AGE-RELATED DIFFERENCES IN THE STOPOVER OF FALL LANDBIRD MIGRANTS ON THE COAST OF ALABAMA

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ABSTRACT.—We estimated fat load, length of stopover, and rate of mass change for six Neotropical migrant landbird species at a site along the northern coast of the Gulf of Mexico. Swainson's Thrushes (*Catharus ustulatus*), Gray Catbirds (*Dumetella carolinensis*), White-eyed Vireos (*Vireo griseus*), Red-eyed Vireos (*V. olivaceus*), Magnolia Warblers (*Dendroica magnolia*), and American Redstarts (*Setophaga ruticilla*) were captured on Fort Morgan Peninsula in coastal Alabama during fall migration, 1990 to 1992. In Swainson's Thrushes, White-eyed Vireos, and American Redstarts, adults carried significantly higher fat loads than young birds, whereas no age-related differences in fat loads were evident in the other species. The likelihood of staying beyond the day of capture and the rate of change in body mass did not differ between age classes. One consequence of differences in fat load is reflected in flight range in relation to the Gulf of Mexico. On average, adult Swainson's Thrushes, White-eyed Vireos, American Redstarts, and both age classes of Magnolia Warblers carried sufficient energy stores to complete a trans-Gulf flight, whereas young Swainson's Thrushes, White-eyed Vireos, American Redstarts and both age classes of Gray Catbirds carried insufficient stores for such a flight, based on flight-performance simulations. *Received 17 October 1996, accepted 13 May 1997.*

A SUCCESSFUL MIGRATION is dependent on how effectively migrants satisfy energy demands and meet en-route contingencies. Problems that arise during passage undoubtedly are magnified for hatching-year birds on their first migration (e.g. Ralph 1978, Gauthreaux 1982, DeSante 1983, Moore 1984, Lindström and Alerstam 1986). If the high cost of migration (i.e. reduced fitness, increased mortality) is absorbed largely by inexperienced, hatching-year birds (Nisbet and Medway 1972; Johnson 1973; Alerstam 1978; Greenberg 1980; Goss-Custard et al. 1983; Ketterson and Nolan 1982, 1983, 1985; DeSante 1983), differential costs should be reflected in age-dependent differences in stopover biology. Moreover, individuals with different levels of migratory experience can be expected to respond differently to the exigencies of migration (e.g. Metcalfe and Furness 1984; Ketterson and Nolan 1985, 1988; Terrill 1988; Ellegren 1991).

An important constraint during migration is the acquisition of adequate fat stores. Individuals in migratory disposition (sensu Berthold

1975) become hyperphagic and deposit fat, increasing their body mass by 30 to 50% (Berthold 1975, Blem 1980). If young migrants satisfy the energy requirements of migration and meet en-route contingencies with less proficiency than adults, they may carry less fat than adults when encountered at migratory stopovers. Alternatively, young migrants may deposit more fat than adults to increase their "margin of safety" if they anticipate greater difficulty solving en-route problems by virtue of their inexperience or subordinate social status. Finally, fat loads may be independent of age, but young migrants may take longer to achieve the same level of preparation (i.e. they deposit fat at a slower rate than adults). Age-dependent differences may arise not only because of constraints on the performance of young migrants, but also because young birds invest less time and energy in migration than adults because of disproportionate costs (see Wiley 1981, Curio 1983).

We estimated fat stores, length of stay, and rate of mass change during stopover for young and adult landbirds at a stopover site along the northern coast of the Gulf of Mexico. We also examined the consequences of differences in fat load in relation to a simulated trans-Gulf flight. The movement of landbird migrants in relation to the Gulf of Mexico is a prominent feature of

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the Nearctic-Neotropical migration system (Buskirk 1980). Coastal habitats give spring migrants a place to rest and replenish energy stores immediately after a trans-Gulf flight (Rappole and Warner 1976, Moore and Kerlinger 1987) and give fall migrants a final place to deposit stores sufficient for a nonstop flight (18–24 h) of more than 1,000 km should atmospheric conditions favor a trans-Gulf crossing (see Able 1972, Sandberg and Moore 1996). Based on our ability to capture adequate numbers of after-hatching-year (AHY; i.e. adults) and hatching-year (HY; i.e. young) individuals, we examined age-dependent aspects of stopover biology in Swainson's Thrushes (*Catharus ustulatus*), Gray Catbirds (*Dumetella carolinensis*), White-eyed Vireos (*Vireo griseus*), Red-eyed Vireos (*V. olivaceus*), Magnolia Warblers (*Dendroica magnolia*), and American Redstarts (*Setophaga ruticilla*).

METHODS

Study sites.—Data were collected at two sites near the western end of Fort Morgan peninsula, coastal Alabama (30°10′N, 88°00′W). The first site was the "Stables Area," a 5-ha woodland characterized by scattered slash pines (*Pinus elliottii*) interspersed among hummocks of sand live oak (*Quercus geminata*) and yaupon (*Ilex vomitoria*). The second site was a 6-ha portion of the Bon Secour National Wildlife Refuge located 2 km east of the Stables Area. This site is comprised of two relatively distinct habitats. The pine/shrub habitat is dominated by a slash pine overstory with a dense understory of yaupon, redbay (*Persea borbonia*), and saw palmetto (*Serenoa repens*), and the scrub/shrub habitat is dominated by thickets of sand live oaks 2 to 4 m high, but includes some rosemary (*Ceratiola ericoides*) mixed with saw palmetto. Data were collected at the Stables Area from 30 August to 1 November 1990 and 28 August to 18 October 1991 and at the second site from 27 August to 28 October 1992.

Field methods.—We used mist nets (12 × 2.6 m, 30-mm mesh) to capture birds. Except in rain or high winds, mist nets were opened shortly after sunrise, sometimes closed during midday because of high temperatures, and reopened for a few hours in the afternoon. Data collected for each bird banded with a U.S. Fish and Wildlife Service aluminum leg band included: (1) body mass (± 0.1 g using an electronic balance), (2) tarsus length, (3) unflattened wing chord, (4) fat class (see below), (5) age (when possible), and (6) sex (when possible). To get an accurate assessment of age, all captured birds were skulled using methods outlined in Pyle et al. (1987). Recaptured birds were assigned to a fat class without reference to previous records, and their body mass was remeasured.

Visible subcutaneous fat deposits were quantified according to a six-point scale developed by Helms and Drury (1960). Fat scoring provides a fairly precise method of indexing fat stores as long as comparisons are made within species (e.g. between age classes) and between-observer variability is controlled (Krementz and Pendleton 1990). We minimized variability in fat scoring by making comparisons within species, and between-observer variability was minimized by having one observer determine fat levels for each of the three years of the study.

Data analysis.—We used a Wilcoxon two-sample test to analyze differences in the distribution of fat scores by age class within species. Although subcutaneous fat stores can account for most of the variation in body mass between individual migrants, individual size differences also can contribute to variation in body mass (Connell et al. 1960). If standardized for body size, body mass is a reasonable predictor of an individual's fat content (Connell et al. 1960, Rogers and Odum 1964). To determine if age classes within species differed in body size, we compared age classes using wing chord and tarsus length with a two-sample t-test (Zar 1984). After determining that age classes differed significantly in body size, we used Pearson's correlation analysis to look for a linear relationship between wing chord or tarsus length and body mass. Because of the significant differences in size and the significant linear relationships between measures of body size and body mass, we used one-way ANCOVA to examine age differences in body mass within species. Prior to conducting the ANCOVA, we tested for homogeneity of slopes and found no significant differences. We arbitrarily chose wing chord as the covariate to standardize for individual differences in body size. We used a two-sample t-test to compare fat scores between age classes (Zar 1984).

Simple linear regression was used to determine mass change in migrants during stopover. Based on samples of birds captured only once throughout the day, regression analysis was used to examine the relationship between body mass and time of capture (see Winker et al. 1992). We used this approach in addition to the more traditional approach of using recapture data from individuals (see Rappole and Warner 1976, Moore and Kerlinger 1987, Safriel and Lavee 1988) because few migrants were recaptured during this study. Regression lines were fitted to the data using least-squares analysis.

To compare differences in the location of the distribution of passage times between age classes, we used Mann-Whitney tests (Wilkinson 1989). Passage data for Swainson's Thrushes, Red-eyed Vireos, Magnolia Warblers, and American Redstarts in 1990 and 1991 are from Woodrey and Chandler (1997).

Flight-range estimates for migrants captured at

TABLE 1.   Passage data (Julian dates) for six species migrating through Fort Morgan, Alabama, 1990 to 1992. P-values are from Mann-Whitney U-tests comparing differences in median passage times between age classes (AHY = after-hatching-year; HY = hatching-year).

Species	AHY			HY			P
	n	Median	Range	n	Median	Range	
1990							
Swainson's Thrush	22	278	258–303	71	273	250–301	0.14
Gray Catbird	61	292	274–300	234	279	266–305	<0.0001
White-eyed Vireo	8	272	267–290	72	288	261–299	0.09
Red-eyed Vireo	20	257	244–296	75	274	243–299	0.004
Magnolia Warbler	28	285	266–294	59	266	259–293	<0.0001
American Redstart	30	267	247–294	87	267	248–294	0.91
1991							
Swainson's Thrush	14	264	251–281	51	271	255–281	0.02
Gray Catbird	29	276	267–281	331	270	264–281	0.004
White-eyed Vireo	42	271	255–281	71	271	264–281	0.61
Red-eyed Vireo	28	256	244–279	69	257	245–281	0.06
Magnolia Warbler	23	276	264–281	35	270	251–281	<0.0001
American Redstart	61	279	245–281	133	267	246–281	<0.0001
1992							
Swainson's Thrush	27	276	255–288	34	278	255–292	0.32
Gray Catbird	127	284	272–294	863	285	255–301	0.11
White-eyed Vireo	41	282	259–295	79	284	255–301	0.13
Red-eyed Vireo	9	249	244–260	238	269	243–297	<0.0001
Magnolia Warbler	9	286	281–292	39	284	255–299	0.07
American Redstart	16	275	243–287	126	274	243–298	0.40

our study sites were derived from the model developed by Pennycuick (1989). His approach allows calculation of mechanical power in relation to airspeed on the basis of body mass and wing span of an individual bird (e.g. Pennycuick 1975, 1989). Using methods outlined in Pennycuick (1989), we measured wing span for at least 10 individuals within each age class for each species and used mean values in the calculations. To estimate the amount of fat available for migration in our simulation of trans-Gulf migration, we calculated mean body mass for each age class of a species and then subtracted the average fat-free body mass from the mean body mass and assumed the difference was fat available for migration. Although we assumed that mass differences reflected differences in fat stores, other factors may have contributed to observed differences (e.g. hypertrophy of flight muscles contributes to increased premigratory body mass; Marsh 1984). Nevertheless, because we were interested in making flight-range comparisons between age classes within species, we assumed that other factors contributing to differences between mean and lean body mass were the same across age classes.

Estimates of mean fat-free body mass are given by Connell et al. (1960) and Rogers and Odum (1964, 1966) for all species except the White-eyed Vireo. Estimation of the mean fat-free mass of White-eyed Vireos was based on the average body mass of transient individuals in the eastern United States (Dun-

ning 1993). Flight-range calculations were made using still-air conditions, and we assumed that migrants traveled at an average altitude of 500 m (air density = 1.17 kg/m^3; Kerlinger and Moore 1989) during their trans-Gulf flight.

RESULTS

Pattern of passage and age ratios.—Each of the six species showed age ratios skewed toward young birds, although the bias varied among species: Swainson's Thrush (71% HY, $n = 219$), Gray Catbird (87% HY, $n = 1,645$), White-eyed Vireo (71% HY, $n = 313$), Red-eyed Vireo (87% HY, $n = 439$), Magnolia Warbler (69% HY, $n = 192$), and American Redstart (76% HY, $n = 543$). Although age-specific passage dates varied among species and among years (Table 1), these differences do not mean that AHY and HY migrants do not co-occur during stopover on Fort Morgan peninsula; they do, but the extent of overlap varies among species (Table 1).

Fat load and body mass.—Few lean birds were captured during our study (see Figs. 1 to 6). With the possible exception of HY Swainson's Thrushes (Fig. 1), fat-score estimates (i.e. fat loads) were high for most birds captured re-
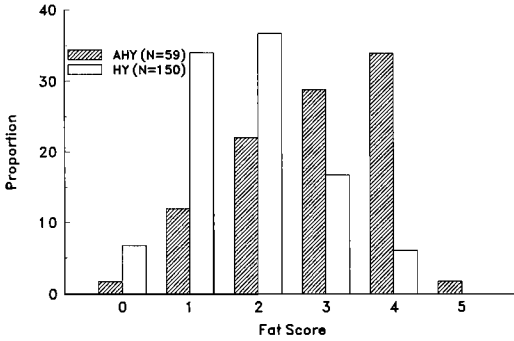
SWAINSON'S THRUSH

FIG. 1. Distribution of fat scores for after-hatching-year (AHY) and hatching year (HY) Swainson's Thrushes captured during fall migration, 1990 to 1992.
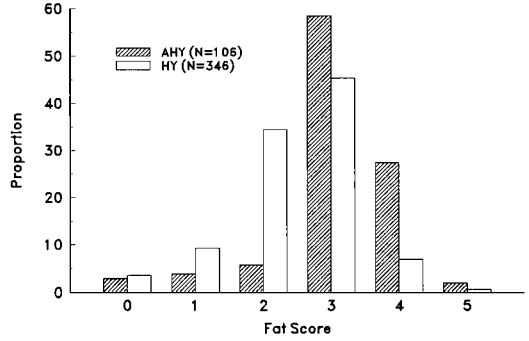
AMERICAN REDSTART

FIG. 3. Distribution of fat scores for after-hatching-year (AHY) and hatching year (HY) American Redstarts captured during fall migration, 1990 to 1992.

gardless of species and age. Age-specific differences in the distribution of fat scores were evident among Swainson's Thrushes ($Z = 5.85$, $P < 0.0001$), White-eyed Vireos ($Z = 2.22$, $P = 0.026$), and American Redstarts ($Z = 7.04$, $P < 0.0001$), with adults carrying larger fat loads (Figs. 1 to 3). Differences in the distribution of fat scores between age classes coincided with similar differences in mass for those three species (Table 2). Mean fat scores also differed significantly among Swainson's Thrushes ($t = 6.64$, df = 207, $P < 0.00001$), White-eyed Vireos ($t = 2.15$, df = 290, $P = 0.03$), and American Redstarts ($t = 6.45$, df = 450, $P < 0.00001$), with adults carrying significantly more fat than young birds (Table 2).

The distribution of fat scores did not differ between age classes for Gray Catbirds ($Z = 0.529$, $P = 0.597$; Fig. 4), Red-eyed Vireos ($Z = 0.141$, $P = 0.888$; Fig. 5), and Magnolia Warblers ($Z = 1.24$, $P = 0.215$; Fig. 6). Comparison of average mass between age classes revealed that young Gray Catbirds and Magnolia Warblers were heavier than adults (Table 2). Despite being significantly heavier than adults, neither young Gray Catbirds ($t = 0.60$, df = 1,577, $P = 0.55$) nor Magnolia Warblers ($t = 1.21$, df = 186, $P = 0.23$) carried significantly more fat, on average, than adults (Table 2). Given the lack of difference in average body mass for AHY and HY Red-eyed Vireos, it is not surprising that age classes did not differ in the amount of fat
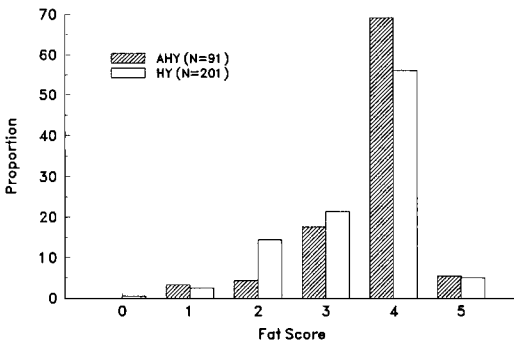
WHITE–EYED VIREO

FIG. 2. Distribution of fat scores for after-hatching-year (AHY) and hatching year (HY) White-eyed Vireos captured during fall migration, 1990 to 1992.
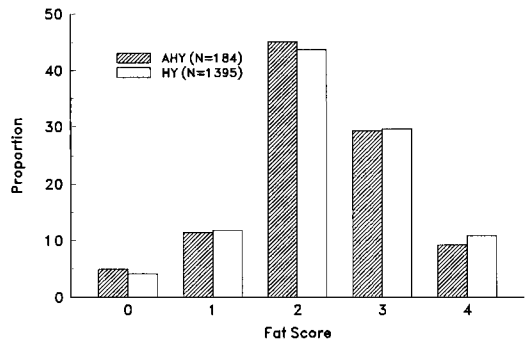
GRAY CATBIRD

FIG. 4. Distribution of fat scores for after-hatching-year (AHY) and hatching year (HY) Gray Catbirds captured during fall migration, 1990 to 1992.
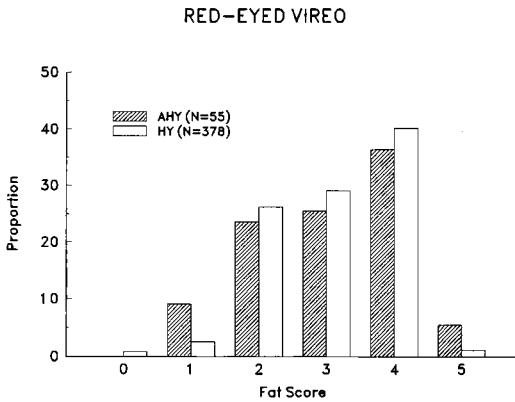
RED−EYED VIREO

MAGNOLIA WARBLER

FIG. 5.   Distribution of fat scores for after-hatching-year (AHY) and hatching year (HY) Red-eyed Vireos captured during fall migration, 1990 to 1992.
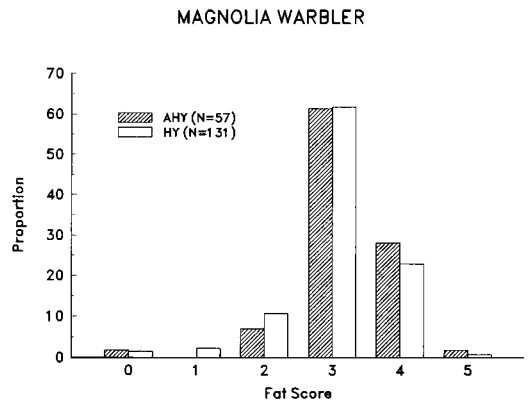
FIG. 6.   Distribution of fat scores for after-hatching-year (AHY) and hatching year (HY) Magnolia Warblers captured during fall migration, 1990 to 1992.

they carried ($t = 0.22$, df $= 431$, $P = 0.83$; Table 2).

Flight-range estimates.—Flight-range estimates indicated that for Swainson's Thrushes, Red-eyed Vireos, and Magnolia Warblers, fat scores ≥ 3 were sufficient to cross the Gulf of Mexico under still-air conditions, whereas scores ≥ 4

represented sufficient energy stores for Gray Catbirds and White-eyed Vireos to complete such a flight. Very few (ca. 10%) Gray Catbirds, regardless of age, could have crossed the Gulf of Mexico on the fat stores we estimated at the time of capture (see Fig. 4). The proportion of

TABLE 2.   Fat score, body mass, adjusted body mass (values are $\bar{x} \pm$ SE), results of one-way ANCOVA for age differences in body mass within species (using wing chord as the covariate), and flight-range estimates for six species migrating through Fort Morgan, Alabama. The minimum distance across the Gulf of Mexico is 1,200 km.

Age	n	Fat score	Mass (g)	Adjusted mass (g)	F	P	Flight-range estimate (km)
			Swainson's Thrush				
AHY	63	2.9 ± 0.15	33.3 ± 0.72	33.1 ± 0.72	25.33	<0.0001	1,290
HY	156	1.8 ± 0.08	29.5 ± 0.35	29.6 ± 0.35			740
			Gray Catbird				
AHY	217	2.3 ± 0.07	36.8 ± 0.26	36.3 ± 0.26	10.63	0.001	625
HY	1,428	2.3 ± 0.03	37.0 ± 0.09	37.1 ± 0.09			690
			White-eyed Vireo				
AHY	91	3.7 ± 0.08	13.7 ± 0.12	13.6 ± 0.12	10.52	0.001	1,250
HY	222	3.4 ± 0.06	12.9 ± 0.11	13.0 ± 0.11			850
			Red-eyed Vireo				
AHY	57	3.1 ± 0.15	19.5 ± 0.43	19.5 ± 0.43	0.24	0.628	1,300
HY	382	3.1 ± 0.05	19.7 ± 0.15	19.7 ± 0.15			1,375
			Magnolia Warbler				
AHY	60	3.2 ± 0.10	9.3 ± 0.12	9.2 ± 0.12	5.18	0.024	1,150
HY	132	3.0 ± 0.07	9.5 ± 0.09	9.5 ± 0.09			1,290
			American Redstart				
AHY	107	3.1 ± 0.09	9.4 ± 0.09	9.3 ± 0.09	60.33	<0.0001	1,460
HY	346	2.4 ± 0.05	8.3 ± 0.06	8.4 ± 0.06			1,050

birds carrying fat loads sufficient to cross the Gulf of Mexico was much higher for the other five species. Almost all Magnolia Warblers, HYs (85%) and AHYs (91%), were fat enough for a trans-Gulf flight (Fig. 6), and about two-thirds of all Red-eyed Vireos, HYs (70%) and AHYs (67%), were sufficiently fat (Fig. 5). The other species were characterized by age-dependent differences: 53% of the HY American Redstarts (Fig. 3) and 88% of the AHYs carried sufficient fat stores for a nonstop flight across the Gulf. A three-fold difference in the proportion of birds capable of a trans-Gulf flight existed between AHY (64%) and HY (23%) Swainson's Thrushes (Fig. 1), and a two-fold difference characterized AHY (80%) and HY (38%) White-eyed Vireos (Fig. 2).

If we assume that the difference between lean body mass and body mass upon capture represents the migrant's fat load, age-dependent differences in the average migrant's ability to complete a trans-Gulf crossing were evident for some species. Adult Swainson's Thrushes, White-eyed Vireos, and American Redstarts (Table 2) had deposited energy stores sufficient to cross the Gulf of Mexico under still-air conditions. This trend was reversed for Magnolia Warblers (Table 2); the average HY migrant could complete a trans-Gulf crossing with fat to spare, whereas the average AHY migrant had no margin of safety in relation to a flight across the Gulf of Mexico. Neither AHY nor HY Gray Catbirds, of average mass, carried sufficient stores for a successful trans-Gulf flight (Table 2). The average Red-eyed Vireo, regardless of age class, carried sufficient fat deposits to complete a trans-Gulf flight (Table 2).

Wing span, a major component in Pennycuick's (1989) flight-performance model, was similar between age classes of the focal species (Swainson's Thrush: AHY, 29.2 ± SE of 0.16 cm, $n = 22$; HY, 29.0 ± 0.18 cm, $n = 22$; Gray Catbird: AHY, 27.7 ± 0.15 cm, $n = 19$; HY, 27.6 ± 0.18 cm, $n = 26$; White-eyed Vireo: AHY, 19.6 ± 0.08 cm, $n = 21$; HY, 19.2 ± 0.40 cm, $n = 22$; Red-eyed Vireo: AHY, 24.7 ± 0.32 cm, $n = 10$; HY, 24.3 ± 0.12 cm, $n = 38$; Magnolia Warbler: AHY, 18.7 ± 0.21 cm, $n = 11$; HY, 18.2 ± 0.10 cm, $n = 24$; American Redstart: AHY, 18.9 ± 0.15 cm, $n = 11$; HY, 18.5 ± 0.11 cm, $n = 22$). Consequently, differences in wing span had no appreciable effect on flight range-estimates.

Recapture and length of stopover.—With the ex-ception of White-eyed Vireos, less than 10% of the individuals we captured were recaptured on subsequent days: American Redstarts and Gray Catbirds (8%), Magnolia Warblers (3%), Swainson's Thrushes (2%), and Red-eyed Vireos (< 1%). More than a quarter (26%) of the White-eyed Vireos captured at our study site were recaptured on a subsequent day; AHYs (31%) and HYs (23%) were equally likely to be recaptured ($\chi^2 = 1.98$, $P = 0.159$). The average length of stay for White-eyed Vireos that were recaptured beyond the day of first capture did not differ between HYs (3.9 ± 2.9 days) and AHYs (3.6 ± 2.5 days; $t = -0.45$, df = 70, $P >$ 0.05). The average length of stay for Gray Catbirds recaptured after the day of first capture was highly variable for both age classes (AHY, 4.1 ± 3.2 days; HY, 4.7 ± 4.5 days). The likelihood of recapture on a subsequent day did not differ between the two age classes of Gray Catbirds ($\chi^2 = 0.144$, $P = 0.704$).

Change in mass and fat score.—Neither body mass nor fat scores changed appreciably during stopover regardless of species or age within species. HY and AHY White-eyed Vireos that were recaptured gained, on average, only 0.2 ± 0.3 g/day, and fat scores did not differ between initial and final captures (AHY: initial, 3.4 ± 0.9; final, 3.8 ± 0.9; $t = 0.60$, $n = 27$, $P > 0.05$; HY: initial, 3.3 ± 1.0; final, 3.6 ± 0.9; $t = 1.50$, $n = 45$, $P > 0.05$). Recaptured Gray Catbirds lost 0.10 g/day during their stopover regardless of age, and fat scores remained unchanged for the species (AHY: initial, 2.4 ± 0.9; final, 2.6 ± 1.0; $t = 0.61$, $n = 16$, $P > 0.05$; HY: initial, 2.4 ± 0.9; final, 2.5 ± 1.0; $t = 0.83$, $n = 109$, $P > 0.05$). The American Redstarts that we recaptured the day after initial capture exhibited only slight changes in mass and fat scores (AHY, $t = 0.00$, $n = 20$, $P > 0.05$; HY, $t = 1.43$, $n = 20$, $P > 0.05$) between recaptures. Infrequent recaptures prevented analysis of change in mass based on recaptured individuals of other species.

An analysis of body mass at initial capture and time of day indicated that birds maintained their mass regardless of species and age class within species (Table 3). Only HY American Redstarts and HY White-eyed Vireos showed a significant linear relationship between body mass and time of day (Table 3). Pearson correlation analysis failed to discern a

TABLE 3. Summary of linear regression models ($Y = b + mX$) of the relationship between body mass and capture time. The slope (m) is defined as the change in body mass (g) per hour. The correlation coefficient (r) is a measure of strength of the relationship between capture time and body mass. Δ mass/day is the change in body mass (g) for a 12-h day of mist-netting. Flight range (km) is the estimated distance an average migrant could fly for the given Δ mass/day. Flight-range estimates derived from computer program of Pennycuick (1989).

Age	n	b	m	r	F	P	Δ mass/day	Flight range
				Swainson's Thrush				
AHY	61	35.2	−0.002	0.09	0.55	0.462	−0.024	—
HY	154	31.2	−0.002	0.09	1.42	0.236	−0.024	—
				Gray Catbird				
AHY	195	35.5	0.001	0.09	1.64	0.202	0.012	1.63
HY	1,310	36.7	0.001	0.03	1.71	0.191	0.012	1.63
				White-eyed Vireo				
AHY	62	14.1	−0.0001	0.10	0.58	0.449	−0.0012	—
HY	168	11.6	0.001	0.25	11.52	0.001	0.012	4.68
				Red-eyed Vireo				
AHY	55	18.7	0.001	0.09	0.42	0.520	0.012	3.64
HY	378	19.8	−0.0001	0.01	0.05	0.818	−0.0012	—
				Magnolia Warbler				
AHY	60	8.9	0.0001	0.08	0.41	0.525	0.0012	0.68
HY	126	9.4	0.0001	0.003	0.003	0.957	0.0012	0.67
				American Redstart				
AHY	97	9.4	0.0001	0.01	0.01	0.910	0.0012	0.78
HY	314	7.8	0.001	0.15	7.75	0.006	0.012	7.30

relationship between body-size measures (tarsus length and wing chord) and time of day.

If body condition upon arrival affects the duration of stopover, then birds that are recaptured should be leaner when first captured than those captured only once (i.e. birds that presumably departed soon after stopping). No difference existed between fat-score distributions (see Fig. 7) of recaptured and "not recaptured" White-eyed Vireos ($\chi^2 = 3.71$, df = 4, $P = 0.447$) and American Redstarts ($\chi^2 = 4.82$, df = 4, $P = 0.191$), although recaptured redstarts were lighter ($\bar{x} = 8.2 \pm$ SD of 1.0 g) upon initial capture than individuals not recaptured ($\bar{x} = 8.6 \pm 1.1$ g; $Z = 2.25$, $P = 0.024$). Fat-score distributions did differ for Gray Catbirds ($\chi^2 = 9.98$, df = 4, $P = 0.041$), and recaptured birds were leaner ($\bar{x} = 36.4 \pm 3.2$ g) upon initial capture than those that were not recaptured ($\bar{x} = 37.1 \pm 3.7$ g; $Z = 2.28$, $P = 0.023$). Small samples of recaptured adults precluded age-specific comparisons.

DISCUSSION

Pattern of passage and age ratios.—Age-specific patterns of passage varied among species and across years. In no species, however, did one age class complete its passage before the arrival of the other age class. Consequently, the possibility for competitive interactions existed between young and adults.

Although more HY than AHY migrants stopped on Fort Morgan Peninsula, the age bias in our capture data was less pronounced for four of six species than has been reported for other coastal sites during fall migration. HY birds comprised 85 to 95% of the captures along the Atlantic (Drury and Keith 1962, Murray 1966, Ralph 1981, Morris et al. 1996) and Pacific (Ralph 1971, Stewart et al. 1974) coasts. The phenomenon of heavily skewed age ratios along the Atlantic and Pacific coasts is referred to as the "coastal effect" (Ralph 1981) and is thought to result from different migratory routes followed by young and adults (Leberman and Clench 1975) or from high percentages of young on the periphery of a species' migration route (Ralph 1981).

Other testable explanations come to mind for the skewed age ratios we observed. For example, adults may be better able to "predict" atmospheric conditions conducive to migratory
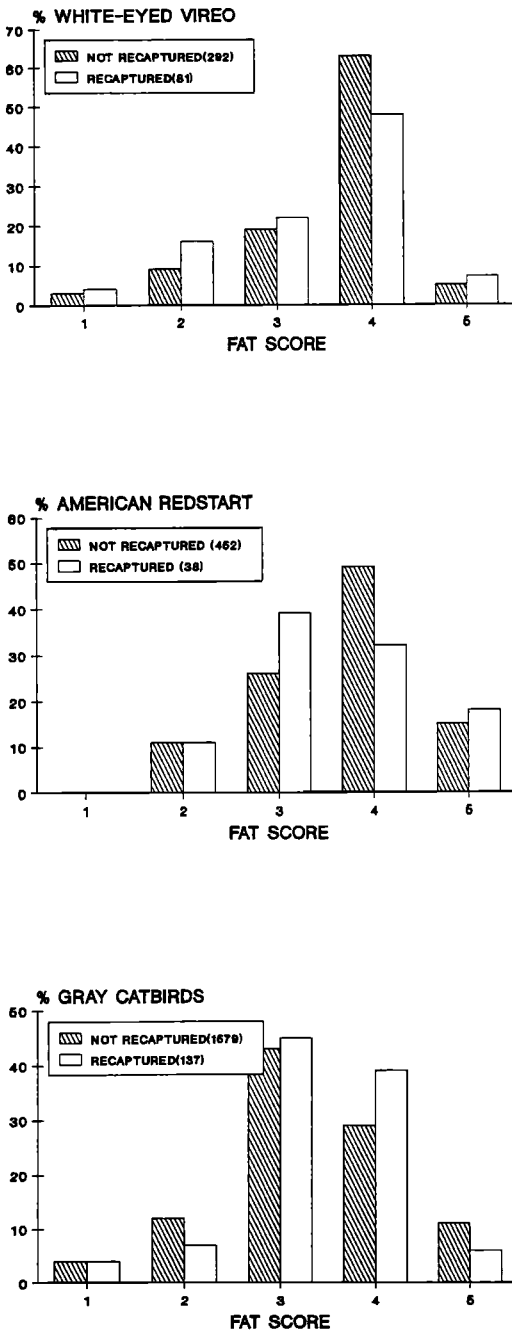
FIG. 7. Distribution of fat scores for birds recaptured and birds not recaptured during the fall migration, 1990 to 1992. Only Gray Catbird, White-eyed Vireo, and American Redstart are shown because of insufficient sample sizes for other species. Sample sizes are shown in parentheses.

flight (see Kerlinger and Moore 1989) and be less uncertain about continuing migration in relation to the Gulf of Mexico and therefore occur in fewer numbers immediately along the coast. Also, adults may be more likely to stopover before reaching coastal areas or to reorient inland away from the coast to avoid the high density of migrants that sometimes characterizes coastal habitat. Although Lindström and Alerstam (1986) found evidence of reorientation in relation to a coast primarily among young migrants and argued that young birds did so because they were competitively inferior to adults, there is no *a priori* reason why adults should not reorient in relation to an ecological barrier. For example, predators often concentrate along coasts (Kerlinger 1989), and adults may be better able to assess the potential for predation than are inexperienced birds.

Energetic condition.—Adult Swainson's Thrushes, White-eyed Vireos, and American Redstarts carried more fat, on average, than young birds, and a higher proportion of adults was prepared energetically to cross the Gulf of Mexico should they have chosen to do so (see Able 1972, Sandberg and Moore 1996). Similar age-specific differences in fat loads occurred in Pied Flycatchers (*Ficedula hypoleuca*) in Spain (Veiga 1986), Sedge Warblers (*Acrocephalus schoenobaenus*) in northern Italy (Spina and Bezzi 1990), and Bluethroats (*Luscinia svecica*) in Sweden (Ellegren 1991). Murray (1979) found that adult Yellow-rumped Warblers (*Dendroica coronata*) and Blackpoll Warblers (*Dendroica striata*) weighed significantly more than young birds when they stopped during fall migration along the mid-Atlantic coast of the United States, but differences in mass may have reflected more than just fat (see Lindström and Piersma 1993). Blackpoll Warblers probably increased their flight-muscle mass in anticipation of a long, nonstop flight over the western Atlantic Ocean (Nisbet et al. 1963, Nisbet 1970; but see Murray 1989), and observed differences in mass may have reflected age-dependent differences in the ability to increase muscle mass or differences in migratory routes. Recently, Morris et al. (1996) found that young birds were significantly lighter than adults in one-third of the 15 Neotropical landbird migrant species examined during fall passage on Appledore Island, Maine, including Red-eyed Vireos and American Redstarts. Interestingly, AHY and HY Swainson's

Thrushes in our study area had the same av-
erage body masses as at Appledore Island.

In our study, AHY Red-eyed Vireos, Mag-
nolia Warblers, and Gray Catbirds carried no
more fat than did HYs, but fat loads varied
among these species vis-a-vis possible nonstop
flights over the Gulf of Mexico. Red-eyed Vir-
eos, regardless of age, deposited more than
enough fat to cross the Gulf of Mexico under
still-air conditions. Extra fat stores would be
especially advantageous should a migrant en-
counter unfavorable weather during a trans-
Gulf flight (see Moore and Kerlinger 1991).
Even if atmospheric conditions were favorable
throughout the flight across the Gulf of Mexico,
birds that arrived at their next stopover with a
margin of safety would be at an advantage
should they experience poor feeding conditions
upon arrival, which would require more time
than usual to locate resources (Sandberg and
Moore 1997). Both adult and young Magnolia
Warblers had deposited sufficient fat stores to
cross the Gulf of Mexico, but only young birds
had deposited a margin of safety based on our
estimates of flight performance.

The average Gray Catbird (AHY or HY) car-
ried sufficient fat to fly 600 to 700 km, but not
enough to cross the Gulf of Mexico. Our sample
of Gray Catbirds undoubtedly included birds
that wintered in peninsular Florida and in
southern Texas (Root 1988), i.e. birds that
would migrate along the coast to reach those
destinations. Other Gray Catbirds that migrate
south of the Gulf of Mexico may elect to forego
a trans-Gulf route (see Eddins and Rogers
1992).

Forgoing a trans-Gulf route may be the Gray
Catbird's better strategy given the relationship
between aerodynamic performance and flight
morphology (see Yong and Moore 1994). Gray
Catbirds have relatively short wings, small
wing area, a low aspect ratio, and greater wing
loading, which may constrain them to shorter
migratory flights. Species or individuals with
relatively long, pointed wings migrate more ef-
ficiently, and the energy demand per unit dis-
tance traveled is lower. Reduced flight costs
means that less fat is required to negotiate a
long-distance flight (e.g. trans-Gulf) and that
less fat need be replenished during stopovers
before migration is resumed. That Gray Cat-
birds were not especially fat when we captured
them does not preclude trans-Gulf migration

should they succeed in depositing adequate
stores. Marsh (1984) reported hypertrophy of
flight muscles in Gray Catbirds captured in fall
along the northern coast of the Gulf of Mexico,
which would be expected in anticipation of a
long, nonstop flight. Also, Gray Catbirds are
common in samples of Neotropical landbird
migrants that stop on barrier islands along the
Mississippi coast in spring, presumably fol-
lowing a trans-Gulf flight (Moore unpubl.
data).

Length of stopover and mass change.—Duration
of stopover during migration varies from a few
hours to several days and depends on several
factors (Moore et al. 1995). Generally, length of
stay is negatively correlated with fat load (Bair-
lein 1985, Pettersson and Hasselquist 1985, Bie-
bach et al. 1986, Moore and Kerlinger 1987,
Yong and Moore 1993), and fat loads often are
age-dependent (Veiga 1986, Ellegren 1991,
Morris et al. 1996, this study). With the excep-
tion of White-eyed Vireos, we recaptured very
few migrants of either age class. Presumably,
migrants departed soon after capture, which is
not surprising given their energetic condition
(i.e. large fat loads). Even among lean birds,
however, the probability of staying depends on
habitat suitability (Rappole and Warner 1976,
Graber and Graber 1983, Kuenzi et al. 1991)
and is subject to time constraints (Safriel and
Lavee 1988, Alerstam and Lindström 1990,
Winker et al. 1992). When a lean migrant ex-
periences a low rate of fat deposition during
stopover, the best decision might be to move on
(Rappole and Warner 1976, Graber and Graber
1983).

Migrants that reach the northern coast of the
Gulf of Mexico in fall might be better off con-
tinuing to move along the coast regardless of
energetic condition or prospects for fat depo-
sition, because atmospheric conditions favora-
ble for a trans-Gulf flight do not occur with any
regularity until later in the fall (Able 1972).
Cage-orientation experiments with Red-eyed
Vireos that stop on Fort Morgan Peninsula in
fall revealed condition-dependent directional-
ity (Sandberg and Moore 1996). Birds carrying
sufficient fat stores to cross the Gulf of Mexico
oriented their activity toward the south, where-
as leaner birds oriented in a westerly direction
parallel with the coast. If a lean migrant suc-
ceeded in depositing sufficient fat to make a
trans-Gulf flight, and if atmospheric conditions

were favorable, we would expect the bird to depart across the Gulf.

Rates of mass change during stopover are used to measure fat-deposition rates (e.g. Kuenzi et al. 1991, Winker et al. 1992). We could apply this approach to only two species because few migrants were recaptured. In an attempt to draw inferences about rates of mass change for transients, we used a modified version of linear regression analysis (see Winker et al. 1992) to examine body mass in relation to time of day among birds captured only once. Although HY American Redstarts and White-eyed Vireos showed a significant positive relationship between capture time and body mass, the increased mass represented a flight distance of only a few kilometers, assuming the increased mass was in the form of fat. Migrants that stop on Fort Morgan Peninsula do so briefly, and during stopover they neither gain nor lose fat stores; rather, they maintain substantial fat loads. Migrants with insufficient fat stores may move inland in search of habitats more favorable for fat deposition (Alerstam 1978, Lindström and Alerstam 1986), or they may continue migration along the coast in a circum-Gulf manner.

In summary, the age-specific differences that we observed among Swainson's Thrushes, American Redstarts, and White-eyed Vireos may reflect the difficulty hatching-year birds experience trying to solve en-route "problems" on their first migration. Younger birds often are less proficient foragers (Burger 1988, Wunderle 1991) and are usually socially subordinate to adults (Terrill 1987, Sherry and Holmes 1989). The latter could be a serious handicap for a young migrant if status affected the opportunity to deposit necessary energy stores (see Ekman and Askenmo 1984, Piper and Wiley 1990). A migrant that departs a stopover site with relatively low fat stores has a smaller margin of safety to buffer variation in food availability at the next stopover, or it may arrive at its destination in poor nutritional condition (Moore and Kerlinger 1991). Migrants that arrive in poor condition or later than normal may jeopardize opportunities to secure a place in high-quality habitat or to attract a mate in the case of spring migration (e.g. Askenmo 1982, Ojanen 1984, Sandberg and Moore 1996). If a bird expects to "catch-up" with the overall time schedule of migration, it must refuel faster

than average during its next stopover. Yet, a penalty may be attached to late arrival at the next stopover if resource levels have been depressed by earlier migrants (see Moore and Yong 1991).

The age-specific differences in fat load that we observed also may reflect a mass-dependent predation effect (i.e. young birds carry less fat in relation to predation risk). Several measures of flight capacity are reduced with an increased amount of fat (Hedenstrom 1992); hence, the capacity to escape a predator should be adversely affected by high fat loads (Witter et al. 1994). If young are more vulnerable to predation, then young birds may deposit and maintain less fat.

Observed differences in fat loads between young and adult migrants also may reflect different migration strategies, including differences in passage routes and destinations. Young Swainson's Thrushes, for example, may be more likely to migrate along a circum-Gulf route than follow a trans-Gulf route. Because flight costs increase as fat stores accumulate (Alerstam 1991), a migrant's flight range becomes a negatively accelerating function of its fat load (see Alerstam and Lindström 1990). The large fat stores that provide a margin of safety during long flights across ecological barriers may not be necessary for overland flights.

Finally, we found no age-specific differences in fat loads in Red-eyed Vireos, Magnolia Warblers, and Gray Catbirds. Although we cannot rule out the possibility that HYs of these species deposit fat at a slower rate than adults, our results reveal that HY Red-eyed Vireos and Magnolia Warblers are as well prepared energetically as are adults for long, nonstop migratory flights.

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