

FLIGHT ENERGY AND ESTIMATED FLIGHT RANGES OF  
SOME MIGRATORY BIRDS\*

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SINCE fat provides virtually all of the fuel for extended migratory flights, the energy available for flight is easily calculated if the total available body fat is known. As described in detail in a previous paper (Odum, 1960a), migration in the sense of long-continued, sustained flight is possible only within fairly narrow metabolic limits. A reasonable estimate of the flight range can be made on the assumption that the energy required for sustained flight is between two and four times "maintenance" or "existence" metabolism, herein defined as the metabolized energy required by caged birds that are not subjected to energy demands above those needed for day-to-day maintenance of body weight and health at room temperatures. Since metabolic rate per gram of fat-free weight appears to be similar for passerines of 10-40 g, the flight range of an individual bird having a given amount of fat can be estimated. Furthermore, the amount of fat in a living bird, or intact specimen, can be estimated from the total weight if the fat-free, weight-wing length relationship has been worked out for the species involved (Connell, Odum, and Kale, 1960). It is the purpose of this paper (1) to illustrate how patterns of migratory behavior are related to lipid deposition, and (2) to present estimates of the flight ranges of migrating birds killed at a Gulf coast television tower located near Tallahassee, Florida.

## METHODS

Daily collections of birds killed at the Florida Gulf coast tower have been made by Stoddard during both spring and fall migration periods since the tower was first constructed in the fall of 1955.

Birds killed by striking the tower during nocturnal migration were collected at dawn, or in some cases during the night as they fell to the ground, and stored in deep freeze. Total body fat was determined by a simple, rapid method previously described (Odum, 1960a), which consisted of vacuum dehydration followed by extraction in petroleum ether. Three weights were taken: total wet weight, total dry weight (after dehydration), and nonfat dry weight (after extraction). The differences between the latter two weights provide an accurate estimate of

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total body fat. Wet weight minus fat equals the fat-free weight, which was the weight used as a basis for computing weight-specific metabolic rates.

#### PATTERNS OF LIPID DEPOSITION

For the sake of discussion it is convenient to consider three classes of migrants in so far as fat deposition is concerned: (1) short-range migrants that become moderately obese, but begin migration before peak deposition, (2) short-range migrants that attain moderate obesity but begin migration after the peak deposition levels have been reached, (3) long-range migrants that become extremely obese just prior to long flights.

The Savannah Sparrow, *Passerculus sandwichensis*, is an example of the first pattern. Birds leaving their wintering grounds in April at the latitude of Augusta, Georgia, generally carry little fat, while many individuals striking the television tower at the same locality on the southward return in late October are moderately fat (Connell, 1959). Although not demonstrated experimentally, it would appear that migratory unrest, or *Zugunruhe*, develops to some degree at the onset of fat deposition, with the result that birds begin short flights before there is very much buildup in fat reserves. In the Savannah Sparrow such flights, which may involve only a local shifting from one field to another, begin in late February. When individuals disappear from their winter locations in March and April, only a small increase in weight is evident. The last birds to leave in May may be moderately fat; it is suspected that these individuals began migration from points to the south, since birds locally banded in winter have disappeared by this time.

A pattern involving increasing body-fat levels as the bird travels northward is probably characteristic of early spring migrants that winter in continental United States. The absence of a pronounced pre-migratory increase in weight as reported for the Song Sparrow (*Melospiza melodia*) and Tree Sparrow (*Spizella arborea*) by Helms and Drury (1960) and the Purple Finch (*Carpodacus purpureus*) by Bartleson and Jensen (1955) indicates that these species belong to the first category. The triggering of the migratory urge before maximum fat deposition is clearly of adaptive value, since low energy reserves at the start of migration would prevent long flights that might move the bird into unfavorable early spring weather conditions. Also, it appears that a gradual increase in fat reserves during migration is characteristic of land migrants that breed in the far north. It is well known from the

early observations of Cooke (see Lincoln, 1950) that many spring migrants increase their speed of travel as they approach northern breeding grounds, suggesting increasing fuel reserves. Furthermore, many species of small land birds are quite fat on arriving at the breeding grounds in Alaska (Irving, 1960; D. W. Johnston, pers. corr.). Again, such a pattern has survival value, since maximum fat reserves towards the end of the migratory journey would enable the bird to complete the journey quickly when the weather becomes favorable, and, what is perhaps more important, enable the individual to withstand periods of bad weather that often occur early in the breeding season. Less is known about fall migration, but it seems logical to assume that many species, especially those that start early, begin the southward journey with low fat reserves and hence move in short hops. At each stop for refueling the amount of body fat is increased, permitting longer flights as the bird moves southward.

In the second type of pattern as illustrated by the White-throated Sparrow (*Zonotrichia albicollis*) and the White-crowned Sparrow (*Z. leucophrys*), migration, in many individuals at least, does not begin until after more or less maximum deposition of fat is achieved. Maximum levels in these species are only moderate (up to 25 per cent of wet weight as observed in nature, or as induced experimentally by long photoperiods), but more or less complete deposition occurs on the wintering grounds. Thus, banded individuals that have been present all winter exhibit a striking increase in weight just before they disappear from the locality (Odum, 1949). A pattern of this type is probably characteristic of late spring migrants in continental regions.

The third pattern of migratory obesity is characteristic of long-range migrants that breed in North America but winter in the tropics. Scarlet Tanagers (*Piranga olivacea*) and Ruby-throated Hummingbirds (*Archilochus colubris*) are typical of a group of small land birds that are trans-Gulf migrants, that is, they fly nonstop over at least 1,000 km (600 miles) of open water. Such birds become extremely obese just prior to long flights. In terms of the per cent of live weight, individual Scarlet Tanagers are the fattest birds we have extracted with up to 52 per cent fat (see Table 1). From the standpoint of percentage nonfat dry weight, hummingbirds range higher, up to 350 per cent fat; that is, the dry weight of fat may be three and a half times the dry weight of all other tissues in premigratory hummingbirds. A tabular analysis of the three patterns of lipid deposition together with data on the daily rates of fat accumulation in experimental and wild birds are given in another paper (Odum, 1960b).

TABLE 1  
EXTRACTED FAT AND ESTIMATED FLIGHT RANGES OF PASSERINE BIRDS KILLED  
DURING NOCTURNAL MIGRATION AT A FLORIDA GULF COAST TELEVISION TOWER

Migrating population	Dates	No.	Fat levels		Estimated flight range in km*	
			Mean fat (grams)	per cent wet wt.	average	extremes
<i>Zonotrichia albicollis</i> White-throated Sparrow (Fall)	Oct.-Nov. 1956	45	1.45	6.2	1.9-14.2	180 0-580
<i>Passerculus sandwichensis</i> Savannah Sparrow (Fall)	Oct.-Nov. 1956	40	2.25	13.8	6.3-27.6	560 180-1340
<i>Piranga olivacea</i> Scarlet Tanager (Fall)	5 Oct. 1956	29	17.62	42.6	35.3-51.8	2360 1850-3075
<i>Piranga rubra</i> Summer Tanager (Fall)	5 Oct. 1956	44	16.61	40.7	32.6-46.6	2180 1650-2650
<i>Piranga rubra</i> Summer Tanager (Spring)	April 1957	5	5.34	19.0	13.8-25.9	850 520-1240
<i>Dolichonyx oryzivorus</i> Bobolink (Sept.)	8-16 Sept. 1956-57	8	10.25	29.8	21.7-40.9	1490 940-2240
<i>Dolichonyx oryzivorus</i> Bobolink (Oct.)	1-8 Oct. 1956-57	19	17.50	42.0	32.8-49.1	2340 1680-2850
<i>Hyalocichla fuscescens</i> Eastern Veery (Fall)	5 Oct. 1957	101	16.57	38.0	9.8-49.1	2040 380-2850
<i>Vermivora peregrina</i> Tennessee Warbler (Fall)	5 Oct. 1957	72	5.26	39.8	30.2-47.9	2160 1510-2760

<i>Wilsonia citrina</i> Hooded Warbler (Fall)	3 Aug.-11 Oct. 1958	30	4.80	30.0	15.5-43.0	1500	650-2380
<i>Wilsonia citrina</i> Hooded Warbler (Spring)	26 Mar.-30 Apr. 1958	99	1.53	13.4	1.0-22.9	540	0-1060
<i>Dendroica castanea</i> Bay-breasted Warbler (Fall)	8-30 Oct. 1956	10	4.92	33.0	27.4-37.6	1700	1320-2000
<i>Vireo olivaceus</i> Red-eyed Vireo (Entire fall)	Aug.-Oct. 1956	101	5.47	25.7	4.0-43.4	1220	80-2420
<i>Vireo olivaceus</i> Red-eyed Vireo (Early fall, lean group)	3 Aug.-10 Sept. 1956	13	2.24	13.7	4.0-25.7	560	80-1220
<i>Vireo olivaceus</i> Red-eyed Vireo (Early fall, fat group)	3 Aug.-10 Sept. 1956	16	9.07	38.5	30.8-43.4	2070	1550-2420
<i>Vireo olivaceus</i> Red-eyed Vireo (Single night)	6 Oct. 1956	29	6.92	30.8	8.1-42.2	1550	280-2330
<i>Vireo olivaceus</i> Red-eyed Vireo (Single night)	30 Sept. 1957	48	3.43	18.2	5.9-33.2	800	175-1700
<i>Vireo olivaceus</i> Red-eyed Vireo (Spring)	4-21 Apr. 1957	81	3.09	18.1	3.8-27.9	790	75-1350
<i>Passerina cyanea</i> Indigo Bunting (Fall)	23 Sept.-9 Oct. 1956	55	2.00	13.4	4.4-35.2	550	100-1820

\* Estimates based on curve 2 of Figure 1.

## FLIGHT RANGES OF GULF COAST MIGRANTS

As previously described (Odum, 1960a), we have used two approaches to estimate flight ranges of birds having a given amount of fat. In the first method the range was calculated for each species on the assumption that the energy required for migratory flight at a speed of 50 km (about 30 miles) per hour is three times the existence level. Since existence energy of passerine birds of 10-30 g fat-free weight averages about 0.05 kcal/gm/hr, flight energy requirement would be 0.15 kcal/gm/hr or 0.003 kcal/gm/km. A bird of 10 g fat-free weight that had 45 kcal (5 g) of usable fat would thus require 0.03 kcal/km and have a flight range of 1,800 km (1,000 miles). Since a small portion of the body fat is a necessary constituent of the physiological machinery and cannot be used as fuel, we have considered the available fuel to be the total fat minus 0.5 g for birds of tanager and thrush size, and minus 0.3 g for warblers and vireos. These estimates for unavailable fat are based on the minimum amounts found in post-migratory individuals.

In the second method flight ranges of hypothetical birds having a fat-free weight of 20 g plus from one to 20 g of fat were calculated, and these estimates plotted against fat as percentage of total weight (*i.e.*, the fat index). Such a curve can be used to estimate the flight range of any species or individual, since the fat index automatically adjusts for different body sizes, at least within the size range of most migratory passerines. Two such curves are shown in Figure 1. The concave curve (dotted line, curve 1) is based on the assumption that flight energy is three times existence energy and varies with the fat-free but not the fat weight. In the previous paper (Odum, 1960a) preliminary flight-range estimates were based on this assumption, since the evidence available at that time indicated that three times the existence level could account for extra energy needed to transport the large amount of fuel present. However, the assumption that the increment in flight range per unit increment of fat is constant (as in curve 1, Figure 1) would tend to underestimate the range of a moderately fat bird.

As pointed out to us by I. C. T. Nisbit of Cambridge University (pers. comm.), the energy required by a small, flapping bird to overcome gravity is probably more important than the energy needed to overcome drag (especially since migratory birds usually fly with the wind). Therefore, Nisbit suggests that energy requirement should increase proportional to total weight. The difficulty with this assumption, of course, is that the bird changes weight as it migrates and metabolizes its fat. Curve 2 in Figure 1 is based on a compromise assumption as

follows: Flight energy of a lean bird is two times existence energy (0.1 kcal/gm/hr or 0.002 kcal/gm/km) and increases proportional to average weight of the bird during the trip, which is to say, in proportion to half of the fat weight at the beginning of the trip. Thus, a bird with a 25 per cent fat index would be 50 per cent heavier at the start of the journey, but average 25 per cent heavier and hence require 2.25 times the existence level. Likewise, three times existence level would be required at the maximum fat level of 50 per cent. Two times existence level for a lean bird fits in very well with what we know about energy requirements of an active bird in the field, while, as already indicated, three times this level is logical for a very heavy bird.

If we are to deal only with laboratory extractions, fat as a per cent of nonfat weight is a better index than fat as per cent total weight. However, the latter index can be at least approximately determined on living birds or intact specimens. As previously indicated, a good esti-

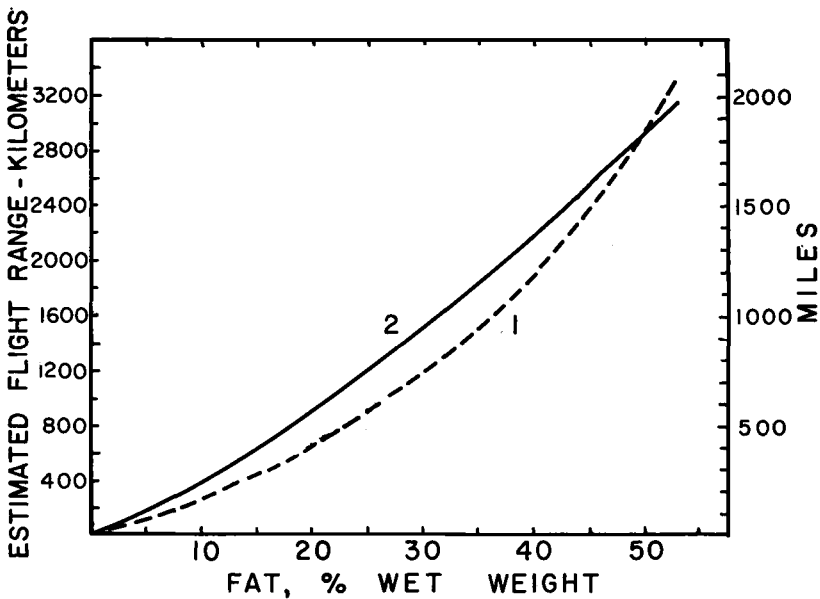


Figure 1. Estimated flight range of small, migratory birds plotted against total body fat in per cent of wet (live) weight. Curve 1 (dotted line) is based on assumption that flight energy is three times the "existence energy" requirement irrespective of weight of the fat. Curve 2 (solid line) is based on the assumption the flight energy is two times existence energy for the lean bird and increases in direct proportion to the average fat weight. See text for explanation.

mate of total fat (and hence the fat index) can be made without extraction simply by weighing the bird and taking its wing length, provided the fat-free, weight-wing length relationship has been worked out for the species in question. Thus, the utility of the graphic method for estimating fat reserves and flight ranges in banded birds or large samples of tower birds is obvious.

Estimated flight ranges (averages and extremes) of birds killed at the television tower based on curve number 2 of Figure 1 are given in Table 1. Included are samples from the entire migratory season as well as samples from single nights when large flights were in progress. Species include two that winter in southeastern United States (White-throated and Savannah sparrows), several that are generally considered trans-Gulf migrants (tanagers), and others whose migratory routes are not well understood at present. All of our data are now being coded and entered on IBM cards so that detailed statistical analyses of relationships between fat and numerous factors such as age, season, year, wind direction, etc. can be made with the aid of computers. For the purposes of this preliminary paper we shall indicate only a few relationships that seem clear at the moment.

White-throated Sparrows, which reach the very southern edge of the wintering range at the Gulf coast, have proved to be the leanest birds killed at the tower; many individuals had no more fat or potential flight range (theoretically zero in some individuals) than nonmigratory birds. Samples of Savannah Sparrows, also winter residents in the region, had greater flight ranges, but would still not have been able to fly across the Gulf. In contrast, fall samples of both species of tanagers indicated that every individual could have crossed the Gulf with large reserves of fuel to spare. In fact, many of these birds had an estimated flight range of over 2,400 km (1,500 miles); such individuals should have been able to continue nonstop all the way to South America had they not been killed at the tower!

Comparison of Summer Tanagers (*Piranga rubra*) and Hooded Warblers (*Wilsonia citrina*), two species that are believed to be habitual trans-Gulf migrants, taken in spring and fall indicates that our flight estimates are of the right order of magnitude. Spring tanagers were by no means depleted of fat (Table 1); the difference between spring and fall flight ranges in this species was about 1,300 km (850 miles). Likewise, difference in spring and fall estimates for Hooded Warblers was about 1,000 km (600 miles). Assuming that the tanagers and warblers started northward across the Gulf with the same high level of fat as recorded in the fall, then the observed moderate levels in birds



arriving in Florida are what would be expected after a flight of 1,000 km (the minimum overwater distance from Yucatan to the Gulf coast) or more. Furthermore, both species still had ample fat left to continue several hundred miles inland if the weather had been more favorable. The "Gulf coast hiatus" as described by Lowery (1945) is thus easily accounted for by fat reserves still present in birds killed by the Gulf coast tower when they were forced down by thick cloud cover on their northward flight. These results also support our contention that long-distance migrants accumulate more fat than is normally needed to complete any given flight. The reserve is of survival value not only under adverse flying conditions but, also, should food be temporarily scarce at the termination of the flight.

Referring again to Figure 1, we see that a bird with a fat index of 25 per cent would have an estimated flight range of 1,200 km (750 miles). Consequently, allowing for a margin of safety, we would expect that habitual trans-Gulf migrants should have a fat index greater than 25. All 73 fall tanagers, all but six of 101 Veeries, and all 75 Tennessee Warblers so far extracted had a fat index greater than 30, indicating an ability to make trans-Gulf or other long, nonstop flights. The October flight of Bobolinks (*Dolichonyx oryzivorus*) has proved to be consistently fatter than the September flight. During each of three years for which we have specimens, October Bobolinks equalled the tanagers in obesity, while some individuals in September were low in fat content and would probably not have been able to make it across the Gulf. These data strongly suggest that the early flight of Bobolinks follows the Florida-West Indian route while the later flight is trans-Gulf.

Red-eyed Vireos (*Vireo olivaceus*) were the most frequent victims of the tower, and were also the most variable in fat content. As shown in Table 1, the range of variation was great not only for a season as a whole, but also for samples taken from a single night's kill (as on 6 October 1956 or 30 September 1957). In large samples from the 1956 season frequency distribution early in the season was bimodal, with very fat and very lean birds in the same flight; later in the season birds showed a more intermediate condition. Only about half of the total sample of 100 fall birds had an index of over 30 per cent. Since Red-eyed Vireos presumably follow both the Florida-West Indian route and the trans-Gulf route, it may be that the fat birds would have gone by sea and the lean birds by land!

In general, daily observations of mortality in relation to weather conditions have led Stoddard to conclude that west and northwest

winds in fall bring Florida-West Indian migrants, while northeast winds (the most common direction during nights of heavy mortality) bring trans-Gulf migrants. In regard to vireos, we do not have enough data so far to determine if fat condition is related to wind direction. Interestingly enough, vireos had almost as much fat in spring as in fall (see Table 1), although the maximum in spring was not as great and the minimum less than in fall.

For the most part species that we have found to be consistently very fat in the fall are those that Lowery (1946) and/or Stevenson (1957) list as probable trans-Gulf migrants. An exception is the Indigo Bunting (*Passerina cyanea*), one of the species Lowery recorded as appearing on ships in the middle of the Gulf. According to our estimates only about six individuals out of a sample of 55 birds extracted would have been able to continue across the Gulf. Most of the individuals would have had to follow the coast or stop for extensive refueling, since the average fat index for the whole group was only about 13 per cent.

Extracted fat and estimated flight range for three species on non-passerines are shown in Table 2, including small samples of swifts and hummingbirds taken far inland from the Gulf Coast. The swifts were collected from a chimney at a season when the species was beginning to disappear from the locality; likewise, hummingbirds were taken from an aggregation described by Norris, Connell, and Johnston (1957) a day or two before the birds disappeared from the flower patch. Flight-range estimates in Table 2 are on less certain grounds, since the long-winged swifts and hummingbirds and the short-winged Soras may have different flight metabolic rates as compared with those of passerines. The flight range of swifts may be underestimated, for example, since these birds may fly with less effort than passerines. On the other hand, the range of hummingbirds may be overestimated, since their small size requires a very high metabolic rate per gram. For hummingbirds an interesting comparison can be made between estimates based on the curve in Figure 1 and estimates based on Pearson's (1950) measurements of the energy required for hovering flight in a bell jar. Using his measurement of 0.4 kcal/gm/hr and a flight speed of 80 km (50 miles) per hour, 2.2 g (19.8 kcal) of fat would result in a flight range of about 1,250 km (800 miles) (see Odum and Connell, 1960) as compared with the estimate of 2,400 km (1,500 miles) as shown in Table 2. Since Pearson found hummingbirds could not maintain hovering for very long, it is reasonable to assume that hovering flight requires more energy than straightaway, migratory flight (with favorable tail winds also a probability). Thus, we are inclined to think that the esti-

TABLE 2  
EXTRACTED FAT AND ESTIMATED FLIGHT RANGES OF THREE NONPASSERINE SPECIES OF BIRDS

Species	Date and location of collection	No.	Fat levels		Estimated flight range in km
			Mean fat	Per cent wet wt.	
			(grams)	average extremes	
<i>Porzana carolina</i> Sora Rail	Tallahassee TV tower 30 Sept.-30 Oct. 1956	8	19.86	27.6 15.1-38.2	1340 630-2020
<i>Chaetura pelagica</i> Chimney Swift	Athens, Georgia—roosting in chimney, 13 Oct. 1959	21	10.51	34.6 29.5-40.6	1800 1450-2210
<i>Archilochus colubris</i> Ruby-throated Hummingbird	Daytime premigratory aggregation, near Augusta, Georgia, 23 Sept. 1955	3	2.25	43.8 41.2-45.9	2450 2260-2590

mate of 2,400 km is more nearly correct. If so, then hummingbirds can easily begin a fall trans-Gulf flight several hundred miles inland. Frequent observations of September aggregations of hummingbirds that suddenly disappear from inland locations when the birds become very fat suggest that these tiny birds may do just that!

Finally, we would like to suggest that bird students obtain weights and wing measurements from birds killed at television towers, as well as from birds captured for banding. From these two simple measurements we believe a good estimate of fat level, and hence flight range, can be made for many species as soon as the wing-length, fat-free weight relationship has been investigated. We will be glad to supply information on the latter for any species for which we have data (see also Connell *et al.*, 1960).

#### SUMMARY

Three patterns of fat deposition in relation to migration are now evident: (1) short-range migrants (*e.g.*, Savannah Sparrow) that become moderately obese but begin migration before peak deposition; (2) short-range migrants (*e.g.*, White-throated Sparrow) that begin migration after peak deposition; (3) long-range migrants (*e.g.*, Scarlet Tanager prior to trans-Gulf flights) that become extremely obese (fat up to 50 per cent of body weight) just prior to long flights.

Measured lipid levels and estimated flight ranges are presented for samples of birds (totaling 853 individuals of 15 species) killed during nocturnal migration at a Gulf coast television tower located near Tallahassee, Florida, or collected from premigratory aggregations at inland localities (see Tables 1 and 2).

In general, species of tanagers, thrushes, and warblers, which are now considered to be trans-Gulf migrants, proved to have more than enough fat to make the overwater journey nonstop (estimated flight ranges 1,000-2,500 km or 600-1,500 miles). The Indigo Bunting was an exception; most individuals in the fall sample did not have enough stored energy for a flight from West Florida to Yucatan. The difference between fall and spring Summer Tanagers and Hooded Warblers indicated a northward flight of about 1,000-1,300 km (600-850 miles) for these species, which would account for a trans-Gulf flight. Furthermore, spring specimens killed at the Gulf coast tower still had ample fat to account for the "coastal hiatus" as well. Likewise, fat levels in swifts and hummingbirds at inland localities in the fall indicate that these species could begin a fall trans-Gulf flight from points several hundred miles inland from the Gulf coast.

The possibility of distinguishing between Florida-West Indian and trans-Gulf migrants on the basis of lipid levels is discussed. Bird students are urged to take weights and wing measurements on specimens killed at television towers, as well as birds captured for banding, since good estimates of fat and flight range can eventually be made on the basis of these two easily taken measurements.

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