi et al. 1991). Many individuals in our study had fat scores ≥ 1 and gained mass through the morning, which combined may provide sufficient reserves to continue on that night. Migrants at

stopover sites in Costa Rica would also not cross a major geographic barrier until they reached the Gulf of Mexico and it may not be necessary to build reserves beyond what is required for a few hours of flight (e.g., Schaub and Jenni 2000b, Rubolini et al. 2002). Individuals that did stopover typically remained for ~1 to 4 days, similar to lengths observed for this species in temperate areas further north (Winker et al. 1989, Wang and Moore 1997).

Rates of mass gain through the morning averaged ~0.18 g/hr, which equates to 0.67% of the lean body mass (average mass of individuals with no visible fat) (Dunn (2002). This is similar to the pooled estimates for spring migrants across Canada (0.40% of lean body mass), although rates for Swainson's Thrushes in that study were low (average = −0.06% of lean body mass/hr, Dunn 2001, 2002). Daily mass gain for Swainson's Thrushes in Minnesota (Winker et al. 1989) was ~4.08 g/day in spring, slightly higher than our data. Variation in rates of mass gain among sites could be due to differences in food availability (Dunn 2001) or whether migrants are using a site for other purposes such as to rest or rehydrate (Kuenzi et al. 1991).

Entire populations of some neotropical migrant species may pass through a narrow geographic corridor during early stages of spring migration because of the small landmass of southern Central America. Habitat disturbance in these regions could negatively impact populations of these species (Sillett and Holmes 2002, Newton 2006). We know little about migratory routes, habitat requirements, and stopover behavior of neotropical migrants in tropical regions. Our study revealed that Swainson's Thrush use lowland habitats along Costa Rica's Pacific coast in spring; high numbers relative to North American sites indicate thrushes are particularly concentrated during this period. Recapture rates, stopover lengths, and rates of mass gain were similar to those in temperate areas suggesting these behaviors may be consistent across the spring migratory period. Studies that use a combination of mist netting and counts in high and low elevation habitats of southern Central America would further our knowledge of stopover ecology of neotropical migrant songbirds within the tropics.

LITERATURE CITED

ACHARD, F., H. D. EVA, H. J. STIBIG, P. MAYAUX, J. GALLEGO, T. RICHARDS, AND J. P. MALINGREAU. 2002. Determination of deforestation rates of the world's humid tropical forests. Science 297:999–1002.

ALERSTAM, T. AND Å. LINDSTRÖM. 1990. Optimal bird migration: the relative importance of time, energy and safety. Pages 331–351 *in* Bird migration: physiology and ecophysiology (E. Gwinner, Editor). Springer-Verlag, Berlin, Germany.

BLAKE, J. G. AND B. A. LOISELLE. 2001. Bird assemblages in second growth and old-growth forests, Costa Rica: perspectives from mist nets and point counts. Auk 118:304–326.

CHANDLER, C. R. AND R. S. MULVIHILL. 1990. Interpreting differential timing of capture of sex classes during spring migration. Journal of Field Ornithology 61:85–89.

CHERRY, J. D. 1982. Fat deposition and length of stopover of migrant White-crowned Sparrows. Auk 99:725–732.

COCHRAN, W. W. AND M. WIKELSKI. 2005. Individual migratory tactics of New World *Catharus* thrushes: current knowledge and future tracking options from space. Pages 274–289 *in* Birds of two worlds (R. Greenberg and P. P. Marra, Editors) Johns Hopkins University Press, Baltimore, Maryland, USA.

COLLISTER, D. M., R. D. DICKSON, AND G. SMILEY. 2005. 2004 Calgary Bird Banding Society Annual Technical Report. Calgary, Alberta, Canada.

DEAN, K. L., H. A. CARLISLE, AND D. L. SWANSON. 2004. Age structure of neotropical migrants during fall migration in South Dakota: is the northern Great Plains region an inland ''coast''? Wilson Bulletin 116:295–303.

DIERSCHKE, V., B. MENDEL, AND H. SCHMALJOHANN. 2005. Differential timing of spring migration in northern wheatears *Oenanthe oenanthe*: hurried males or weak females? Behavioral Ecology and Sociobiology 57:470–480.

DUNN, E. H. 2001. Mass change during migration stopover: a comparison of species groups and sites. Journal of Field Ornithology 72:419–432.

DUNN, E. H. 2002. A cross-Canada comparison of mass change in birds during migration stopover. Wilson Bulletin 114:368–379.

FRANCIS, C. M. AND F. COOKE. 1986. Differential timing of spring migration in wood warblers (Parulinae). Auk 103:548–556.

GALINDO, P., E. MENDEZ, AND A. J. ADAMES. 1963. Banding of migrant thrushes in Almirante, Panama. Bird Banding 34:202–209.

GREENBERG, R. 1980. Demographic aspects of long-distance migration. Pages 493–516 *in* Migrants in the Neotropics: ecology, behavior, distribution and conservation (A. Keast and E. S. Morton, Editors). Smithsonian Institution Press, Washington, D.C., USA.

GRIFFITHS, R., M. C. DOUBLE, K. ORR, AND R. J. G. DAWSON. 1998. A DNA test to sex most birds. Molecular Ecology 7:1071–1075.

HELMS, C. W. AND W. H. DRURY. 1960. Winter and migratory weight and fat: field studies on some North American buntings. Bird-Banding 31:1–40.

HOLDRIDGE, L. R. 1967. Life zone ecology. Tropical Science Center, San José, Costa Rica.

KELLY, J. F. AND D. M. FINCH. 2000. Effects of sampling design on age ratios of migrants captured at stopover sites. Condor 102:699–702.

KUENZI, A. J., F. R. MOORE, AND T. R. SIMONS. 1991. Stopover of neotropical landbird migrants on East Ship Island following Trans-Gulf migration. Condor 93:869–883.

LACK, D. 1954. The natural regulation of animal numbers. Oxford University Press, London, United Kingdom.

LINDSTRÖM, Å. 1990. The role of predation risk in stopover habitat selection in migrating Bramblings *Fringilla montifringilla*. Behavioral Ecology 1:102–106.

MACK, D. E. AND Y. WANG. 2000. Swainson's Thrush (*Catharus ustulatus*). The birds of North America. Number 540.

MARRA, P. P., K. A. HOBSON, AND R. T. HOLMES. 1998. Linking winter and summer events in a migratory bird by using stable-carbon isotopes. Science 282:1884–1886.

MOORE, F. R. AND D. A. ABORN. 2000. Mechanism of *en route* habitat selection: how do migrants make habitat decisions during stopover? Studies in Avian Biology 20:34–42.

MOORE, F. R. AND P. KERLINGER. 1987. Stopover and fat deposition by North American wood warblers (Parulinae) following spring migration over the Gulf of Mexico. Oecologia 74:47–54.

MOORE, F. R. AND Y. WANG. 1991. Evidence of food-based competition during migratory stopover. Behavioral Ecology and Sociobiology 28:85–90.

MORRIS, S. R. AND J. L. GLASGOW. 2001. Comparison of spring and fall migration of American Redstarts on Appledore Island, Maine. Wilson Bulletin 113: 202–210.

MORRIS, S. R., C. R. PUSATERI, AND K. A. BATTAGLIA. 2003. Spring migration and stopover ecology of Common Yellowthroats on Appledore Island, Maine. Wilson Bulletin 115:64–72.

MORRIS, S. R., D. A. LIEBNER, A. M. LARRACUENTE, E. M. ESCAMILLA, AND H. D. SHEETS. 2005. Multiple day constancy as an alternative to pooling for estimating mark-recapture stopover length in Nearctic-neotropical migrant landbirds. Auk 122:319–328.

NEWTON, I. 2006. Can conditions experienced during migration limit the population levels of birds? Journal of Ornithology 147:146–166.

PETIT, D. R. 2000. Habitat use by landbirds along Nearctic-neotropical migration routes: implications for conservation of stopover habitats. Studies in Avian Biology 20:15–33.

PYLE, P. 1997. Identification guide to North American birds. Part I. Slate Creek Press, Bolinas, California, USA.

R DEVELOPMENT CORE TEAM. 2006. R: a language and environment for statistical computing, reference index version 2.3.1. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org (accessed 24 February 2007).

RALPH, C. J. 1981. Age ratios and their possible use in determining autumn routes of migrant passerines. Wilson Bulletin 93:164–188.

RALPH, C. J., M. J. WIDDOWSON, R. I. FREY, P. A. HERRERA, AND B. P. O'DONNELL. 2005. An overview of a landbird monitoring program at Tortuguero, on the Caribbean coast of Costa Rica. USDA, Forest Service, General Technical Report PSW-GTR-191. Albany, California, USA.

RAPPOLE, J. H. AND D. W. WARNER. 1976. Relationships between behavior, physiology and weather in avian transients at a migration stopover site. Oecologia 26:193–212.

REMSEN, J. V. AND D. A. GOOD. 1996. Misuse of data from mistnet captures to assess relative abundance in bird populations. Auk 113:381–398.

RICHARDSON, W. J. 1978. Timing and amount of bird migration in relation to weather: a review. Oikos 30:224–272.

RIDGELY, R. S. AND J. A. GWYNNE. 1989. A guide to the birds of Panama. Princeton University Press, Princeton, New Jersey, USA.

RUBOLINI, D., A. G. PASTOR, A. PILASTRO, AND F. SPINA. 2002. Ecological barriers shaping fuel stores in Barn Swallows *Hirundo rustica* following the central and western Mediterranean flyways. Journal of Avian Biology 33:15–22.

RUEGG, K. C. AND T. B. SMITH. 2002. Not as the crow flies: a historical explanation for circuitous migration in Swainson's Thrush (*Catharus ustulatus*). Proceedings of the Royal Society of London Series B 269:1375–1381.

SANCHEZ-AZOFEIFA, G. A., B. RIVARD, J. CALVO, AND I. MOORTHY. 2002. Dynamics of tropical deforestation around national parks: remote sensing of forest change on the Osa Peninsula of Costa Rica. Mountain Research and Development 22:352–358.

SCHAUB, M. AND L. JENNI. 2000a. Body mass of six long-distance migrant passerine species along the autumn migration route. Journal für Ornithologie 141:441–460.

SCHAUB, M. AND L. JENNI. 2000b. Fuel deposition of three passerine bird species along the migration route. Oecologia 122:306–317.

SCHAUB, M., R. PRADEL, L. JENNI, AND J. D. LEBRETON. 2001. Migrating birds stopover longer than usually thought: an improved capture-recapture analysis. Ecology 82:852–859.

SCHULTE-HOSTEDDE, A. I., B. ZINNER, J. S. MILLAR, AND G. J. HICKLING. 2005. Restitution of mass-size residuals: validating body condition indices. Ecology 86:155–163.

SILLETT, T. S. AND R. T. HOLMES. 2002. Variation in survivorship of a migratory songbird throughout its annual cycle. Journal of Animal Ecology 71:296–308.

SMITH, R. J. AND F. R. MOORE. 2005. Arrival timing and seasonal reproductive performance in a long-distance migratory landbird. Behavioral Ecology and Sociobiology 57:231–239.

SMITH, S. B. AND C. J. NORMENT. 2005. Nocturnal activity and energetic condition of spring landbird migrants at Braddock Bay, Lake Ontario. Journal of Field Ornithology 76:303–310.

STEWART, R. L. M., C. M. FRANCIS, AND C. MASSEY. 2002. Age related timing of spring migration within sexes in passerines. Wilson Bulletin 114:264–271.

STILES, F. G. AND A. F. SKUTCH. 1995. A guide to the birds of Costa Rica. Cornell University Press, Ithaca, New York, USA.

SWANSON, D. L., H. A. CARLISLE, AND E. T. LIKNES. 2003. Abundance and richness of neotropical migrants during stopover at farmstead woodlots and associated habitats in southeastern South Dakota. American Midland Naturalist 149:176–191.

SWANSON, D. L., E. T. LIKNES, AND K. L. DEAN. 1999. Differences in migratory timing and energetic condition among sex/age classes in migrant Ruby-crowned Kinglets. Wilson Bulletin 111:61–69.

WANG, Y. AND F. R. MOORE. 1993. Relation between migratory activity and energetic condition among thrushes (Turdinae) following passage across the Gulf of Mexico. Condor 95:934–943.

WANG, Y. AND F. R. MOORE. 1997. Spring stopover of intercontinental migratory thrushes along the northern coast of the Gulf of Mexico. Auk 114:263–278.

WANG, Y., D. M. FINCH, F. R. MOORE, AND J. F. KELLY. 1998. Stopover ecology and habitat use of migratory Wilson's Warblers. Auk 115:829–842.

WILSON, S., K. A. HOBSON, D. M. COLLISTER, AND A. G. WILSON. 2008. Breeding destinations and

spring migration patterns of Swainson's Thrush at a Costa Rican stopover site. Auk 125: In Press.

WINKER, K., D. W. WARNER, AND A. R. WIESBROD. 1989. The Northern Waterthrush and Swainson's Thrush as transients at a temperate inland stopover site. Pages 384–404 *in* Ecology and conservation of neotropical migrant landbirds (J. M. Hagan III and D. W. Johnston, Editors). Smithsonian Institution Press, Washington D.C., USA.

WINKER, K., D. W. WARNER, AND A. R. WIESBROD. 1992. Daily mass gains among woodland migrants at an inland stopover site. Auk 109:853–862.