

SPRING STOPOVER OF INTERCONTINENTAL MIGRATORY THRUSHES ALONG THE NORTHERN COAST OF THE GULF OF MEXICO

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ABSTRACT.—The narrow woodlands and wooded barrier islands along the northern coast of the Gulf of Mexico provide the first available landfall for Neotropical landbird migrants after their spring trans-Gulf flight. We studied the timing, volume, fat stores, length of stay, and fat deposition of thrushes ($n = 1,903$) during stopover at a coastal Louisiana woodland in 1987, 1988, and 1990. Peak migration occurred around mid-April in Wood Thrushes (*Hylocichla mustelina*) and was one to two weeks later for *Catharus* thrushes. More than one-third of the thrushes carried no observable subcutaneous fat stores upon initial capture, and only 5% of the birds had estimated fat stores that exceeded 20% of lean body mass. Body mass and condition index (mass/wing length) were negatively related to time of capture, suggesting that birds captured later in the day arrived with lower fat stores. Wing size varied negatively with capture date, suggesting differential migration between sexes and among age classes and/or populations. Recapture probability was related to the amount of fat stores upon initial capture, and length of stay was predictable from estimated fat stores, rate and amount of fat replenishment, and capture date. Flight range estimates suggest that most thrushes captured in spring along the northern coast of the Gulf of Mexico are unable to reach breeding destinations in a single flight. A series of short flights may represent a better migratory strategy than attempting to cover the same distance in one long flight. Received 22 July 1996, Accepted 13 December 1996.

THE MORTALITY associated with intercontinental migration, although difficult to estimate, is probably substantial (Lack 1946, Ketterson and Nolan 1982). Hence, migration may be a major limiting factor in the population dynamics of migratory birds, and factors that increase the cost of migration could have a disproportionate influence on overall population size. Many studies have shown that migratory landbirds have evolved behavioral and physiological responses to cope with contingencies that arise en route. These responses may involve the amount and rate of fat deposition (Alerstam and Lindström 1990), stopover length (Bairlein 1985, Biebach et al. 1986, Moore and Kerlinger 1987), habitat selection (Hutto 1985, Bairlein 1992, Moore et al. 1995), foraging decisions (Rappole and Warner 1976, Loria and Moore 1990, Martin and Karr 1990, Moore 1991), predator avoidance (Metcalf and Furness 1984, Lindström 1990, Aborn 1994, Moore 1994), competition for food resources

(Rappole and Warner 1976, Moore and Yong 1991), and selection of favorable weather conditions (Gauthreaux 1971, Richardson 1978, Buskirk 1980).

The Wood Thrush (*Hylocichla mustelina*), Veery (*Catharus fuscescens*), Swainson's Thrush (*C. ustulatus*), and Gray-cheeked Thrush (*C. minimus*) are Nearctic-Neotropic migrants. The average distances between their wintering and breeding grounds are about 2,200, 5,200, 5,500, and 6,200 km, respectively (Fig. 1). Most individuals of these species that breed in eastern North America make a trans-Gulf flight during spring passage (Rappole et al. 1979). The narrow woodlands and wooded barrier islands along the northern coast of the Gulf of Mexico are the first available landfall for migratory birds that cross the Gulf in spring. Migrant landbirds occur at high densities in these habitats (Gauthreaux 1971, 1975; Moore and Kerlinger 1987; Moore et al. 1990; Kuenzi et al. 1991) and use them to rest, replenish fat stores, or wait for favorable weather.

Several questions form the basis of this study: (1) What is the seasonal and diel stopover patterns of these thrushes in spring? Synchrony in the time of passage may be tied to wintering lati-

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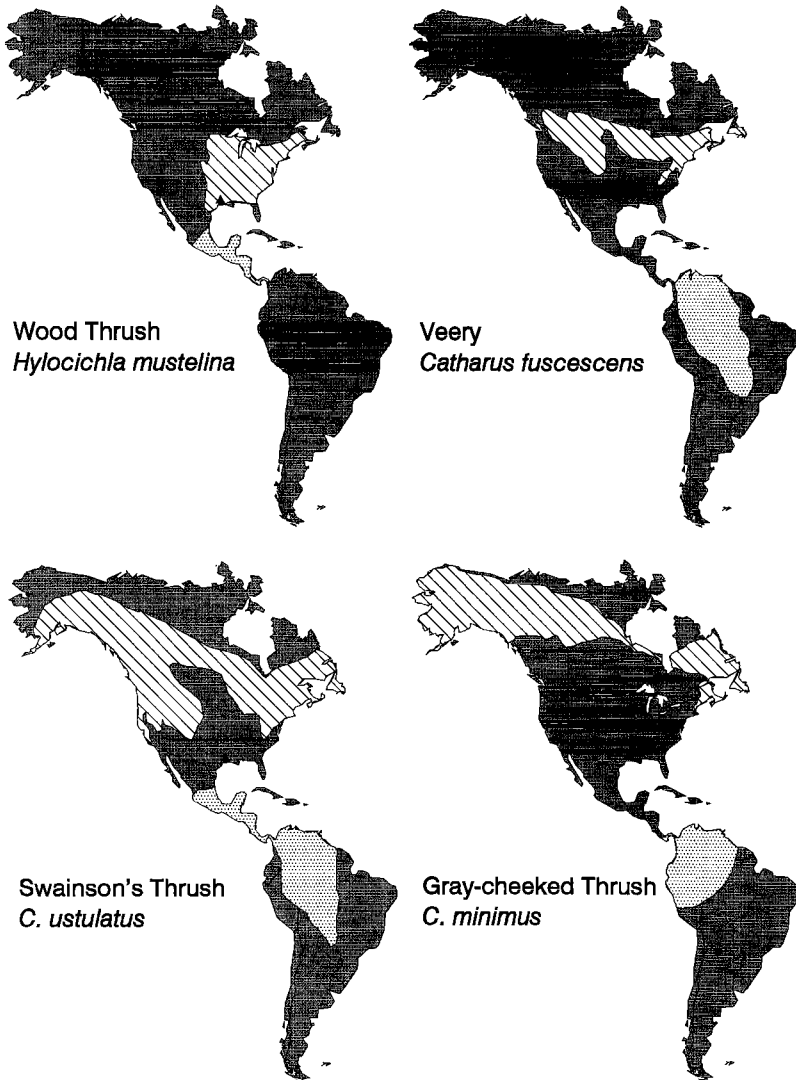


FIG. 1. Breeding and wintering distributions of trans-Gulf migratory Wood Thrush, Veery, Swainson's Thrush, and Gray-cheeked Thrush (after AOU 1983, Rappole et al. 1983). The study site (solid triangle) is located on the southwestern coast of Louisiana.

tude and reflect the degree to which the onset of migration is endogenously controlled (Hagan et al. 1991; see also Gwinner 1986). The diel pattern of capture presumably reflects variation in time of arrival at a stopover site, which influences time available to replenish energy stores. Migrants that arrive late in the day may be more likely to stay for a day or more. (2) What is the energetic condition of migrants when they arrive along the northern coast of the Gulf of Mexico? Fat stores, which represent the principal source of energy during migration, vary

within and among species (Moore and Kerlinger 1987, Kuenzi et al. 1991) as well as within and among seasons. A migrant's fat load affects allocation of time to different activities (Metcalf and Furness 1984), foraging behavior (Loria and Moore 1990), and the likelihood of migratory activity (Yong and Moore 1993), in addition to migratory orientation (Able 1977, Sandberg and Moore 1996). (3) How does fat deposition rate and stopover length vary within and among species? Lean migrants compensate for their poor energetic condition and restore fat loads

more rapidly than fatter migrants (Loria and Moore 1990); they also might remain at stopover sites longer than fatter migrants (Bairlein 1985, Biebach et al. 1986, Moore and Kerlinger 1987, Kuenzi et al. 1991). Otherwise, fat deposition and length of stay vary among species (e.g. Moore and Kerlinger 1987) and are affected by various factors, including distance of migration (Yong and Moore 1993), sex (Morris et al. 1994), migratory experience (Ellegren 1991), habitat preference, and flight morphology (Yong and Moore 1994). (4) What are the potential flight ranges of thrushes after their trans-Gulf flight? Besides the obvious importance of atmospheric conditions (Kerlinger and Moore 1989), flight range depends on the migrant's flight morphology and "fuel" load. Although long-distance migrants are capable of depositing large fat stores over a short period of time (see Berthold 1975, Blem 1980), we do not necessarily expect migrants to replenish fat stores to maximum levels because increased mass following fat storage increases cost of transport and risk of predation (Witter and Cuthill 1993), and increasing fat loads require more foraging time and a longer stopover, which may delay arrival at the migrant's destination.

Conservation implications follow from the answers to these questions. Long-term data sets have revealed population declines for some Nearctic-Neotropical landbird migrants over the past 20 years (Askins et al. 1990, Peterjohn et al. 1995). Although debate continues over the causes of population changes among landbird migrants (see Rappole and McDonald 1994, Sherry and Holmes 1995), the persistence of migrant populations depends on the ability of these birds to find favorable conditions for survival throughout their annual cycle. Hence, factors associated with the en-route ecology of migrants must figure into any analysis of population change (Moore et al. 1995). As stopover habitat is transformed or degraded, the cost of migration increases, and the likelihood of successful migration is jeopardized. High-quality stopover areas probably are especially critical before and after migrants cross ecological barriers.

STUDY AREA AND METHODS

Study site.—Field work was conducted on the Holleyman Migratory Bird Sanctuary (Baton Rouge Audubon Society) located about 2 km east of Johnson's

Bayou, Cameron Parish, Louisiana (29°45'N, 93°37'W; Fig. 1) during spring migration of 1987 (17 March to 28 April), 1988 (25 March to 13 May), and 1990 (1 April to 10 May). The site is a 3-ha coastal woodland (chenier) that supports a vegetation cover dominated by hackberry (*Celtis laevigata*). The understory is composed of honeysuckle (*Lonicera japonica*), poison ivy (*Toxicodendron radicans*), dewberry (*Rubus trivialis*), and greenbrier (*Smilax* spp.). Additional information on the field site is available in Moore and Kerlinger (1987).

Capture and recapture.—Twenty standard mist nets (12 m × 2.6 m) were used to capture thrushes. Unless rain, high winds, or temperature dictated a change, mist nets were operated daily from just before sunrise until after sunset (total of 21,553 net hours during the three field seasons). For each thrush we measured body mass (± 0.1 g using an electronic balance) and unflattened wing chord (± 0.5 mm). Each individual was banded with a numbered aluminum leg band. Recaptured thrushes were reweighed without reference to previous records.

We estimated the amount of stored fat by two methods. First, the visible subcutaneous fat in the interclavicular fossa and on the abdomen was scored following a 6-point scale (see Helms and Drury 1960). Fat scores provide a fairly precise index of fat stores as long as the variability between observers is controlled (Krementz and Pendleton 1990). One observer determined fat levels on all individuals for each of the three years of the study. Second, fat-free body mass was estimated following Ellegren (1989, 1992). Thrushes of each species were divided into groups with common wing lengths (1-mm increments). For each group, body mass was related to fat class by a linear regression. The body mass corresponding to fat class 0 was taken as the estimate of fat-free mass for birds corresponding to a particular wing length. The estimated value of the fat-free mass for each wing-length value was then related to the corresponding wing lengths by a second linear regression. The size-specific, fat-free body mass derived from the second linear regression was subtracted from body mass at capture to estimate fat stores of individual thrushes. A fat index was obtained by dividing estimated fat mass by estimated fat-free mass ($\times 100$).

We estimated stopover length by subtracting the date of first capture from the date of last capture. This yielded a conservative estimate because we assumed that thrushes arrived on the day of initial banding and departed on the day of last recapture (Cherry 1982). Individuals that were not recaptured were assumed to have departed from the study site the same day that they were banded and were assigned a stopover length of zero. For convenience, we referred to the thrushes captured after the day of initial capture as "recaptures" and the rest as "non-recaptures."

Body-mass change during stopover was estimated as the difference in mass between initial capture and

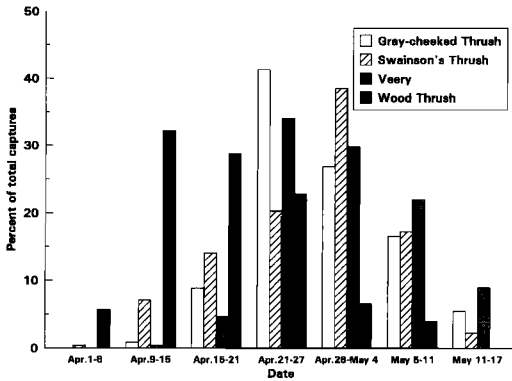


FIG. 2. Distribution of weekly captures of thrushes during migratory stopover along the northern coast of the Gulf of Mexico in spring. Julian date 90 was 30 March 1988 and 31 March 1987 and 1990. See Table 1 for sample sizes.

last capture, and as the correlation between condition index (mass/wing length) and time of capture for all individuals captured (following Winker 1995). We assumed that water gain or loss was negligible (Nisbet et al. 1963, Rogers and Odum 1966). The rate of mass change was calculated by dividing mass change by stopover length (g per day) (Moore and Kerlinger 1987). We applied a forward-selection regression model (SPSS 1994) to evaluate the relative effects of (1) amount of fat stores at initial capture, (2) amount of fat stores at last capture, (3) fat redeposition rate, and (4) capture date on the stopover length of recaptured thrushes.

Potential flight range.—Following Biebach (1992), we estimated energetic consumption for migratory flight based on the amount of fat stores. The maximum range speed (speed in m/s at which the least power per unit distance is consumed) is calculated according to Rayner (1990):

$$V_{mr} = 10.00 M^{0.413} B^{-0.553} S^{-0.095}, \quad (1)$$

where M = body mass (kg), B = wing span (m), and S = wing area (m^2). Energy for metabolism during migratory flight comes mainly from fat (Odum et al. 1964, Piersma and Brederode 1990). An energy equivalent of 31 kJ per gram change in body mass was used (Biebach 1992). To estimate the power (W) required for migratory flight, we used a power input model (following Biebach 1992, Masman and Klaassen 1987, Rayner 1990):

$$P_{met} = 107.47 M^{1.153} B^{-1.378} S^{0.276}, \quad (2)$$

where P_{met} = power input (W), M = body mass (kg), B = wing span (m), and S = wing area (m^2). We then estimated the maximum range speed and power input during flight for every individual in each species

and applied quadratic regressions between body mass and estimated flight range. All statistical analyses were performed with SPSS5.0-PC (SPSS 1994).

RESULTS

Seasonal and daily patterns of capture.—We captured 724 Wood Thrushes, 255 Veerys, 689 Swainson's Thrushes, and 235 Gray-cheeked Thrushes during the three field seasons. Capture rates were 9.59, 8.01, and 10.51 birds/100 net-hours for 1987, 1988, and 1990, respectively.

Seasonal capture patterns differed among species (Kruskal-Wallis test on capture date, $\chi^2 = 597.65$, $df = 3$, $P < 0.0001$). The Wood Thrush occurred first at the site every year followed by Swainson's Thrush, Gray-cheeked Thrush, and Veery (Fig. 2). Median capture dates between Wood Thrushes and the *Catharus* thrushes varied between 11 and 18 days. During the last week of March and the first week of April, Wood Thrush captures increased gradually, while only a few *Catharus* thrushes were captured. The cumulative percentage of Wood Thrush captures increased from about 10 to 90% in the three weeks after this period. Whereas 70% of the Wood Thrushes were captured by the end of the third week of April, only 22%, 10%, and 5% of the Swainson's Thrushes, Gray-cheeked Thrushes, and Veerys were captured, respectively. The number of *Catharus* thrushes increased from mid-April to the first week of May, and their passage was more synchronous than the passage of Wood Thrushes (variance of capture dates = 67.30, 53.50, 53.36, 53.57 for Wood Thrush, Veery, Swainson's Thrush, and Gray-cheeked Thrush, respectively; $F = 301.46$, $df = 3$ and 1,899, $P < 0.0005$).

The daily timing of captures did not differ among species. Thrushes were caught throughout the day, with a peak between 0700 and 1000 (CST) for each species (Fig. 3). Gray-cheeked Thrushes that were recaptured were more likely to have been initially captured later in the day of (presumptive) arrival (median time of initial capture = 1500) than were birds that were never recaptured (median time = 1100; Mann-Whitney $U = 2,682$, $n_1 = 40$, $n_2 = 195$, $P < 0.01$). Recaptured Wood Thrushes also arrived later on the day of initial capture (median time = 1300) than individuals that were never recaptured (median time = 1100; $U = 35,437$, $n_1 = 134$, $n_2 = 589$, $P < 0.05$). Veerys and Swainson's Thrushes did not show any difference in diel capture patterns.

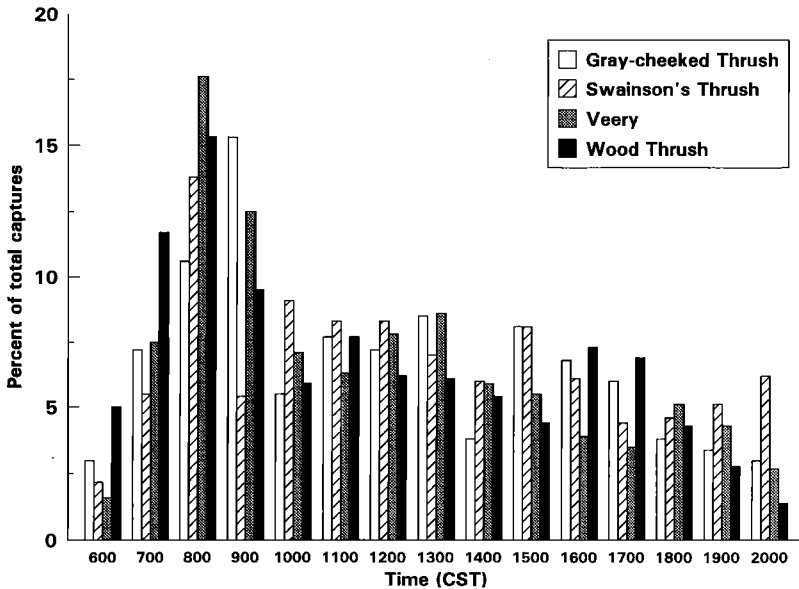


FIG. 3. Temporal distribution of daily captures of thrushes during migratory stopover along the northern coast of the Gulf of Mexico in spring. See Table 1 for sample sizes.

With the exception of Wood Thrushes, recaptured birds were more likely to be captured two to three hours earlier on the day following initial capture than on their "arrival" day.

Fat stores upon initial capture.—Migrants that have crossed the Gulf of Mexico would be expected to have reduced fat stores. More than one-third (39%) of all thrushes captured did not have any observable subcutaneous fat (fat class 0), and the body mass of 23% of the birds was equal to or below the estimated fat-free body mass (Rogers and Odum 1966, Hicks 1967, Child 1969, Yong and Moore 1993). Average body-mass and fat-index values were especially low for Gray-cheeked Thrush ($24.75 \pm \text{SE of } 0.18 \text{ g}$, $6.81 \pm 0.57\%$ fat) and Veery ($24.72 \pm 0.17 \text{ g}$, $5.15 \pm 0.66\%$ fat). Wood Thrush ($40.84 \pm 0.16 \text{ g}$, $11.58 \pm 0.45\%$ fat), and Swainson's Thrush ($26.39 \pm 0.11 \text{ g}$, $9.43 \pm 0.42\%$ fat) arrived heavier in relation to lean body mass and carried a little more fat. The initial mass of thrushes that were later recaptured was significantly lower (5 to 9%, depending on species) than the initial mass of thrushes that were not recaptured (Table 1). The mass differences between the two groups were not due to body-size difference (ANCOVA with wing length as covariate, $P < 0.45$ for all species).

Seasonal and daily changes in wing size, body mass, and fat stores.—Wing length declined with

capture date, suggesting that individuals captured earlier during spring were larger. Body mass and the amount of stored fat also decreased during the season in every species except the Gray-cheeked Thrush (Table 1). The combination of the negative relationship between capture date and wing length and the positive relationship between capture date and fat stores suggested that individuals captured later were smaller and carried more fat.

Wing length also declined with time of capture, suggesting that thrushes captured later in the day were smaller (Table 1). Body mass, fat stores, and condition index decreased significantly through the day in the *Catharus* species. Fat stores declined 0.07 g, 0.09 g, 0.10 g, and 0.23 g per hour for Gray-cheeked Thrush, Swainson's Thrush, Veery, and Wood Thrush, respectively.

Recapture rate, mass change, and stopover length.—We recaptured 268 thrushes (14% of captures) at least one day after the first capture. The recapture rate of Swainson's Thrush (7%) was much lower than that of Gray-cheeked Thrush (17%), Veery (19%), and Wood Thrush (19%), and the frequency of recaptures varied among species ($\chi^2 = 41.4$, $df = 3$, $P < 0.001$).

Recaptured thrushes gained body mass during stopover (average % gain = 2.6%, 2.3%, 2.1%, and 3.4% for Gray-cheeked Thrush,

TABLE 1. Relationship (*r*-values) between dependent variables wing length, body mass, fat stores, and condition index (mass/wing length) and independent variables date of capture and daily timing of capture for four species of thrushes captured during spring migration in Louisiana.

	Gray-cheeked (<i>n</i> = 234)	Swainson's Thrush (<i>n</i> = 688)	Veery (<i>n</i> = 254)	Wood Thrush (<i>n</i> = 721)
Wing length				
Date of capture	-0.19**	-0.29***	-0.45***	-0.02
Time of capture ^a	-0.05	-0.08*	-0.24***	0.09*
Body mass				
Date of capture	-0.07	-0.14***	-0.24***	-0.10
Time of capture	-0.12	-0.15***	-0.24***	-0.19***
Fat stores				
Date of capture	0.15*	-0.05	-0.07	-0.10**
Time of capture	-0.10	-0.13***	-0.16*	-0.22***
Condition index				
Date of capture	0.14*	-0.06	-0.09	-0.10**
Time of capture	-0.11	-0.13***	-0.17**	-0.23***

*, *P* < 0.05; **, *P* < 0.01; ***, *P* < 0.001

^a Time of day bird was captured.

Swainson's Thrush, Veery, and Wood Thrush, respectively). The corresponding daily rate of mass gain was 1.96%, 1.16%, 0.57%, and 1.14% for the four species, respectively.

Thrushes that stopped for shorter periods tended to lose body mass, or to gain less mass, during their stopover (Fig. 4). About 50% of recaptured birds lost body mass during their first day of stopover, and body size had no effect on body-mass loss (Table 2). When thrushes stayed

for more than one day, body mass and rate of gain increased significantly in all species (Table 2).

The average stopover length of recaptured birds varied among species and ranged from 3.16 days for the Wood Thrush to 1.55 days for the Swainson's Thrush (Fig. 4). The Gray-cheeked Thrush stayed 2.40 days and the Veery 2.17 days, on average. Stopover lengths differed significantly when all four species were consid-

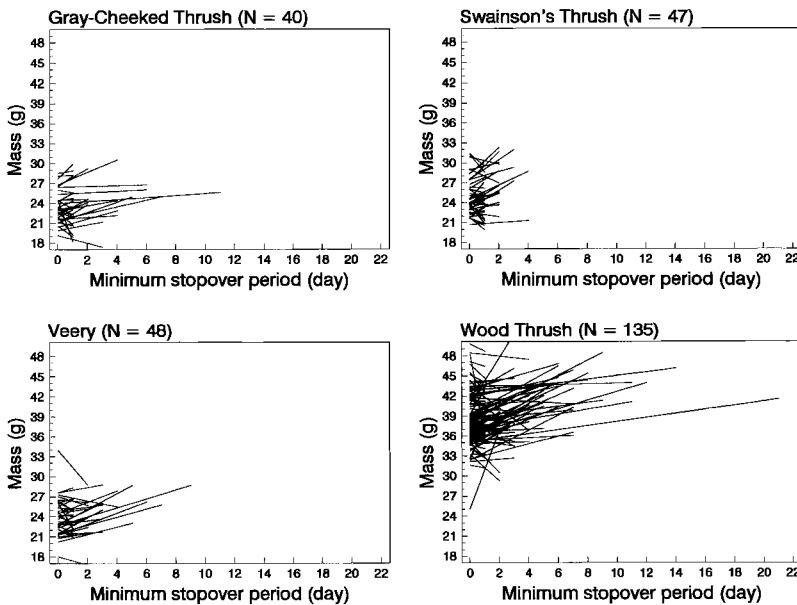


FIG. 4. Body-mass changes of thrushes as a function of days between initial capture and last capture.

TABLE 2. Wing length (mm), body mass (g) at initial capture, mass change (g), rate of mass change, and probability of body mass loss among individuals with different stopover lengths. Values are $\bar{x} \pm$ SD.

Group ^a (n)	Wing length	Initial mass	Mass change ^b	Mass change per day ^c	% change per day ^d	Probability of mass loss ^e
Gray-cheeked Thrush						
1 (195)	101.6 ± 3.78	25.0 ± 2.82				
2 (23)	102.4 ± 3.24	23.9 ± 2.15	-0.3 ± 1.70	-0.3 ± 1.70	-1.5 ± 7.06	47
3 (17)	101.9 ± 3.72	22.9 ± 2.43*	1.9 ± 1.54**	0.5 ± 0.52*	8.1 ± 6.99*	6**
Swainson's Thrush						
1 (642)	97.6 ± 3.08	26.5 ± 2.90				
2 (28)	98.2 ± 3.01	24.4 ± 2.63	-0.2 ± 1.44	-0.2 ± 1.44	-0.7 ± 5.84	54
3 (19)	98.7 ± 2.97	25.4 ± 2.76*	1.7 ± 1.94**	0.7 ± 0.83*	6.6 ± 7.39*	21**
Veery						
1 (207)	97.9 ± 3.50	25.0 ± 2.60				
2 (24)	96.2 ± 3.63	24.0 ± 1.91	-0.4 ± 1.26	-0.4 ± 1.26	-1.4 ± 5.13	63
3 (24)	96.1 ± 3.78	23.3 ± 3.29*	1.3 ± 2.55**	0.2 ± 0.78*	6.4 ± 10.64*	25**
Wood Thrush						
1 (589)	105.7 ± 3.25	41.2 ± 4.24				
2 (57)	104.8 ± 4.12	38.5 ± 3.91	-0.1 ± 2.36	-0.1 ± 2.36	0.1 ± 5.60	46
3 (78)	105.7 ± 3.70	37.9 ± 3.57*	2.4 ± 3.46**	0.5 ± 1.08*	6.8 ± 9.94*	23**

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; ANOVA among groups

^a 1 = not recaptured; 2 = stopover length of 1 day; 3 = stopover length of ≥ 2 days.

^b Body mass at initial capture - body mass at last capture.

^c Mass change/stopover length.

^d (Mass change/body mass at 1st capture) \times 100/stopover length; t -test between groups 2 and 3.

^e % of individuals in group that lost body mass; χ^2 goodness-of-fit between groups 2 and 3.

ered (Kruskal-Wallis test, $\chi^2 = 12.40$, $df = 3$, $P < 0.01$) but were not different among the three *Catharus* thrushes ($\chi^2 = 1.96$, $df = 2$, $P > 0.05$). Stopover length was not affected by body size because wing length was essentially the same among individuals that stopped for different lengths of time (Table 2).

We predicted stopover lengths of recaptured thrushes by applying forward-selection regressions using amount of fat stores at initial capture and last capture, rate of mass gain, and date of capture (Table 3). The analysis suggested that length of stopover was negatively related with the amount of fat stores at initial capture, rate of mass-gain, and capture date. The order of the variables that were selected into the model was consistent among species, with fat stores at last capture entering first followed by the fat stores at initial capture, rate of mass gain, and capture date. The amount of fat stores at last capture accounted for 24–44% of the total variance in stopover length. Fat stores at initial capture accounted for 11–29% of the total variance, and the rate of mass gain accounted for another 13–20% of the total variance in stopover length.

The potential flight ranges under still air or tailwinds for various fat loads are depicted in Figures 5–8. These simulations suggested that

most birds (especially *Catharus* spp.) did not have sufficient fat stores to migrate to their breeding grounds by a single nonstop flight, even under favorable wind conditions. Assuming that a thrush flies 6 to 8 h per night at a maximum range speed of 38.5 km/h (10.7 m/s, Pennycuik 1989), then a thrush would travel about 270 km in one night. This migration capacity requires a fat load of 1.55 g, 1.60 g, 1.59 g, and 2.61 g for the Gray-cheeked Thrush, Swainson's Thrush, Veery, and Wood Thrush, respectively.

DISCUSSION

Seasonal patterns.—The seasonal timing of captures for the four thrush species along the northern coast of the Gulf of Mexico is consistent with their arrival times near or on their breeding grounds (Dilger 1956, Graber et al. 1971, Hagan et al. 1991, Winker et al. 1992). Wood Thrushes breed across most of eastern North America. On average, they have the shortest migration distance among four species studied. Hagan et al. (1991) found a 7- and 12-day difference in mean arrival dates between Wood Thrushes and Veerys and between Wood Thrushes and Swainson's Thrushes, respectively. The later migration

TABLE 3. Forward-selection regression analysis on the influence of fat stores at initial capture, fat stores at last capture, rate of mass change (g per day), and capture date on stopover length.

Step	Variable	R	β	df	F ^a
Gray-cheeked Thrush					
1	Last fat stores	0.24	2.18	1,38	2.31
2	Initial fat stores	0.50	-1.61	2,37	9.70**
3	Rate of mass change	0.70	-1.02	3,36	17.02***
4	Capture date	0.70	-0.06	4,35	0.23
Swainson's Thrush					
1	Last fat stores	0.35	2.58	1,45	6.36*
2	Initial fat stores	0.53	-2.12	2,44	9.98**
3	Rate of mass change	0.68	-1.04	3,43	14.65***
4	Capture date	0.69	0.06	4,42	0.22
Veery					
1	Last fat stores	0.44	1.52	1,46	11.04**
2	Initial fat stores	0.72	-1.37	2,45	30.01***
3	Rate of mass change	0.82	-0.63	3,44	20.95***
4	Capture date	0.83	-0.14	4,43	2.54
Wood Thrush					
1	Last fat stores	0.41	1.20	1,131	27.11***
2	Initial fat stores	0.53	-1.04	2,130	18.91***
3	Rate of mass change	0.65	-0.65	3,129	33.68***
4	Capture date	0.66	-0.06	4,128	0.84

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

^a F-value associated with change in sum of squares at each step.

and more synchronous passage of *Catharus* thrushes conforms with Lack's (1951) hypothesis that later-migrating species have a greater urgency to reach the breeding grounds because of their later departures. Additionally, the timing of spring migration of thrushes may be affected by migratory distance between the breeding and wintering grounds (Hagan et al. 1991), food availability en route and on the breeding grounds, competition for breeding space (Cox 1985, Greenberg 1986), physiological tolerance for unpredictably low temperature in early spring (Swanson 1995), and the endogenous migration schedule (Safriel and Lavee 1988).

The seasonal decline in wing length that we observed may be related to differential migration between the sexes, among age classes, or among populations. Among thrushes, males tend to have longer wings than females and yearlings (Pyle et al. 1987). Also, other breeding studies have suggested that arrival times of thrushes vary with sex and age. Consequently, such factors are likely to contribute to seasonal changes in wing length of thrushes captured during migration. For example, male thrushes arrive on the breeding grounds ahead of females, based on behavioral observations (Dilger 1956), and Francis and Cooke (1986) found a ten-

dency for older birds within each sex to arrive earlier. Among Dark-eyed Juncos (*Junco hyemalis*), differential timing of migration among and within age/sex classes accounted for most of the temporal variation in wing shape (Chandler and Mulvihill 1990).

At least two factors could explain the seasonal decrease in fat stores among thrushes: (1) later migrants used more fat stores during trans-Gulf flight, and/or (2) they deposited lower fat stores before the crossing Gulf. Weather conditions are more favorable and predictable for trans-Gulf flight later in the spring (Buskirk 1980), which would reduce the energetic cost of a trans-Gulf flight. Optimal fat storage and time-minimization models (Alerstam and Lindström 1990) predict that with more favorable weather conditions and higher food availability en route, migrants should deposit lower fat stores to reduce the cost of transport. Furthermore, the demand for a large safety margin of stored fat would be reduced under conditions of predictable weather and increased food availability (Moore and Kerlinger 1991). On the other hand, younger birds (i.e. second-year), which have little experience and less efficient flight morphology than adults (Alatalo et al. 1983, Yong and Moore 1994), probably would mobilize

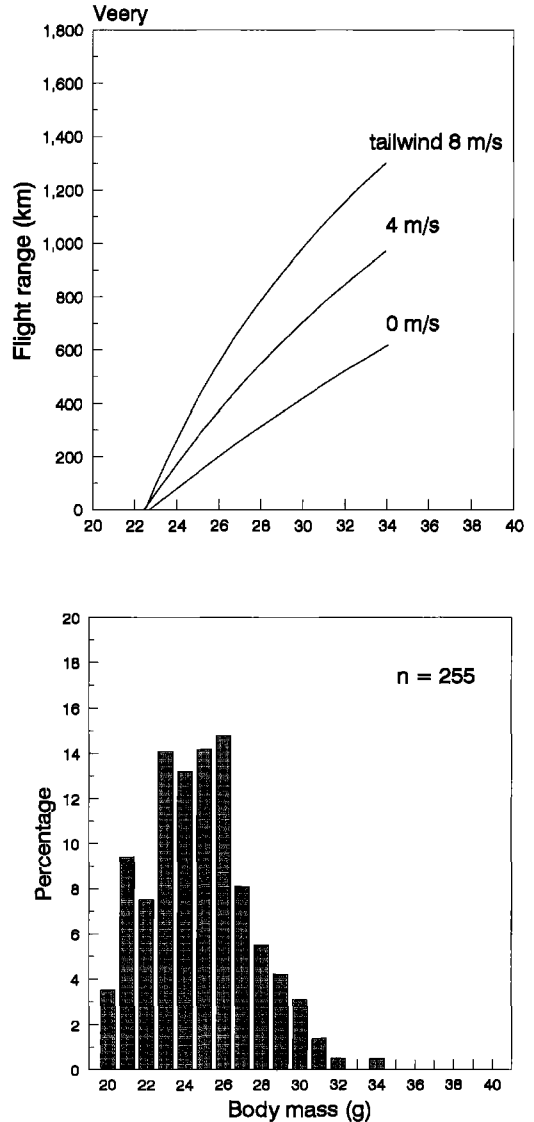
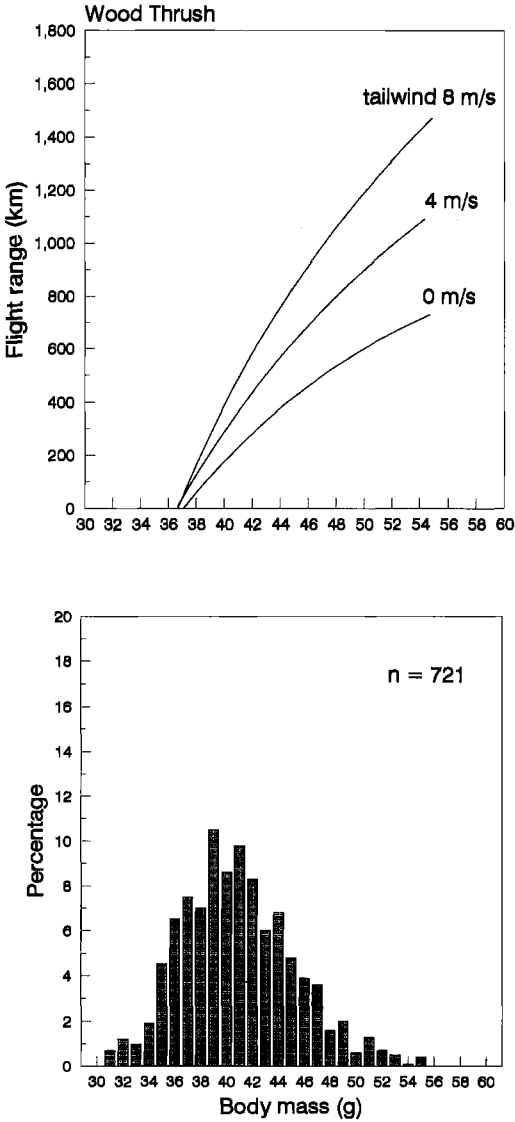


FIG. 5. Frequency distribution of body mass (lower) and potential flight ranges of Wood Thrushes under still air and with tailwinds (upper).

FIG. 6. Frequency distribution of body mass (lower) and potential flight ranges of Veerys under still air and with tailwinds (upper).

greater fat stores during trans-Gulf flight. This would result in an apparent seasonal decline in fat stores if the later migrants were comprised mostly of younger birds. A more complete understanding of seasonal aspects of fat storage will not be possible until more attention is paid to sex- and age-dependent aspects of spring passage.

Daily patterns.—Radar observations of spring landbird migration in southwestern Louisiana (Gauthreaux 1971) revealed that peak arrival of

migrants along the northern coast of the Gulf of Mexico varied from late morning through mid-day to late in the afternoon and depended largely on prevailing weather conditions during passage. Day-to-day differences in peak capture time of migrants at our study site were consistent with the radar observations (i.e. thrushes arrived at various times during the day). The diel pattern of capture was consistent among the four species, with a peak skewed toward the mid-morning hours. This discrepancy between

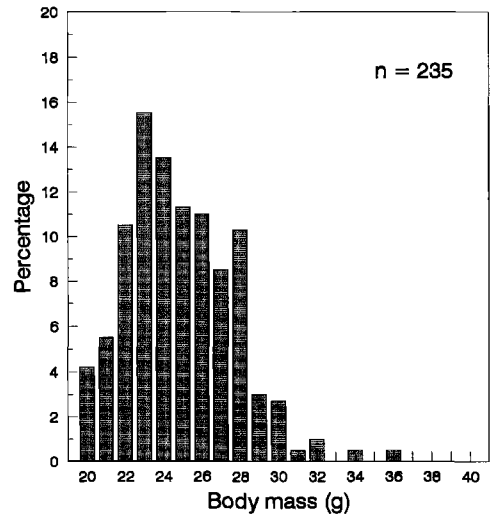
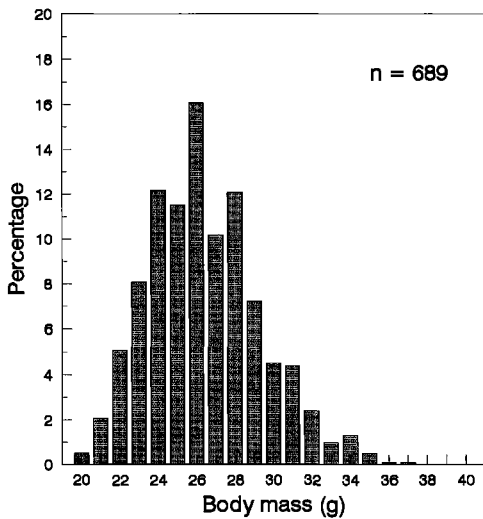
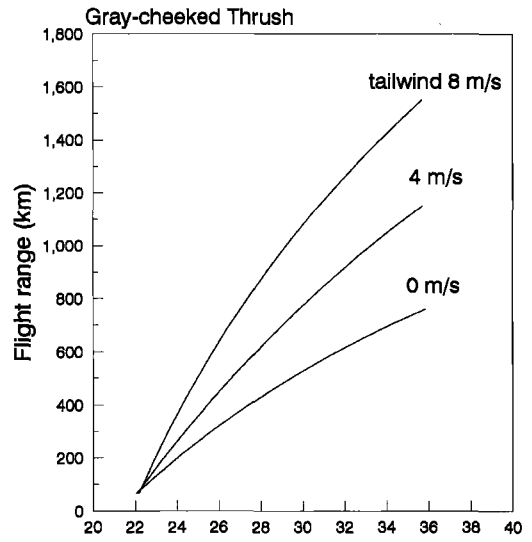
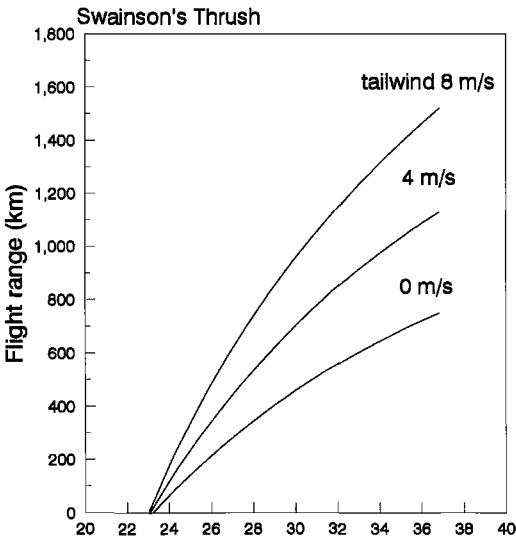


FIG. 7. Frequency distribution of body mass (lower) and potential flight range of Swainson's Thrushes under still air and with tailwinds (upper).

FIG. 8. Frequency distribution of body mass (lower) and potential flight range of Gray-cheeked Thrushes under still air and tailwinds (upper).

radar observations, which would lead us to expect a midday peak, and the mist-net data probably represents a confounding of the daytime activity pattern of birds that stayed overnight and newly arrived migrants. We tested this hypothesis by comparing the hour-by-hour capture pattern with the diel pattern of recaptures because recaptured birds arrived at the study site during the previous day(s) and their pattern of capture is affected only by movement during stopover. The results confirmed our expectation. Moreover, many of the individuals detected by

radar were probably flying over our coastal site toward more extensive forested areas north of the coastal prairie (Gauthreaux 1971), whereas the thrushes we captured represented individuals that probably made landfall in the first available woodlands.

The relationship between estimated fat stores and daily time of capture was negative for each species, which might reflect loss of mass over the course of a day. Winker et al. (1992) pointed out that many transients that stopover are not recaptured and do not contribute to estimates of

fat deposition, because such estimates are usually based on recaptured birds. They recommended simple linear regression to examine the relationship between time of day (capture) and energetic condition (fat score and size-adjusted mass). A linear regression of mass on time of day should yield a significant positive slope among birds gaining or maintaining fat stores (Winker 1995). The application of this approach depends on species, site, and season because the models assume that within species, individuals behave similarly and have the same foraging opportunities. Although these assumptions are probably true for some migrants (such as landbirds that migrate through relatively continuous forest habitat), arrival of trans-Gulf migrants along the northern coast of Gulf of Mexico is highly variable.

The negative relationship between fat stores and daily time of capture in our study could be the result of lower fat loads among later-captured thrushes. According to flight mechanical theory (Pennycuik 1975), flight speed among individuals of similar flight morphology is slower in individuals with lower body mass. Possibly, later-captured thrushes consumed more fat stores during trans-Gulf migration because they originated from more southerly wintering grounds. The flight metabolic rate of thrushes is about 0.19 g fat/h (based on Pennycuik 1975), which is very similar to the hourly rate of body mass decrease detected among thrushes. Alternatively, thrushes caught later in the day may have originated from the same wintering grounds as birds captured earlier in the day, but deposited less fat prior to their trans-Gulf flight because they had settled in low-quality habitat, were socially subordinate (e.g. second-year birds) to older migrants and had greater difficulty finding food, or both (see Sherry and Holmes 1996). Finally, later-captured thrushes with lower fat stores may have been less successful in replenishing fat stores and continued to be active later in the day, whereas birds that gained mass earlier were less active (and less likely to be captured). Information on the body condition of migrants prior to departure from the wintering grounds and detailed foraging observations of individually marked migrants during stopover are needed to test these hypotheses.

Fat stores, body-mass change, and stopover length.—Thrushes that stopped for more than a day tended to loss mass initially, but thereafter gained mass at a rate of 6 to 8% of their initial

mass per day. That rate equals or exceeds theoretically calculated maximum fat deposition rates for thrush-sized passerines (Lindström 1991). Based on fat deposition rate alone, coastal woodlands such as our study site represent suitable places for thrushes (as well as other passerines; see Moore and Kerlinger 1987) to replenish depleted fat stores during migration.

Although we assume that mass differences reflect differences in fat stores, other factors may contribute to changes in mass (see Lindström and Piersma 1993). Some mass gain may be attributed to water uptake, especially if migrants become dehydrated during long flights (Biebach 1991, Leberg et al. 1996). An increase in body mass also may reflect a return to premigratory levels of fat-free mass if migrants catabolize some of their reserves (see King and Murphy 1985) to offset heightened energy demands during long, nonstop flights (Bairlein and Totzke 1992).

Initial declines in body mass upon arrival at stopover sites are typical among long-distance migrants (e.g. Rappole and Warner 1976, Moore and Kerlinger 1987, Lindström 1995). Explanations for this mass loss include effects of capture and handling (Nisbet and Medway 1972), recovery from poor physiological condition after migration (Carpenter et al. 1993), competition among conspecifics (Rappole and Warner 1976, Moore and Yong 1991), and inefficient foraging because of unfamiliarity with the stopover site. Capture and handling could deprive birds of foraging time and cause stress or injury. However, we found no relationship between mass change and number of times individuals were recaptured. We also found that the initial body mass was similar among individuals that lost body mass and those that gained mass, which suggests that the initial body mass decline was not related to body condition at arrival. We speculate that unfamiliarity with stopover habitat, and competition for food resources among migrants, are the most important factors contributing to the initial loss of body mass in thrushes.

Length of stopover often depends on the migrant's energetic condition (i.e. fat stores) upon arrival (e.g. Bairlein 1985, Biebach et al. 1986, Moore and Kerlinger 1987), and our results are consistent with this pattern, although energetic status is not the only contributing factor. Arrival date, rate of fat deposition, and amount of fat gain affected length of stopover. The latter two are probably related to habitat quality at stopover sites (Hutto 1985). Moreover, migrants that

stopover a day or two are more likely to arrive later in the day, which provides less time to familiarize themselves with the local habitat, locate food, and cope with nutritional constraints before the end of the day.

Length of stopover undoubtedly is sensitive to time constraints during passage, especially in spring (Safriel and Lavee 1988, Alerstam and Lindström 1990). If a migrant stays longer than usual at a stopover site and does not make up the lost time, then arrival on the wintering or breeding grounds is necessarily delayed. Migrants that arrive late on the breeding grounds, for example, jeopardize opportunities to secure a territory and a mate. If a bird expects to "catch-up" with the overall time schedule of migration, then it must refuel faster during its next stopover. Yet, a penalty may be attached to late arrival at the next stopover site if resource levels have been depressed by earlier migrants (Moore and Yong 1991).

Flight range, stopover pattern, and conservation implications.—Our data suggest that migrant thrushes that stop along the northern coast of the Gulf of Mexico rapidly replenish fat stores that are sufficient to sustain about one night of migratory flight (ca. 300 km). The difference in median capture dates of Swainson's Thrushes passing our study site and the Minnesota study site of Winker et al. (1992; i.e. Julian day 125 vs. 138, respectively) is consistent with our estimate of a migration speed of 300 km per day. Bent (1949) estimated that the average migration speed of the Gray-cheeked Thrush in spring was 213 km per day.

Rates of fat deposition, stopover lengths, and fat loads attained among the thrushes that stopped at our study site reflect in part the quality of the habitat (see Moore et al. 1995). In general, lean migrants stay longer than birds that have not mobilized fat stores (e.g. Bairlein 1985, Pettersson and Hasselquist 1985, Biebach et al. 1986, Moore and Kerlinger 1987, Kuenzi et al. 1991). Even among lean birds the probability of staying is dependent on habitat quality (Rappole and Warner 1976). The combination of low fat stores and a high probability of replenishing stores should induce a migrant to stay at a stopover site. Low fat combined with a low probability of replenishment should favor departure to search for more suitable stopover habitat (Rappole and Warner 1976). For example, although Gray-cheeked Thrushes can expect to gain mass at our study site, our simulation sug-

gests that a stopover of about four days would be necessary to deposit fat stores sufficient for a flight of 600 km, which is a much shorter distance than that needed to reach their high-latitude breeding grounds.

A migration strategy characterized by brief stopovers, reduced fat loads upon departure, and a series of short flights may be advantageous (Piersma 1987). Our simulations suggest that if thrushes stop 10 times en route and take on fat stores equal to 5% of body mass during each stop, then they would achieve a flight distance that is 20% longer than if they deposited the entire fat stores (50% body mass) at a single stopover site. This "low fat stores-short stopover" strategy depends on the predictability of stopover sites, the availability of food resources, and the cost of settlement among potential stopover sites (see Alerstam and Lindström 1990).

A migrant that departs a stopover site with reduced fat stores has a smaller "margin of safety" to buffer the prospects of experiencing a poor-quality site or arriving during adverse weather at the next stopover (see Moore and Kerlinger 1991). Moreover, migrants arriving on their breeding grounds with endogenous fat stores to spare may be better able to meet contingencies that arise during the onset of the breeding season and to offset time constraints associated with breeding at high latitudes (Sandberg and Moore 1996). It is well established, for example, that the prebreeding nutritional condition of parents affects reproductive success (Drent and Daan 1980). Hence, the availability of resources in the form of endogenous fat stores acquired during passage should improve parental condition and influence reproductive success in migrant landbirds.

Undertaking long flights that require large fat loads may be the best strategy if high-quality stopover sites are limited in availability or occur unpredictably along the migratory route (Weber et al. 1994). The migration of *Catharus* thrushes, for example, evolved against a landscape that is quite different from what they encounter today. Deforestation and habitat fragmentation may reduce the number as well as the quality of stopover sites (see Moore et al. 1993). If landbird migrants cannot periodically replenish fat stores, or cannot do so quickly because they experience difficulty locating high-quality sites, then the probability of successful migration will be reduced.

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