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Stopover and fat deposition by North American wood-warblers (Parulinae) following spring migration over the Gulf of Mexico

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Summary. Length of stopover and rate of weight gain (fat deposition) were studied in several species of passerine birds that stopped in southwestern Louisiana along the northern coast of the Gulf of Mexico after a trans-Gulf flight. Fat-depleted birds were more common among the birds that arrived at our study site in southwest Louisiana, though variability characterized our samples. Migrants that landed after encountering opposing winds or rain over the northern Gulf of Mexico were, on average, fatter than migrants that landed when weather was favorable for continued migration. Some of the variation in the energetic condition of arrivals may be explained by the location where migrants initiated crossings. Our simulation of flight over the Gulf of Mexico showed that with following winds a warbler can cross the Gulf of Mexico from Yucatan with fat reserves to spare, and stronger tailwinds make flights from as far south as Honduras energetically permissible. The length of stay after a trans-Gulf flight was related to the extent of fat-depletion upon arrival: lean birds stayed longer than fat migrants. Migrants stopped over for 1–7 days and replenished energy reserves at rates that varied from 0.19 g/d for Hooded Warblers (*Wilsonia citrina*) to 0.87 g/d for Ovenbirds (*Seiurus aurocapillus*). Within each species, most individuals gained weight at a rapid rate, though a few individuals lost or maintained weight during their stay.

Key words: Migration – Wood-Warblers – Gulf of Mexico – Energetics

Nearctic-neotropical migrants may experience the 'best of two worlds': increased survivorship associated with neotropical wintering and a productive temperate environment for breeding. Whether benefits associated with the evolution of migration accrue through increased productivity or increased probability of surviving an unfavorable season or both, they must be balanced against the cost of long distance migration (Greenberg 1980; Morse 1980; Ketterson and Nolan 1982; Pienkowski and Evans 1985). Besides the energetic cost of transport (see Pennycuick 1969, 1975), migrants must contend with fluctuations of food availability (Bibby et al. 1976; Mehlum 1983a), predators (Fry et al. 1970; Page and Whitacre 1975; Metcalfe and Furness 1984), competition among energy-depleted migrants and residents at stopover sites (Rappole and Warner 1976; Laursen 1978; Abramsky and Safriel 1980; Bibby and Green 1980; Schneider and Harrington 1981; Bairlein 1983; Mehlum 1983a), unfavorable weather (Gauthreaux 1971), as well as possible orientation errors (Ralph 1978). How well migrants respond to the contingencies that arise en route influences their survival and future reproductive success.

A striking feature of North American bird migration is the mass movement of individuals over the Gulf of Mexico (Lowery 1946, 1951; Gauthreaux 1971, 1972; Able 1972; Buskirk 1980). After the first week in April migration across the Gulf is rarely interrupted until mid-May (Gauthreaux 1971). Isolated woodlands and wooded barrier islands along the northern coast provide the last stopover before fall migrants cross the Gulf of Mexico and the first landfall for birds returning north in the spring. These habitats are crucial to fall migrants because they provide a place to deposit energy reserves for a nonstop flight (18–24 h) of >1,000 km (Caldwell et al. 1963; Marsh 1983) and to spring migrants by giving them a place to rest and replenish energy reserves following trans-Gulf flight.

The energy necessary for migration is derived mostly from fat reserves (triglycerides) accumulated before a flight. The principal mechanism of fat (re)deposition is hyperphagia, when food intake may increase 40%–50% (Berthold 1975, Blem 1976, 1980). As fat stores are depleted, birds that restore reserves rapidly improve their chances of successful migration (see Graber and Graber 1983; Bairlein 1985b; Moore and Simm 1985, 1986). Hence, the selection of favorable en route habitat, where energy reserves can be rapidly replenished, is especially important (Sprunt 1975; Bradstreet et al. 1977; Schneider and Harrington 1981; Martin 1985; Martin and Karr 1986). Adequate energy reserves are especially important before and after crossing ecological barriers (see Caldwell et al. 1963; Dolnik and Blyumenthal 1967; Moreau 1972; Wood 1982; Marsh 1983; Yom-Tov 1984; Bairlein 1985a; Biebach et al. 1986).

According to Keast (1980), the largest number of nearctic-neotropical migrants are wood-warblers (subfamily Parulinae), many of which are abundant along the northern coast of the Gulf of Mexico in spring. Our analysis focuses on the behavior and physiology of these migrants following a trans-Gulf flight and addresses these questions:

1) What is the energetic condition of migrants that stopover along the northern coast of the Gulf of Mexico in spring? Is energetic condition upon arrival related to weather conditions during a crossing?

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2) How long do migrants stopover after crossing the Gulf of Mexico?

3) Is a migrant's length of stay related to its energetic condition upon arrival?

4) At what rate do migrants replenish energy reserves during stopover following trans-Gulf migration?

Methods

Field work was conducted at Peveto Beach, Louisiana (29°90′N, 93°30′W), a 10 hectare "chenier" (coastal woodland) located along the northern coast of the Gulf of Mexico west of Cameron, Louisiana (Fig. 1). The narrow cheniers along the southwest coast of Louisiana and the wooded islands along the Alabama, Mississippi and east Louisiana coasts are thought to be important stopover sites for trans-Gulf migrants (Sprunt 1975). The cheniers support a luxuriant vegetation dominated by hackberry (*Celtus laevigata*) and live oak (*Quercus virginiana*). Migrants often occur at very high densities in coastal habitats in response to weather that is unfavorable for continued migration (Gauthreaux 1971, 1972). Even with favorable weather, migrants are found in large numbers within these habitats.

Data were gathered in April 1985 and 1986. Migrants were captured (and recaptured) in mist-nests (12×2.6 m, 4 shelves, 30 mm-mesh) which were checked every 20 min. Birds were weighed with a Pesola 50-g spring balance to the nearest 0.25 g, fat classed, banded with a USFWS aluminum leg band, sexed and aged (when possible). Visible (subcutaneous) fat was quantified according to an ordinal scale developed by Helms and Drury (1960): (0) no visible fat, (1) traces of fat in the furcular and abdominal regions, (2) small reserves of fat, furcular region deeply concave and subcutaneous fat on abdomen not continuous, (3) moderate reserves forming a continuous sheet of fat, but not conspicuously mounted, (4) considerable reserves filling fossa and abdominal fat conspicuously mounted, (5) furcular and abdominal fat deposits conspicuously mounted and convex. No birds were classified 5 and the few class 4 birds were analyzed with the class 3 birds. Estimates were made by blowing feathers aside in the interclavicular fossa and abdominal regions. Fat class data should not be interpreted as total lipid, though changes in fat classes represent changes in lipid reserves. Recaptured birds were weighed and assigned to a fat class without reference to previous records.

If comparisons are made from one capture to the next, weights must be taken at the same time of day or corrected to the same time by using the rate of weight gain during the daylight hours (see Cherry 1982). We determined their rate by computing the mean for a sample of birds ($n = 37$) captured >5 h apart on the same day. Of these migrants, 6 lost weight, 8 experienced no weight change, and 23 increased their weight. We standardized the rate of weight gain by computing the percent change/h (average $= 0.609\%/\mathrm{h} \pm 0.097$ SE), which yielded an overall rate of $0.0784\ \mathrm{g/h} \pm 0.013$ SE. This %/h rate was used to correct weights to 1200 for all birds that were captured and recaptured.

The weight change of individual migrants was computed by subtracting the weight upon first capture from the weight upon last capture after correcting the weights to 1200. Minimum stopover time was computed by subtracting the date of first capture from the date of last capture. We computed minimum stopover according to Cherry (1982), i.e. a 1 day stopover is equivalent to 1 night plus part of 2 days. The rate of weight change was computed by dividing the weight change by the length of stopover. This method of computing stopover differs from Borror (1948), Bairlein (1985a), and Biebach et al. (1986) who count each day a migrant is present as a day of stopover. In either case, the calculated minimum stopover period is a conservative estimate because the likelihood of netting a migrant could not assure that the bird was captured on its first and last day of stopover.

Results

Energetic condition of arrivals

Migrants that have crossed the Gulf of Mexico and stopped along the northern coast were expected to be fat-depleted and nearly half (41.1%) of the migrants captured in this study ($n = 627$) were lean (fat class $= 0$). On the other hand, a third (35.1%) of the migrants that stopped had sufficient fat stores remaining to be ranked fat class 2 or greater and presumably sufficient energy reserves to continue migration. Weather conditions along the northern Gulf coast

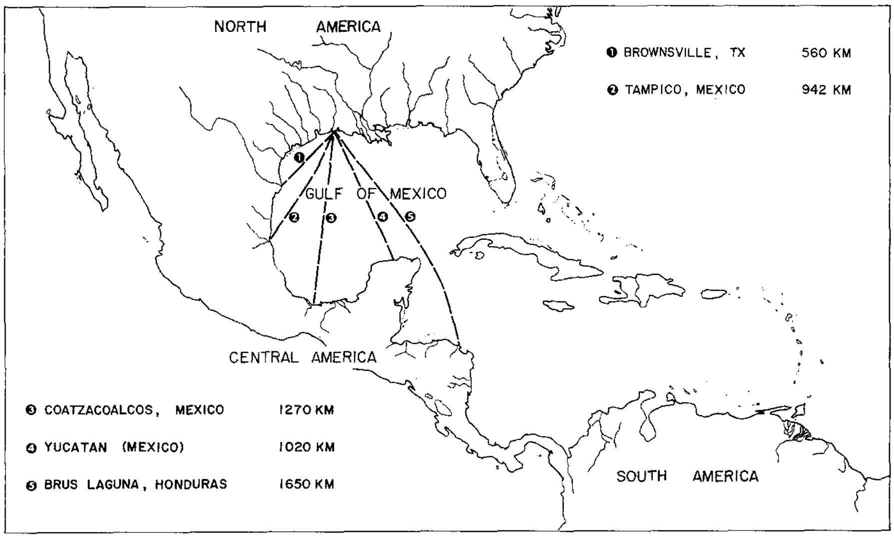

Fig. 1. Study site is a coastal woodland along the northern coast of the Gulf of Mexico where the dotted lines (flight paths) converge. Distances between possible departure points and the Louisiana site are given

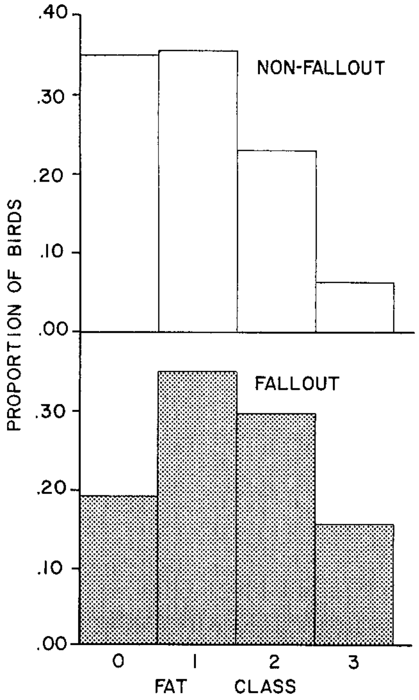

Fig. 2. Frequency distribution of fat class scores for migrants captured when weather over the northern coast of the Gulf of Mexico was unfavorable for ongoing migration (Fallout situation, n = 283) and when weather was favorable (Non-Fallout situation, n = 344)

Table 1. The number of individuals banded and recaptured for the ten species that accounted for 93% of the total banded. Migration distance is based on median breeding latitude

Species	Migration distance	Banded	Recaptured	
			N[a]	%
Hooded Warbler *Wilsonia citrina*	Middle	146	21	14.4
Kentucky W. *Oporornis formosus*	Middle	127	41	32.3
Ovenbird *Seiurus aurocapillus*	Middle-Long	80	20	25.0
Prothonotary W. *Prothonotaria citrea*	Middle	69	15	21.7
Worm-eating W. *Helmitheros vermivorus*	Middle	51	10	19.6
Tennessee W. *Vermivora peregrina*	Long	29	0	0.0
Northern Waterthrush *S. noveboracensis*	Long	27	1	3.7
Black & White W. *Mniotilta varia*	Long-Middle	23	0	0.0
Blue-winged W. *Vermivora pinus*	Middle-Long	23	2	8.7
Swainson's W. *Limnothlypis swainsonii*	Middle	13	6	46.2

[a] 2 birds escaped before they could reweighed

is one factor that could influence the proportion of fat-depleted migrants in a sample. Migrants that encounter headwinds or weather otherwise unfavorable for migration over the northern coast often stop in large numbers at the first suitable habitat (= birdwatcher's fallout). We looked at the arrival condition of migrants as a function of weather by distinguishing between migrants captured on 'fallout' days ($n = 283$) when the weather was unfavorable, i.e. winds from the NW, N, or NE and/or rain, and migrants otherwise captured (Fig. 2). More lean birds and fewer fat birds cease migrating on days when winds are favorable for migration ($X^2 = 27.44$, 3 df, $P < 0.001$). Even with favorable winds, some moderately fat birds do stop along the coast after a trans-Gulf flight.

Length of stopover

Twenty-three species of wood-warblers stopped at our study site. Ten species accounted for >93% of the total, whereas 6 species accounted for >95% of individuals ($n = 116$) recaptured after the day of initial capture (Table 1). With the possible exception of the Ovenbird longer distance migrants, notably the Tennessee Warbler and Northern Waterthrush, were infrequently recaptured (see Table 1).

Migrants that stopover following a trans-Gulf flight most often stay only 1 or 2 days before continuing migration (Fig. 3). The average length of stay varies for different species (see Table 2) ranging from 1.6 days for Worm-eating Warblers to 2.5 days for Kentucky Warblers. The likelihood that a migrant will stopover (and be recaptured) was positively related to the bird's energetic condition upon arrival (Fig. 4). Not surprisingly, comparison of the two distributions plotted in Fig. 4 suggests that learner birds stay over longer than fatter birds ($X^2 = 10.89$, 3 df, $P < 0.025$).

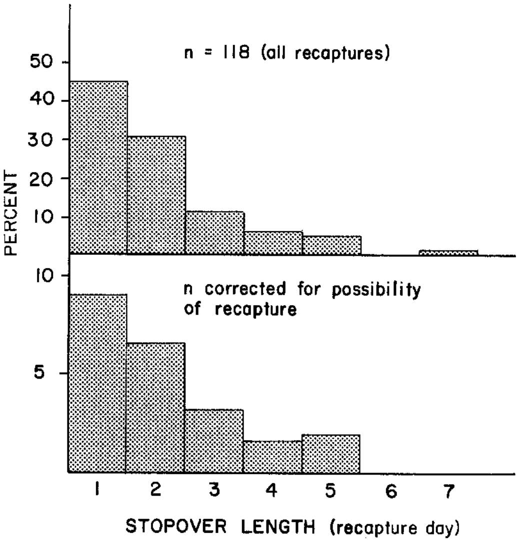

Fig. 3. Frequency distribution of the minimum stopover period fallowing a trans-Gulf flight for all recaptures (top histogram) and after the sample of recaptures was adjusted for the possibility of recapture (bottom histogram). Sample size was corrected by eliminating birds from the analysis which could not be recaptured because we were not at the study site

Rate of weight gain

Data on weight gain and replenishment of energy reserves were available for 6 species (Table 2). Whereas all 6 species

Table 2. Length of stopover, body weight change, and fat accumulation for 6 species of migrant birds at the Peveto Beach, LA, Woodland. Mean ± s.d. given

Spp	*N*	Stopover[a]	Gain (g)	Gain (%)	Gain (g/d)	Gain (%/d)	FC[b]	% that lost wgt
Kentucky Warbler	38	2.45±1.52	1.27±1.00	10.65± 8.52	0.59±0.50	4.80±3.94	1.22±0.99	7.9%
Hooded Warbler	20	2.00±0.97	0.36±0.49	4.46± 4.75	0.19±0.29	2.10±3.14	0.58±1.02	15.0%
Ovenbird	19	1.68±0.89	1.30±1.08	8.08± 6.66	0.87±0.70	5.44±4.35	1.00±1.00	5.3%
Prothonotary Warbler	14	2.00±1.41	1.35±1.27	11.11±10.01	0.62±0.47	5.21±3.91	1.71±1.27	7.1%
Worm-eating Warbler	10	1.60±0.70	0.71±0.80	6.04± 6.43	0.45±0.45	3.97±4.07	0.70±1.06	10.0%
Swainson's Warbler	6	1.67±0.82	0.58±0.49	4.28± 3.87	0.41±0.46	3.00±3.37	0.33±0.82	16.7%

[a] Length of stopover in days

[b] Fat classes gained since initial capture (includes entire sample). Data were not adjusted for stopover length

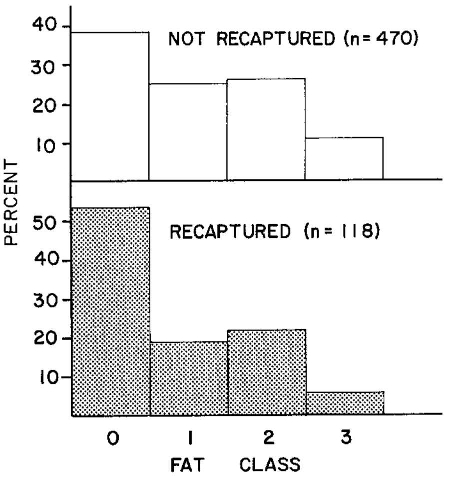

Fig. 4. Frequency distribution of fat class scores for migrants captured only one time (top histogram) and for migrants recaptured at least once following a trans-Gulf flight. The two distributions are significantly different from each other (X^2 test) with $P < 0.025$)

showed a positive rate of gain (grams/day) over the stopover period, species averages ranged from 0.87 g/d for Ovenbirds to 0.19 g/d for Hooded Warblers. A one-way ANOVA for rate of weight gain (4 species with largest sample sizes only) confirmed statistically differences among species ($F = 6.01$, 3,85 df, $P < 0.01$). A post-hoc Tukey Test revealed the rates of gain for Ovenbirds and Prothonotary Warblers to be greater than the rate of gain for Hooded Warblers ($P < 0.05$), but no differences among the other species. Interestingly, the percentage changes in weight gain (%/day) were not different from each other (one-way ANOVA; $F = 2.48$, 3,85 df, $P > 0.10$). Species that gained the greatest amount of weight during their stay also appeared to show the greatest change in fat class (Table 2). Although the increase in weight characteristic of the migratory condition may reflect changes in the mass of flight musculature (see Child 1969; Fry et al. 1972; Marsh 1984), the rapid replenishment of fat by lean migrants accounts for most weight changes of migrants.

When the changes in weight are examined on an individual basis (Fig. 5a–f), variability within each species is striking. Some individuals gained weight at a rapid rate, whereas few lost weight during their stopover (see also Table 2).

Discussion

Energetic condition of arrivals

If stopover habitat is used as a place to replenish energy reserves depleted during migration, lean birds should predominate at the first available habitat following a trans-Gulf flight. Our results are consistent with this expectation, though the arrival condition of migrants is variable (Child 1969; Hicks 1967). Several factors contribute to this variation. Migrants that encounter headwinds or rain over the northern coast of the Gulf of Mexico stop in large numbers along the coast and it is not unusual to capture fat as well as lean migrants at these times. Radar observations (Gauthreaux 1971) indicate that migrants often overfly the coast and land some distance inland, when weather conditions are favorable for ongoing migration. This behavior is consistent with our data which suggest that many migrants arrive on the northern coast with sufficient fat reserves to continue migration (see also Hebrard 1971; Gauthreaux 1971). In contrast, migrants that 'stopover' along the northern Gulf coast during favorable weather are typically leaner and often stay for a day or more to replenish fat reserves.

Physiological and behavioral differences among migrants in their accumulation and subsequent need for energy reserves also contribute to observed variability. Individual differences are likely to be accentuated when there is competition for food (cf. Rubinstein 1981; Milinski 1982). Competition may be a common occurrence during migration, especially when migrants must negotiate an ecological barrier (see Rappole and Warner 1976; Bibby and Green 1980; Schneider and Harrington 1981; Mehlum 1983a and b). The variability we observed in the rate of weight gain within several species may reflect individual differences in energy acquisition.

The energetic condition of migrants arriving on the northern coast of the Gulf of Mexico also depends upon the location of departure and actual flight distance (see Fig. 1). Many trans-Gulf migrants originate from the Yucatan peninsula and fly the approximately 1000 km in 18–24 h depending upon weather conditions (see Lowery 1946, 1951; Gauthreaux 1971). Migrants at our study site may have originated from as near as the southeastern coast of Texas or as far south as Honduras, Panama, or the northern coast of South America (see Monroe 1968). To determine how long it takes a migrant to cross the Gulf of Mexico and the points of departure for trans-Gulf migrants, we

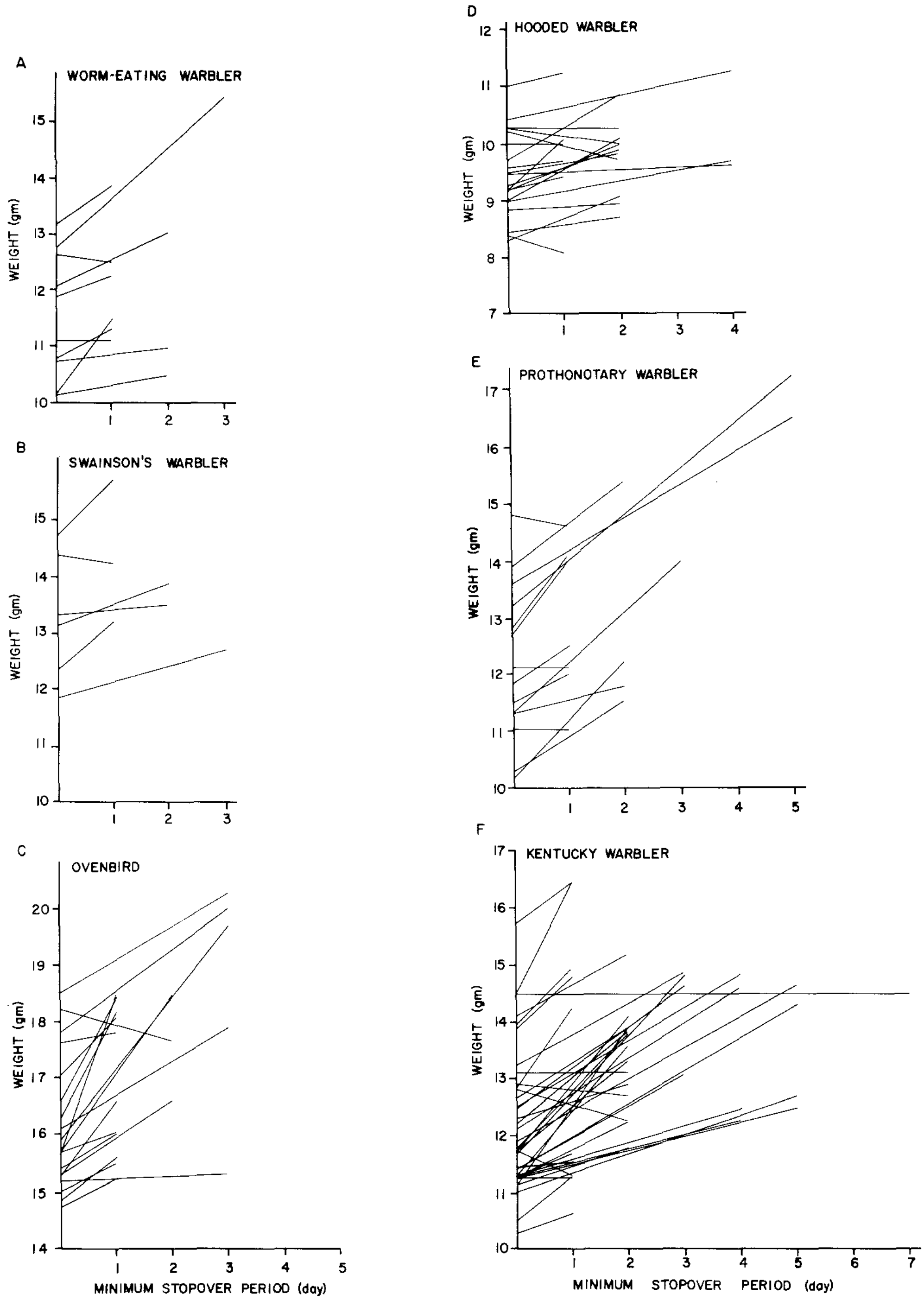

Fig. 5A–F. Changes in the weight of recaptured individuals during their stopover period following trans-Gulf migration

simulated flight over this barrier. By examining the timing of arrival and energetic condition of migrants we may speculate as to where they originated their trans-Gulf flight. For example, how much fat will be used by a warbler in a flight between the coast of Yucatan and the southwest coast of Louisiana (1020 km)? Distance flown per gram of fat (km/g) is given by $E = 800/W\ (L/D)_{\mathrm{eff}}$ (Pennycuick 1969), where L/D is assumed to be 5.5 for small passerines. Thus, a 16 g Kentucky Warbler flying at an air speed of 10 m/s will realize 275 km/g of fat consumed. With no wind, the warbler needs 3.6 g of fat to make the flight from Yucatan to Louisiana and 6.0 g of fat to fly from Honduras to Louisiana. Of course, it is unreasonable to assume no wind. The relationship between fat required and wind condition is curvilinear (Fig. 6). With a tail wind of +2.0 m/s, for example, only 3 g of fat are required to make the >20 h crossing from Yucatan. Stronger tailwinds (6–8 m/s) are not unusual at 1000 m above the Gulf of Mexico (see Buskirk 1980) and would make a flight from as far south as Honduras energetically permissible. Birds leaving Yucatan at 1900 h would arrive at the northern Gulf coast at 1000–1200 the following day, using 2–3 g of fat. Opposing winds >2 m/s make the flight more difficult, requiring >35 h or continuous flight and more than 5 g of fat. With stronger opposing winds, most migrants probably cannot make successful crossings.

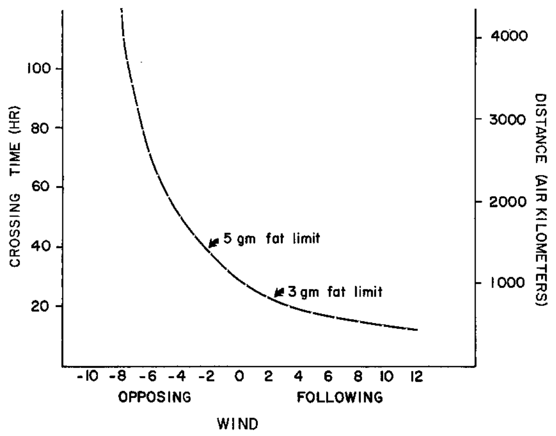

Fig. 6. Flight time across the Gulf of Mexico (Crossing Time) as a function of wind condition

Length of stopover

How long a migrant stops after a trans-Gulf flight depends upon several variables, not the least of which is the degree of fat-depletion upon arrival. We found that lean wood-warblers stayed longer than fat migrants. Both Bairlein (1985a) and Biebach et al. (1986) also reported that trans-Saharan passerine migrants stayed longer at desert oases if they arrived fat-depleted. A similar relation between fat content and stopover length holds for Goldcrests (*Regulus regulus*) and European Robins (*Erithacus rubecula*) that were preparing to cross the Baltic Sea in autumn (Pettersson and Hasselquist 1985). Whereas Cherry (1982) reported that lean White-crowned Sparrows (*Zonotrichia leucophrys*) gained more weight and stayed longer than fat sparrows, DeWolfe et al. (1973) failed to find such a relation among the White-crowned Sparrows migrating through the southern Yukon territory.

The relation between the condition of a migrant upon arrival and how long that bird stays will also depend upon the suitability of the habitat, where suitability is a function of the availability of food. The positive rates at which migrants at our study site gained weight and replenished energy reserves point to its suitability as stopover habitat. Rappole and Warner (1976) found that Northern Waterthrushes defended temporary territories at their study site in coastal Texas. Migrants that secured territories stayed and deposited fat, whereas other individuals departed shortly after arrival regardless of energetic condition. Presumably, fat-depleted migrants are better off continuing their migration when they are unable to find sufficient food or when competition for food precludes defense of sufficient resources. Mehlum (1983a, 1983b) reached a similar conclusion based upon his study of migrating robins in coastal Norway (see also Rabol and Petersen 1973; Bibby and Green 1980). The alternative to moving may be starvation. If the suitability of stopover habitat influences the length of stay, variation between habitats or within a habitat between years should be correlated with length of stay (see Bibby et al. 1976; Bibby and Green 1983; Pettersson and Hasselquist 1985; Hedenstrom and Pettersson 1986 and discussion under *Rate of Weight Gain*).

Rate of weight gain

The rate at which migrants replenish energy reserves is also dependent upon a number of variables. Fat-depleted migrants are likely to forage at higher rates than migrants possessing sufficient fat reserves for continued migration (see Graber and Graber 1983, Moore unpublished field data). Consistent with this expectation are laboratory observations that feeding rates, including handling times of prey items, decrease as birds approach satiation (e.g., Zach and Falls 1978; Krebs et al. 1977; Paszkowski and Moermond 1984; Loria and Moore unpublished work). Consequently, we expect lean migrants to replenish fat at a faster rate than fatter migrants. Yet, some studies have found that migrants loose weight during the first day or two after arrival (e.g., Lebreton 1968; Rappole and Warner 1976; Mehlum 1983a and b). The migrants begin to display a positive rate of gain shortly thereafter, presumably because they secure a temporary territory that provides food for the replenishment of fat. The species that stopped at our study site after crossing the Gulf of Mexico, showed positive rates of gain regardless of the length of stay; many individuals gained weight during the initial 24 h period (see also Bairlein 1985a; Biebach et al. 1986). Moreover, we observed very little evidence of intra- or interspecific aggression indicative of competition for food (Moore unpublished data).

The rate of gain and the likelihood of losing weight during a stopover is evidently a function of the suitability of the stopover habitat. For example, Sedge Warblers (*Acrocephalus schoenobaenus*) gained weight at a rate of 0.42±0.07 g/d at a stopover site near Le Migron, France, but only 0.05±0.10 g/d at a stopover site near Passay, France (Bibby and Green 1983). Similarly, the rate at which migrants replenish energy reserves varies from year-to-year at the same site; Sedge Warblers gained 0.40 and 0.55 g/d in 1973 and 1975, respectively, but only 0.05 g/d in 1974 at the same stopover site in England (Bibby et al. 1976). The same study also revealed that the duration of stay was negatively correlated with rate of weight gain. In 1974, 84% of the Sedge Warblers that stopped stayed ≤ 2 days. In 1973 and 1975, when the rate of gain was substantially greater, 46% of the birds stayed ≤ 2 days, i.e. in a year when the likelihood of gaining weight was low, the migrants stayed for a shorter period of time.

Finally, we observed species differences in the rate of weight gain; Hooded Warblers were slow to replenish energy reserves, whereas Ovenbirds and Prothonotary Warblers did so at a much faster rate. Biebach et al. (1986) reported differences among trans-Saharan migrating passerines that stopped at oases: Lesser Whitethroats (*Sylvia curruca*) showed no change (0.01 g/d) during their study, whereas Willow Warblers (*Phylloscopus trochilus*) and Yellow Wagtails (*Motacilla flava*) gained at rates of 0.11 g/d and 0.37 g/d, respectively. Bairlein's (1985a) study of trans-Saharan migrants also revealed species differences in rate of weight gain which he related to differences in migration distance. Comparisons made at Ottenby, Sweden, suggest that Goldcrests put on fat faster than European Robins (see Petterson and Hasselquist 1985). Several factors probably contribute to observed species differences: (1) differences might be related to the migratory distance between the stopover site and the breeding destination of the migrants. Our recapture data are consistent with the idea that individuals with greater distances to travel stopover for shorter periods (see Bairlein 1985a). (2) At a particular time during migration and at a given site along the migratory route, species differences in the temporal pattern of migration could contribute to differences among species, i.e. it may be late in the migration season for individuals of one species and early for another species. (3) Variation in the availability of preferred food resources at a stopover site could also contribute to differences among species in length of stopover or rate of weight gain (see Bibby and Green 1981, 1983). These questions remain to be examined.

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