ADAPTATIONS OF THE GRAY CATBIRD *DUMETELLA CAROLINENSIS* TO LONG DISTANCE MIGRATION: ENERGY STORES AND SUBSTRATE CONCENTRATIONS IN PLASMA

RICHARD L. MARSH[1]

Division of Biological Sciences, The University of Michigan, Ann Arbor, Michigan 48109 USA

ABSTRACT.—The major body components (water, lean dry, and fat) were measured in the carcasses of Gray Catbirds from which the flight muscles had been removed. Birds were collected from May through October near Ann Arbor, Michigan and during September and October near Gainesville, Florida. Additionally, the glycogen content of muscle and liver and the concentrations of glucose and triglycerides in plasma were determined in catbirds sampled during fall migration in Florida. Catbirds attained maximum body masses of ~50 g in Florida, largely due to the addition of fat. Relatively lean birds (~3–4% body fat) in spring through fall weighed approximately 35 g. Thirteen percent of the birds sampled were estimated to have had sufficient reserves of fat to cross the Gulf of Mexico, although a larger proportion of the population probably makes this crossing. The lean dry mass of the carcass (without the flight muscles) is related significantly to structural body size and time of day, but is not related to molt, sex, or carcass fat content. Plasma glucose and triglycerides in free-living fall migrants do not vary diurnally. Liver glycogen, however, is four times higher in the evening than in the morning (77 and 19 mg/g, respectively), and muscle glycogen is five times higher in the evening (20 and 4 mg/g, respectively). Evening concentrations of glycogen are among the highest values reported for birds and do not confirm the reduction in glycogen reported for some other migrants. *Received 16 February 1982, accepted 30 June 1982.*

DUE to the high metabolic demands of flapping flight, small birds must anticipate long-distance migratory flights by storing large amounts of energy. Energy is stored primarily as fat (triglycerides) before migratory flights, and patterns of premigratory fat deposition have been described for numerous species (see reviews by Farner et al. 1968, King 1972, Berthold 1975). Small passerine migrants show great interspecific variability in such deposition. This variability appears to be related to the distance traveled and the duration of migration (Odum et al. 1961, Johnston 1966, Helms and Smythe 1969), with the greatest reserves being accumulated by birds that must make long, nonstop flights across major geographical barriers (Odum et al. 1961, Fry et al. 1970). The major lipid components of muscle, liver, and plasma also increase in parallel with depot fat content (Farner et al. 1961, King et al. 1963, John and George 1965, de Graw et al. 1979). In contrast to the extensive information available on lipids, the role of carbohydrate before and during migration is less clear. Although glycogen reserves in liver and muscle are depressed and diurnal cycles of glycogen content damped in spring migrants of Gambel's White-crowned Sparrow (*Zonotrichia leucophrys gambelii*), fall migrants of the same species have high glycogen levels (Farner et al. 1961, King et al. 1963). On the other hand, three spring migrants in India, which also accumulate large fat deposits, have elevated levels of glycogen (Naik 1963, Vallyathan and George 1964, John and George 1965) and substantial diurnal glycogen cycles (George and Chandra-Bose 1967) in the premigratory period.

In addition to variations in energy substrates with season and migratory state, various authors have examined the possibility of fluctuations in the lean dry mass or the protein content of migrants. The results obtained from these studies seem contradictory. Odum and several colleagues (Connell et al. 1960, Odum et al. 1964, Rogers and Odum 1964) have proposed that the lean mass remains approxi-

[1] Present address: Department of Biology, Northeastern University, Boston, Massachusetts 02115 USA.

mately constant during fattening, with only fat being added, whereas several more recent studies have documented an increase in the lean dry component of the body mass as birds fatten for migration (Evans 1969, Fry et al. 1970). These increases have been thought to represent an addition of protein, to form a protein "reserve" of use during migration (Fry et al. 1972, Ward and Jones 1977).

In association with studies of adaptations of the flight muscles of the Gray Catbird (*Dumetella carolinensis*) to long-distance migration (Marsh 1979, 1981, in press), I examined the tissue energy stores and blood substrates of this species in samples from Michigan and northern Florida. On the basis of its extensive breeding and wintering range (A.O.U. checklist 1957), this species appears to be highly variable in its migratory pattern. Portions of the population winter in Central America and, at least in the spring, apparently migrate across the Gulf of Mexico. Lowery and Newman (1954) reported the direct sighting of two catbirds over the Gulf during spring migration. Stevenson (1957) lists the catbird among the trans-Gulf spring migrants on the basis of field observations of comparative abundance and sequence of migration dates. In addition, catbirds winter on all of the major groups of Caribbean Islands as well as along the Gulf coast of the United States and throughout peninsular Florida. Small and variable numbers winter as far north as Long Island, New York (A.O.U. checklist 1957, and banding recoveries from the United States Bird-banding Laboratory).

This report concentrates mainly on the components of the carcass exclusive of the flight muscles, which are treated separately (Marsh in press). The term "carcass" here refers to the body minus the two major flight muscles and the heart. The fat content of the carcass has been measured in order to determine whether or not the amount stored is consistent with the hypothesis that some catbirds cross the Gulf of Mexico during the fall migration. The plasma and tissue levels of fats and carbohydrates measured here provide insight into the metabolic state of these long-distance migrants. Additionally, this detailed compositional analysis provides the background necessary for analyzing the premigratory changes in the mass of the flight muscles seen in this species (Marsh in press).

Methods

Capture and initial observations.—Catbirds were mist-netted near Ann Arbor, Washtenaw County, Michigan and Gainesville, Alachua County, Florida. Birds were captured in Ann Arbor during fall, 1975, and spring through early fall, 1977. Florida captures took place in the falls of 1976 and 1977. Except as noted below, the birds were returned to the laboratory alive, and the following data were recorded on the live birds within 2 h of capture: body mass to the nearest 0.1 g, visual fat class (1–5; based on a scheme similar to that of Morton et al. 1973), wing chord and tarsus length to the nearest 0.1 mm, and stage of molt. The molt classes were as follows: 1 = no molt, 2 = light body molt, 3 = heavy body molt, and 4 = wing and body molt. On days on which more birds were collected than could be processed, some of the birds collected were released after these initial observations. Body mass and fat class were used as indicators to help insure that a representative sample was retained.

On the basis of data collected on live birds (particularly, body mass and fat class), some of the birds were selected for the various procedures requiring fresh muscle samples (Marsh 1979, 1981, in press). Birds used for these procedures were reweighed to the nearest 0.01 g and immediately sacrificed by decapitation. Muscle samples were removed from the left side, and the carcasses were then placed in tightly sealed plastic bags and stored at 4°C until dissection (see below). Birds used only for compositional analysis were sacrificed by snapping the cervical vertebrae, reweighed to the nearest 0.01 g, and stored at 4°C in sealed plastic bags until dissection. Use of the entire sample of birds for analysis of carcass composition required correcting water content and lean dry mass for blood lost in the specimens sacrificed by decapitation. For this purpose, the blood was estimated to be 80% water and 20% lean dry mass (Altman and Dittmer 1961), and the water content and lean dry mass of the carcasses were corrected appropriately (see below).

Carcass composition.—The birds were dissected within 24 h of sacrifice. The flight muscles (pectoralis and supracoracoideus) were removed and weighed to the nearest 0.1 mg. (The composition of these muscles was analyzed separately; Marsh in press). The body cavity was opened, the heart removed, and sex identified by examination of the gonads. The ovaries were also removed from females in May and June and weighed to the nearest 0.1 mg. The digestive tract was left intact, because preliminary data indicated that the 1.5–2 h that elapsed between collection and sacrifice were sufficient to empty the stomach and largely to clear the remainder of the digestive tract. Birds were classed as juvenile (first year) or adult, based on the pneumatization of the skull. The dissected carcass (the body minus the pectoralis and

supracoracoideus muscles and the heart and, in May–June birds, the ovaries) was weighed to nearest milligram, and the parts were frozen in plastic bags and stored at −20°C. Care was taken to minimize losses during dissections, particularly from the muscles. The difference between the body mass before dissection and the sum of the masses of the parts after dissection was assumed to represent only water, and this amount was added to the water content of the carcass (water loss during dissection was relatively small, amounting to 0.266 ± 0.019 g; mean ± SE).

After storage in the freezer for 1–6 months, the carcasses were freeze-dried to constant mass and reweighed to the nearest milligram to determine the dry mass. The difference between the fresh mass and the dry mass equals the water content. The dried carcasses were chopped with scissors, placed in cellulose extraction thimbles, and extracted for 24 h with petroleum ether (B.P. 30–60°C) in a Soxhlet apparatus. After extraction the carcasses were redried to constant mass in an oven at 90°C and reweighed to obtain the lean dry mass. The difference between the dry mass and the lean dry mass equals the fat (neutral lipid) content.

Plasma glucose and free fatty acids and tissue glycogen.—A sample of birds was collected in Florida to determine the concentration of plasma glucose and free fatty acids and liver and muscle glycogen contents. An attempt was made to have these samples reflect the substrate levels in normally active, free-living birds. Birds were sacrificed by decapitation within 30–60 s after they entered mist nets placed near a naturally occurring food source. Blood was collected in small, chilled plastic beakers containing sodium oxalate as an anticoagulant, and pectoralis muscle and liver samples were quickly removed and frozen in a bath of ethanol and dry ice. Blood samples were transferred to test tubes and stored on ice. The frozen muscle and liver samples were wrapped in aluminum foil and stored on dry ice. Upon return to the laboratory (within 2 h), the blood was centrifuged and the plasma stored frozen at −20°C for future analysis of glucose and triglycerides. Blood collected by decapitation is probably most representative of arterial blood due to bleeding from the carotid arteries. The frozen samples of muscle and liver were weighed and stored frozen at −20°C until analysed for glycogen content. Glucose was determined by a modification of the glucose oxidase method (Sigma Chemical Co., Bulletin #510) from 0.05-ml samples of plasma. Plasma triglyceride content was determined by calculation from total and free glycerol contents. Glycerol was determined by the method of Eggstein and Kuhlmann (1974) from 0.1-ml samples of plasma. Frozen tissue samples were thawed in chilled 0.06 *N* perchloric acid, homogenized in a glass-glass homogenizer, and glycogen was determined by the amyloglucosidase method of Keppler and Decker (1974).

Statistics.—All statistics were determined with the aid of "Midas," the statistical program developed by the University of Michigan Statistical Research Laboratory (see Fox and Guire 1976). Comparisons between means were made using the Student's *t*-test except between groups that had unequal variances or small sample sizes, for which the Mann-Whitney *U*-test was used. Where parametric statistics were used, the means are reported plus or minus the standard error.

RESULTS

Body mass and carcass composition.—The body mass of the catbird varies considerably at all seasons of the year [Fig. 1A, Table 1 (see also Raynor 1979)]. Maximum body mass is attained during the fall migration in Florida, although many birds captured there still have low body masses (range 30–51 g). As the data in Fig. 1B indicate, much of the variation in body mass reflects variation in the fat content of the carcass. (Recall that in the present context, the term "carcass" refers to the body minus the flight muscles and the heart and, in females during May and June, the ovaries.) This relationship is perhaps better illustrated in Fig. 2, which indicates that fat content of the carcass and body mass vary in a linear fashion ($r = 0.81$, $P < 0.0001$, $n = 95$). It is also clear, however, that considerable variability occurs in the other components of the body mass (water and lean dry). The water content of the carcass is closely correlated with the lean dry mass ($r = 0.79$, $P < 0.0001$, $n = 95$). Neither of these components varies in any systematic way with fat content ($P \gg 0.05$).

The lean dry mass of the carcass is weakly, but highly significantly, correlated with the two linear measures of body size: wing length ($r = 0.37$, $P = 0.0002$, $n = 95$) and tarsus length ($r = 0.31$, $P = 0.0026$, $n = 95$). Other variables measured in this study that are significantly correlated with the lean dry mass of the carcass are time of capture, age, and ovary mass in spring females. The lean dry mass was elevated in birds captured in the evening (Fig. 3). Analysis of covariance demonstrates that, although the slopes of the relationships between lean dry mass and wing length in morning and evening birds are not significantly different, the elevations are ($P = 0.002$). Juvenile catbirds in the fall samples had a significantly smaller mean wing length than adults (86.59 ± 0.24 mm and 89.09 ± 0.63 mm for juveniles and adults, re-

TABLE 1. Body mass and linear measurements of catbirds during various seasons in Michigan and Florida. Values given are the mean ± SE. Sample size is in parentheses.

		Body mass (g)			Wing length (mm)			Tarsus length (mm)		
Month(s)	Location	Male	Female	Both sexes	Male	Female	Both sexes	Male	Female	Both sexes
May–June	Ann Arbor	33.34 ± 0.91 (7)	36.91 ± 2.26 (5)	34.82 ± 1.15 (12)	89.00 ± 0.73 (7)	87.54 ± 0.78 (5)	88.39 ± 0.56 (12)	28.09 ± 0.28 (7)	28.10 ± 0.49 (5)	28.09 ± 0.25 (12)
Aug.–Oct.	Ann Arbor	36.83 ± 0.75 (13)	37.02 ± 1.11 (11)	36.67 ± 0.63 (26)	88.81 ± 0.48 (13)	86.95 ± 0.82 (11)	87.94 ± 0.47 (25)	28.69 ± 0.31 (13)	28.39 ± 0.39 (11)	28.58 ± 0.23 (25)
Sept.–Oct.	Florida	40.92 ± 1.01 (21)	37.76 ± 0.59 (44)	38.91 ± 0.55 (67)	87.38 ± 0.63 (21)	86.36 ± 0.30 (43)	86.66 ± 0.28 (66)	28.03 ± 0.20 (20)	27.94 ± 0.13 (42)	27.95 ± 0.11 (64)
Total		38.33 ± 0.74 (41)	37.55 ± 0.25 (60)	37.88 ± 0.43 (105)	88.11 ± 0.151 (41)	86.57 ± 0.27 (59)	87.17 ± 0.23 (103)	28.26 ± 0.15 (40)	28.04 ± 0.12 (58)	28.12 ± 0.096 (101)

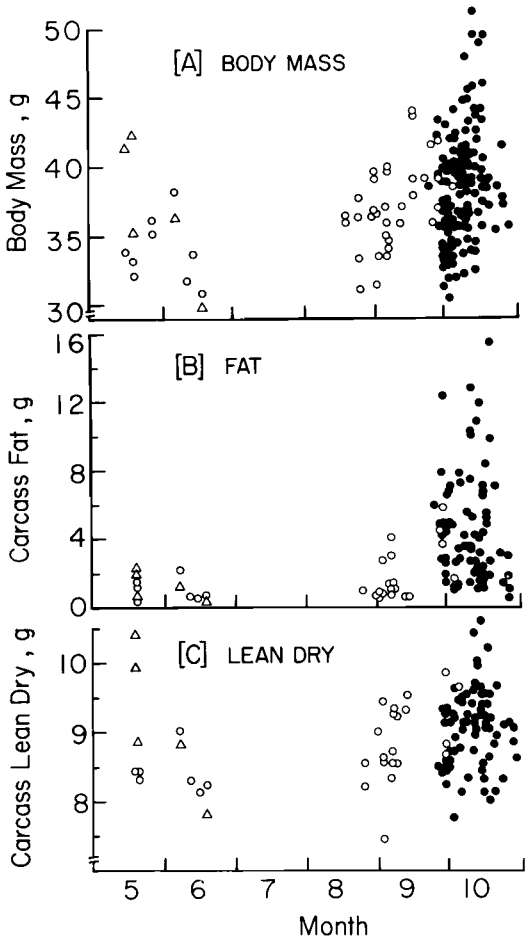

Fig. 1. Seasonal variation in body mass (A), carcass fat content (B), and carcass lean dry mass (C) in the Gray Catbird. ○,△ = birds captured in Michigan; ● = birds captured in Florida; △ = spring and early summer females.

spectively; $P = 0.0001$ for Student's t-test). The fall juveniles also had significantly smaller lean dry masses than did the adults (mean = 8.94 g vs. 9.24 g; $P = 0.0304$ for the Mann-Whitney U-test). Multiple correlation analysis, however, indicates that if the effects of size (wing length) are accounted for, no significant age-related differences in lean dry mass remain. The lean dry mass of the carcass does not appear to be related to molt, season, sex, or place of capture (Michigan vs. Florida). (ANOVA and analyses of covariance $P \gg 0.05$ in all cases.) This was despite the fact that males have a significantly greater mean wing length (Table 1;

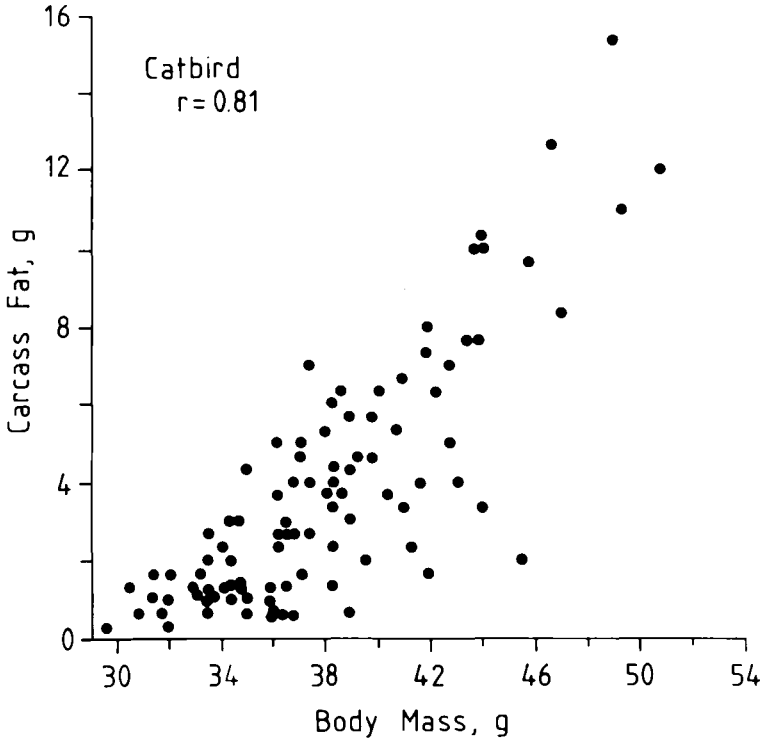

Fig. 2. Carcass fat as a function of body mass in the Gray Catbird.

male vs. female, total sample, $P = 0.0012$). In breeding females a significant positive relationship exists between the lean dry mass of the carcass and ovary mass ($r = 0.96$, $n = 6$ for log ovary mass correlated with log lean dry mass). In contrast, the lean dry mass does not change significantly between May and June in male catbirds.

Tissue glycogen and concentration of substrates in plasma.—Table 2 shows the values for liver and muscle glycogen, plasma glucose, and plasma triglycerides for the group of birds sacrificed in the field in Florida. Plasma concentrations of glucose and triglyceride show no significant difference (Mann-Whitney *U*-test) between morning- and evening-caught birds. Plasma glucose shows little variation, with an overall mean of 3.36 ± 0.15 mg/ml. Plasma triglyceride glycerol, on the other hand, is extremely variable, with values ranging from 1.77

TABLE 2. Plasma and tissue substrates in the catbird during fall migration. Values given are the means with the sample range in parentheses.

Time	Plasma glucose (mg/ml)	Plasma TGG[a] (μmole/ml)	Liver glycogen (mg/g)	Muscle glycogen (mg/g)
Morning[b]	3.28 (2.79–3.74)	4.34 (1.77–7.86)	18.9 (3.4–36.2)	4.08 (0.2–10.7)
Evening[c]	3.43 (3.15–3.77)	6.23 (4.14–8.94)	77.1 (60–103)	19.9 (2.7–34)
P[d]	0.40 (NS)	0.063 (NS)	0.004	0.03

[a] TGG = triglyceride glycerol.
[b] $n = 5$, capture time 0710–1040 EST.
[c] $n = 6$, capture time 1730–1806 EST.
[d] Probability that the morning and evening values are significantly different using the Mann-Whitney *U* two-tailed test.

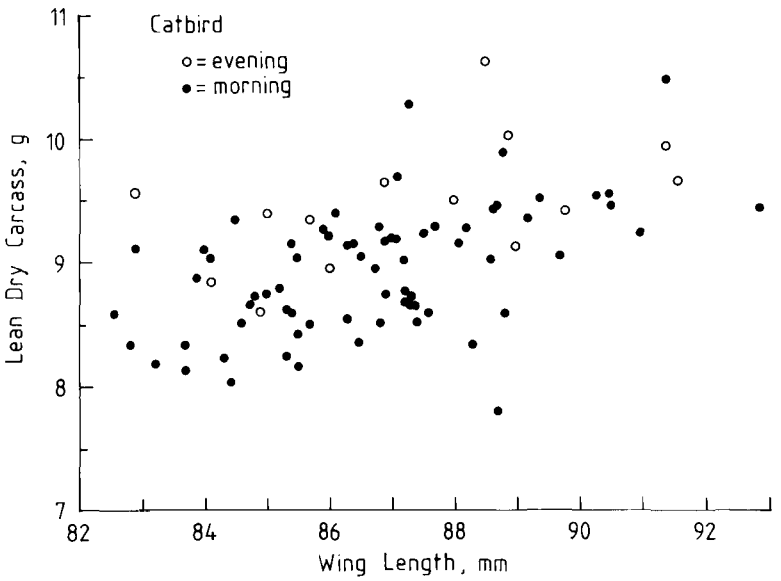

Fig. 3. Lean dry mass as a function of wing length in Gray Catbirds. ○ = birds captured in the evening; ● = birds captured in the morning.

to 8.94 μmole/ml. Glycogen values are four to five times higher in the evening than in the morning (Table 2). Although the birds captured varied in fat content from approximately 1 g to greater than 12 g, neither the blood substrates nor the tissue glycogen levels showed any significant correlation with the amount of fat.

Discussion

Migration pattern.—Because in the present study of the catbird I employed discrete and widely separated sampling locations, some consideration must be given to the overall migratory pattern of the species. On the basis of available banding returns and the known wintering areas (A.O.U. checklist 1957), populations of catbirds from all parts of the breeding range appear to be highly variable in their wintering localities. It is obvious that the catbird as a species does not fit clearly any one of the usual classifications of migrants according to migratory pattern (see Helms and Smythe 1969, King 1972). The sampling locations are such that the fall samples probably contain both premigrants and intramigrants in Michigan and intramigrants and postmigrants in Florida.

Carcass fat content.—The data on fat content collected in this study are consistent with the hypothesis that part of the catbird population migrates across the Gulf of Mexico in the fall. Catbirds collected in Florida have a much higher maximum fat content than Michigan birds (Fig. 1). This pattern of higher fat content in individuals collected near the Gulf is typical of other trans-Gulf migrants (Caldwell et al. 1963).

I have estimated the amount of fat required by catbirds to cross the Gulf based on the formulae of Pennycuick (1975). Although such calculations have a strong theoretical base and are in good agreement with a variety of empirical measurements (see Tucker 1973), they may lack precision in application to natural situations. For example, it is typical to calculate "still-air" range, whereas it is clear from direct observations of migrants that they take advantage of favorable weather conditions to maximize range (Lack 1960, Drury and Keith 1962, Williams et al. 1977). Conversely, migrants may encounter adverse weather in the course of migration, such that fat reserves are depleted and they are forced to land short of their destination (see, for example, Johnston 1968, Williams et al. 1977). Given the possibility of errors in both directions, still-air range may provide a reasonable standard for comparison if the possible errors are kept in mind.

These calculations for the catbird indicate that approximately 8 g of fat would be required to

fly from northern Florida to the Yucatan Peninsula, a distance of 1,000 km. Of the catbirds collected in Florida, 13% had more than 8 g of fat. However, the actual percentage of the catbirds migrating through northern Florida that make a long overwater flight may be much greater. Fry et al. (1970) have suggested, on the basis of their work on trans-Saharan migrants, that long-distance migrants depart soon after reaching high levels of fat. The continuing departure of the fatter birds means that the birds sampled will be distributed in the lower fat categories. Also, in the Florida catbirds fat contents are higher in the evening than in the morning, and 30% of the evening birds collected have greater than 8 g of fat. The overall distribution was skewed by the greater collecting effort in the morning. As Johnston (1966) suggests, caution must be used in inferring potential migratory distance from fat content when one is collecting birds in the process of migration.

Lean dry mass of the carcass.—The lean dry mass of the carcass (carcass = body of the bird minus the flight muscles and heart) is quite variable in catbirds collected at all seasons and stages of fattening (Fig. 1). As has been shown for other small passerines (Connell et al. 1960, Rogers and Odum 1964), some of this variation can be explained by variation in structural body size. This size-related variability is indicated by the correlation with the linear measurements of body size (wing length and tarsus length). The smaller size of the juveniles collected in the fall also appears adequate to explain the age-related differences in lean dry mass. Beyond the correlations with size and age there are only two factors measured in this study that affect the lean dry mass significantly. One factor is the time of day, with evening birds having elevated lean dry masses (Fig. 3). Other small passerines show similar diurnal cycles, and these cycles have been ascribed to a daily cycle of protein content (see Newton 1968). The other factor is the breeding status of the females. Two heavy females were collected in May, and they possessed large ovaries with numerous ripening follicles. The lean dry masses of these females were elevated considerably above the remainder of the May and June sample (Fig. 1C). This large difference was independent of the flight muscles, which were in fact smaller than expected on the basis of body mass (Marsh in press). Clearly, future studies considering the relationship between protein content and breeding should consider the protein content of the whole animal and not just the flight muscles (cf. Jones and Ward 1976, Fogden and Fogden 1979).

In the catbirds sampled, migratory fattening does not influence the lean dry mass of the carcass. These data appear to confirm the suggestions of Odum and colleagues (Connell et al. 1960, Odum et al. 1964, Rogers and Odum 1964) that birds show homeostasis in other body components during the addition of fat. One must also, however, consider the data in light of the significant relationship between lean dry mass of the pectoralis muscles and fat content (Marsh 1979, in press). In the catbird and several other species, these major flight muscles apparently increase in mass with increments in total body mass (see also Marsh and Storer 1981). This hypertrophy is considered to be an adaptation to the increased power requirements for flight. The carcass lean dry mass of the remainder of the animal, however, is so variable in catbirds that the significant changes in the lean dry mass are not evident if one attempts to correlate the lean dry mass of the entire bird (the sum of the lean dry mass of the carcass as defined here and the lean dry masses of the muscles) with the fat content. Thus, it may be possible to reconcile some of the conflicting reports in the literature concerning whether or not body components other than fat change during premigratory fattening (see discussion in Fry et al. 1970, 1972). The detection of a significant relationship between the total lean dry mass and the fat content may depend on a low amount of variability in the lean dry components exclusive of the flight muscles.

Tissue glycogen and blood glucose levels.—The levels of tissue glycogen found in catbirds captured in Florida suggest that glycogen levels are not suppressed during the fall migration in this species (Table 2). In fact, the concentrations of liver and muscle glycogen found in birds collected in the evening are among the highest values reported for any passerine bird (see Farner et al. 1961, John and George 1965) and are within the range reported for man and captive birds and mammals (Hazelwood and Lorenz 1959, Lamb et al. 1969; Baldwin et al. 1973, Keppler and Decker 1974). The diurnal cycles of glycogen found in the catbirds also appear to conform to data from laboratory

studies. Decreases in liver glycogen during the inactive phase of the daily cycle have been found in birds and mammals (e.g. Hazelwood and Lorenz 1959, Bonney et al. 1973). Although less well studied, daily fluctuations in muscle glycogen do occur in skeletal muscles (Pessacq and Gagliardino 1975, Conlee et al. 1976). The largest cycles have been found in high oxidative skeletal muscles (Conlee et al. 1976), and the pectoral muscles of catbird are very high in oxidative capacity (Marsh 1979, Marsh 1981).

The high glycogen concentrations and substantial diurnal fluctuations in glycogen levels in the catbird are in agreement with data on several Indian passerines (see George and Chandra-Bose 1967) and on fall Gambel's White-crowned Sparrows (King et al. 1963). In regard to conflicting reports (see Farner et al. 1961, Baggott 1977), it should be noted that the lability of glycogen stores necessitates care in the design of capture methods and sampling procedures, if glycogen concentrations are to reflect levels present in field animals. Even if substantial variability exists in glycogen storage among migratory species, however, it remains to be determined whether these variations represent intrinsic differences in the regulation of carbohydrate metabolism or are due to extrinsic factors, such as diet.

The importance of carbohydrate in the metabolism of small passerine migrants is difficult to assess on the basis of available data. Glycogen is quantitatively unimportant in terms of energy storage in these animals (this study, Farner et al. 1961), but this does not mean that maintenance of carbohydrate homeostasis is not critical during migration. Indeed, in mammals the maintenance of blood glucose and muscle glycogen concentrations is crucial during periods of high substrate turnover such as exercise and cold stress (Bergström and Hultmann 1967, Saltin and Karlsson 1971, Minaire et al. 1973, Paul and Holmes 1975), even though fat is quantitatively the most important substrate. In these mammals, the turnover and oxidation of plasma glucose are elevated in proportion to the increase in metabolic rate, and the duration of exercise may be limited by the ability to supply this glucose. Additionally, Marsh and Dawson (1982) have suggested that carbohydrate may be the limiting fuel for thermogenesis in the American Goldfinch (*Carduelis tristis*). Whether or not this information applies to the high metabolic rates that must be sustained during migration is not known. Evidence available on catabolic enzymes in the pectoralis muscles of catbirds (Marsh 1979, 1981) indicates that the ability to oxidize FFA increases during fattening. This may represent an adaptation that spares carbohydrate and helps maintain carbohydrate homeostasis. Also, the lack of variation in the concentration of blood glucose found in catbirds (Table 2) indicates precise regulation of this parameter in normally active, wild birds. Of course, my sampling procedures would not have detected the sort of complex seasonal and diurnal cycles described by Dolnik (1973) using caged birds. Because of the limited conclusions that can be drawn from measurements of concentration only, the measurement of rates of carbohydrate use in birds during various stages of the annual cycle is necessary before further conclusions can be drawn concerning the importance of carbohydrate metabolism for migratory species.

Conclusions

Data on fat content are consistent with the hypothesis that a portion of the population of catbirds migrates across the Gulf of Mexico during the fall migration. Calculations of migratory distance based on aerodynamic theory indicate that 13% of the birds collected had accumulated sufficient reserves to cross the Gulf. Due to sampling biases, it is likely that a larger proportion of the population actually makes the crossing.

In contrast to the data on fat content, the lean dry mass and water content of the carcass, exclusive of the flight muscles, do not change significantly in the premigratory period. The flight muscles do increase in size during fattening (Marsh in press), however, which is interpreted as a specific adaptation of these muscles to compensate for increases in the power requirements for flight. These data, combined with information on a more limited sample of breeding females, clearly indicate that the lean dry mass of the flight muscles and of the remainder of the body do not necessarily change in concert. Therefore, studies considering the importance of protein in the annual cycles of birds should consider changes in the entire body and not just the flight muscles.

Field samples during the fall migratory period demonstrate that tissue glycogen levels are

not suppressed during migration in this species. More information on the concentrations and kinetics of carbohydrates is necessary before the role of these substrates in migratory birds can be clarified.

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