The Auk 118(3):665–677, 2001

COMPARATIVE FUEL USE OF MIGRATING PASSERINES: EFFECTS OF FAT STORES, MIGRATION DISTANCE, AND DIET

LEONARD Z. GANNES[1]

Department of Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey 08544, USA; and Mitrani Department of Desert Ecology, Blaustein Institute for Desert Research, Ben-Gurion University of the Negev, Midreshet Ben-Gurion, 84990, Israel

ABSTRACT.—Lipids are the dominant fuel source during migratory flight, but the factors controlling the relative importance of lipid, protein, and carbohydrate to flight metabolism remain unclear. I tested the nonexclusive hypotheses that diet, migration distance, or endogenous lipid reserves mediate variation in the fuels birds catabolize during migration. Blood plasma metabolite concentrations were significantly different among species, and indicated clear differences in protein and lipid utilization among three turdid chat and five sylviid warbler species caught during spring migration in the Negev Desert, Israel. Fruit-eating species (omnivores) catabolized less protein and more lipid during migration than insectivores. Metabolite concentrations of omnivorous Blackcaps (*Sylvia atricapilla*), Garden Warblers (*S. borin*), and Lesser Whitethroats (*S. curruca*) were consistent with low rates of proteolysis (low uric acid), and high rates of lipolysis (high free-fatty acid and β-hydroxybutyrate). On the other hand, metabolite concentrations of insectivorous Redstarts (*Phoenicurus phoenicurus*), Nightingales (*Luscinia megarhynchos*), Thrush Nightingales (*L. luscinia*), Barred Warblers (*S. nisoria*), and Orphean Warblers (*S. hortensis*) indicated increased proteolysis and decreased lipolysis. Blood metabolite concentrations, however, were not correlated with migration distance, and the results do not support the hypothesis that long-distance migrants use fuel differently than short-distance migrants. Triacylglycerol mobilization was positively correlated with the amount of visible subcutaneous fat, but blood metabolite composition was more strongly affected by diet. Omnivores and insectivores exhibit different fuel-use strategies to overcome the physiological challenges of migration. *Received 29 March 2000, accepted 28 February 2001.*

LIPIDS ARE an energy-dense fuel source for volant migrants, and provide the majority of the energy used during long-duration flights in birds (Rothe et al. 1987, Ramenofsky 1990, Jenni-Eiermann and Jenni 1991). Previous authors have suggested that only lipids are catabolized, and that protein mass remains constant during migration (e.g. Odum et al. 1964). However, body-mass changes preceding and during migration (Marsh 1983, 1984; Piersma and Jukema 1990, Wingfield et al. 1990, Lindström and Piersma 1993, Karasov and Pinshow 1998, Klassen et al. 2000) and direct evidence from blood metabolites (Jenni-Eiermann and Jenni 1991, Bairlein and Totzke 1992) indicate that carbohydrates and proteins also are oxidized during migration. Carbohydrate stores are small relative to lipids, but glycogen plays an important role during take-off, burst flight, and fuel delivery to glucose-dependent tissues (e.g. central nervous system; Rothe et al. 1987, Schwilch et al. 1996, Jenni and Jenni-Eiermann 1998). Unlike lipid and carbohydrate reserves, protein is stored as functioning tissues. The roles of oxidized protein during migration are likely multifaceted and may include replacing Krebs cycle intermediaries, maintaining water balance, supplying amino acids for gluconeogenesis, or balancing changes in mass-dependent power requirements (Biebach 1996). However, the mechanisms controlling fuel composition (contribution of lipid, protein, and carbohydrate) during migration remain enigmatic.

Previous studies are compatible with the nonexclusive hypotheses that migration distance or endogenous lipid reserves, or both, mediate variation in the fuels birds catabolize during migration. A long-distance migrant, the Garden Warbler (*Sylvia borin*), used less protein and more lipid during fall migration than a short-distance migrant, the European Robin

[1] Present address: Environmental Studies, Prescott College, 220 Grove Avenue, Prescott, Arizona 86301, USA. E-mail: lgannes@prescott.edu

(*Erithacus rubecula*; Jenni-Eiermann and Jenni 1991). Alternatively, the quantity of endogenous lipid reserves could explain the observed fuel-use differences. In the above study, European Robins had smaller visible fat reserves than Garden Warblers (Jenni-Eiermann and Jenni 1991). Lean passerines, captured in the Sahara during fall migration, had elevated blood concentrations of urea, consistent with increased protein oxidation, compared with fat birds (Bairlein and Totzke 1992). A controlled study of birds varying in both migration distance and fat reserves is required to disentangle these alternative explanations for fuel-use differences among species.

An alternative factor that has not previously been explored in migrating birds is that diet during and preceding migration might affect the composition of fuel oxidized during migration. Days to weeks of eating a diet type changes both substrate utilization and storage rates in exercising humans and rats (reviewed in Volek 1997, Hawley et al. 1998, Spriet and Peters 1998). Similarly, the daily nitrogen requirements of strictly frugivorous and nectarivorous birds are lower than omnivores or carnivores (reviewed in Bairlein and Gwinner 1994; Murphy 1996). Although the effect of diet on the fuel composition of migrating birds is completely unknown, diet affects the rate of mass gain during migratory stopover (Bairlein and Gwinner 1994, Parrish 1997).

In the present study, I used a comparative approach to test the nonexclusive hypotheses that migration distance, fat reserves, or diet explain the differences in fuel use during migration. Old World warblers (Sylviidae) and chats (Turdidae) are an excellent representative system to test these hypotheses. Closely related sylviid and turdid species migrate both short and long distances and eat omnivorous and insectivorous diets (Fig. 1). If migration distance were an important determinant of migratory fuel use, then a species' migration distance should be positively correlated with lipid oxidation and negatively correlated with protein oxidation during migratory flight. Alternatively, if the fuels catabolized during migration were mediated by endogenous lipid reserves, then lean birds should have increased levels of proteolysis and decreased levels of lipolysis compared with fat birds. Finally, if diet mediates the fuels oxidized during migration, fuel composition should group according to diet type rather than lipid reserves or migration distance.

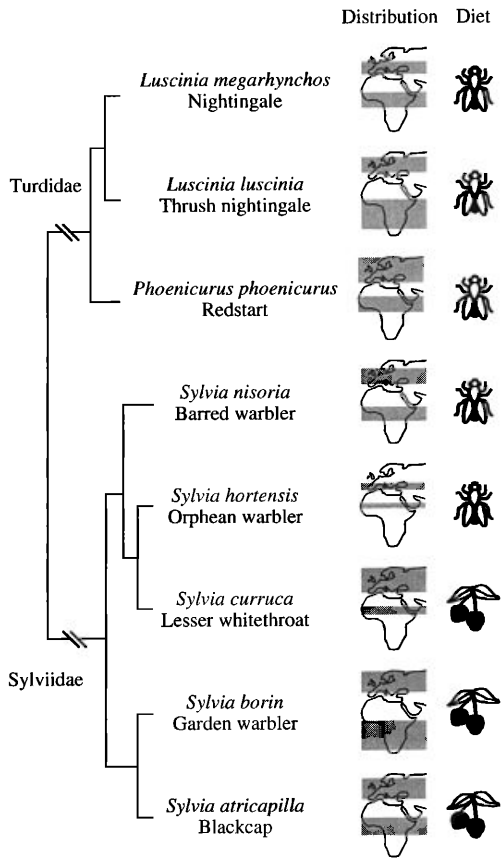

FIG. 1. Closely related sylviid and turdid species migrate both short and long distances, and eat both insectivorous and fruit-based omnivorous diets. The cladogram was adapted from phylogenies by Sibley and Ahlquist (1995) and Blondel et al. (1996). Distribution maps indicate northern and southern extremes of winter and breeding ranges (from Cramp 1988, 1992). Species were categorized as mostly insectivorous (fly) or omnivorous (berry) according to Cramp (1988, 1992), and dietary assignments agree with observations in the field (see methods).

METHODS

This study focused on three turdid chats: Redstarts (*Phoenicurus phoenicurus*), Nightingales (*Luscinia megarhynchos*), and Thrush-Nightingales (*L. luscinia*); and five sylviid warblers: Blackcaps (*Sylvia atricapilla*), Garden Warblers, Lesser Whitethroats (*S. curruca*), Orphean Warblers (*S. hortensis*), and Barred Warblers (*S. nisoria*). Birds were captured in mist nets

in the gardens at Midreshet Ben-Gurion, Israel (30°52′N, 34°46′E, 476 m above sea level). Located in the northern Negev Desert, Midreshet Ben-Gurion receives <100 mm rainfall annually.

Migrants were captured in mist nets daily 4 March to 18 May 1996 and 10 March to 21 May 1997. The nets were checked at 15–20 min intervals from 1 h before sunrise and for approximately 4 h thereafter. High midday temperatures and frequent afternoon windstorms precluded capturing birds all day long. Flattened wing cord and mass (Ohaus electronic balance ±0.1 g) were measured, and birds were banded with aluminum bands obtained from the Israel Banding Center. In addition, visual subcutaneous fat was scored in half-units from 0 for no visible fat to 4 for lipid storage regions overflowing with fat (modified from Helms and Drury 1960). Fat score explains ~50% of the variation in total body fat of other migrant passerines (Rogers 1987, Krementz and Pendleton 1990, Sprengler et al. 1995), particularly when interobserver variation is reduced (Krementz and Pendleton 1990). Throughout both seasons, three observers were frequently crosschecked for internal consistency in scoring fat. Birds were generally held <30 min, including time spent in the net and processing.

Because the same site was intensively trapped daily, individuals captured without a band (after the first 10 days) were called *new arrivals.* Birds captured ≥1 day after their first capture were termed *recaptures.*

Blood metabolite analyses.—Evidence for lipid, protein, and carbohydrate catabolism can be found in the blood, because the majority of an animal's energy reserves are stored externally to metabolizing cells. Lipolysis is associated with elevated concentrations of free-fatty acid, glycerol, and β-hydroxybutyrate, and elevated triacylglycerol levels are associated with net lipogenesis in the liver (Hurley et al. 1986, Jenni-Eiermann and Jenni 1992, 1994). Blood plasma free-fatty acid concentrations were significantly correlated ($r = 0.9446$, Pearson correlation $P = 0.0045$) with lipid turnover in chickens (*Gallus gallus domesticus*) run on a treadmill (reanalysis of data from Vincent and Brackenbury 1988). In addition, free-fatty acid and β-hydroxybutyrate concentrations were positively correlated in flying and resting pigeons (mean $r = 0.783 \pm 0.042$; Gannes et al. 2001). Uric acid is the major end product of protein catabolism in birds. In a variety of birds, blood plasma uric acid concentrations were correlated with protein oxidation measured by excreted nitrogen (Mori and George 1978, Robin et al. 1987, Cherel et al. 1988, Lindgård et al. 1992). In contrast, blood glucose concentrations are not necessarily correlated with glucose oxidation. Many birds regulate blood glucose concentrations within narrow limits (e.g. Hazelwood 1986, Swain 1992a), but some species apparently do not (e.g. Swain 1987, Jenni-Eiermann and Jenni 1997). In this study, I used free-fatty acids and β-hydroxybutyrate concentrations as indicators of lipid turnover, and uric acid as an indicator of protein turnover. However, I do not assume that glycerol, triacylglycerol, or glucose concentrations were correlated with turnover.

Radar data from the Negev Desert indicated that migrating passerines land at dawn (Bruderer and Liechti 1995). Because the goal of this study was to compare fuel use during flight, new-arrival and recapture birds were sampled only during the first 2 h after twilight. Twilight times were calculated using the program available from the Australian Department of Industry, Science and Tourism. Time after twilight was included as a factor in statistical models (see below).

To obtain blood samples, I punctured the vena ulnaris with a 26 gauge hypodermic needle and collected the blood in heparinized capillary tubes (60–120 μL). Blood samples were kept on ice for a maximum of 3 h until they were spun in a microhematocrit centrifuge (5 min, 12,000 g). Blood metabolite concentrations did not change significantly over this time period (L. Gannes unpubl. data). I measured hematocrit and discarded the red blood cells. Blood plasma was diluted gravimetrically by one-half with isotonic saline solution, and diluted samples were stored at −80°C until analyzed.

Triacylglycerol, glycerol, uric acid, β-hydroxybutyrate, glucose (Sigma Diagnostic, St. Louis, Missouri) and free-fatty acid (Boehringer-Mannheim, Indianapolis, Indiana) concentrations were analyzed using spectrophotometric assays modified for small volumes. The triacylglycerol values reported in this study were calculated by subtracting free glycerol from the total bound and unbound glycerol ("true triacylglycerol"). Absorbance values of samples (in duplicate, 3–10 μL) and standards were measured with a spectrophotometer.

Migration distance.—Minimum and maximum migration distances were compared among species. The minimum migration length was calculated by subtracting the northernmost wintering from the southernmost breeding ranges, in degrees latitude (Cramp 1988, 1992). Similarly, the maximum migration distance was calculated by subtracting the southernmost wintering from the northernmost breeding ranges. Because the two measures of migration distance were significantly correlated (pairwise correlation, $R = 0.884$, $P = 0.0036$), only the results from the minimum migration distance were reported below.

Diet.—I used Cramp (1988, 1992) for assigning diet types to species. During the nonbreeding season, Blackcaps, Garden Warblers, and Lesser Whitethroats depend to a large degree on noninsect food sources (berries and fruits), and will be referred to as *omnivores.* On the other hand, Nightingales, Thrush-Nightingales, Redstarts, Barred Warblers,

TABLE 1. Results from separate ANCOVA models for glycerol, triacylglycerol, free-fatty acid, uric acid, β-hydroxybutyrate, and glucose concentration in new-arrival passerine migrants. *Fat* (visible subcutaneous fat score) and *Time of day* (hours after twilight) were included as covariates and *Species* and *Year* were included as factors. Significant effects are in bold.

	Fat			Species		Year		Time of day		
Metabolite	Slope[a]	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*n*
Glycerol	0.046	2.2	0.1432	1.3	0.2418	2.0	0.1599	2.3	0.1305	180
Triacylglycerol	**0.240**	13.9	**0.0003**	2.8	**0.0095**	0.2	0.6240	0.0	0.8916	180
Free-fatty acid	−0.014	0.0	0.8920	2.7	**0.0121**	2.7	0.1000	0.0	0.9236	171
Uric acid	−0.036	0.8	0.3613	5.0	**<0.0001**	2.1	0.1498	3.4	0.0684	180
β-hydroxybutyrate	0.027	0.1	0.7425	4.0	**0.0004**	0.7	0.4199	4.1	**0.0437**	159
Glucose	0.145	0.3	0.5873	4.7	**0.0001**	49.0	**<0.0001**	3.9	0.0514	131
PC1	−0.058	0.6	0.4491	10.3	**<0.0001**	2.0	0.1646	6.0	**0.0159**	122
PC2	**0.195**	5.1	**0.0263**	2.4	**0.0249**	10.0	**0.0020**	0.0	0.9996	122

[a] Slope of ANCOVA effect of fat on metabolite concentrations, significant slopes are in bold.

and Orphean Warblers take almost exclusively insects, and will be referred to as *insectivores*. Although many avian migrants change diets during migration (reviewed in Bairlein and Gwinner 1994), observations from Midreshet Ben-Gurion agreed with Cramp's dietary generalizations. Approximately 20–30% of the Blackcaps, Garden Warblers, and Lesser Whitethroats captured in 1997 had plant parts in their feces, or their bill, forehead, and crown were covered with pollen and nectar (L. Gannes unpubl. data). The defecated seeds were mostly from acacia pods (*Acacia* sp.) and the acacia trees were often covered with feeding Blackcaps and Lesser Whitethroats. In addition, I frequently saw Lesser Whitethroats probing flowers, presumably for nectar. Less than 3% of the Redstarts, Orphean Warblers, Barred Warblers, Nightingales, and Thrush-Nightingales had plant parts in their feces and none were covered with pollen (L. Gannes unpubl. data). In addition, Redstarts and Orphean Warblers fed *ad libitum* in the laboratory refused to eat a fruit-based diet ("banana mash"; Denslow et al. 1987), but readily consumed mealworms (*Tenebrio* larvae; L. Gannes unpubl. data). On the other hand, Blackcaps readily ate and gained mass on either the fruit-based or mealworm diets (L. Gannes unpubl. data).

Statistical analyses.—Separate ANCOVA models for each metabolite were used to interpret interspecific differences in blood metabolites, with fat score as a covariate. We included time after twilight as a covariate in all ANCOVA models, because previous studies have found that metabolite concentrations change over the course of the day (Jenni-Eiermann and Jenni 1997, Jenni and Jenni-Eiermann 1996). Year was also included to control for differences between 1996 and 1997. The least square means (LSM) from the ANCOVA models were used to make ad hoc comparisons of metabolite values independent of fat score, time after twilight, and year. Similarly, ANCOVA models were used to interpret blood-metabolite concentration differences between new-arrival and recaptured birds, and between omnivores and insectivores. Both models included time after twilight as a covariate, and year and species as factors.

Principal component analysis (PCA) was used to clarify interspecific variation in blood-metabolite concentrations. PCA combines correlated variables into independent and interpretable axes. The new PCA values can then be used to compare correlated variables among species. All six blood metabolites were used in the PCA, but birds missing one or more metabolite measures were excluded from the analysis.

The data in the ANCOVA models did not meet the assumptions of normality. Natural-log transformed variables did meet the assumptions of normality, but the transformations did not change the results qualitatively. Therefore, data were not transformed before analysis. Discrepancies in sample size are a result of incomplete samples, and all means are given ±SE. Statistical models and PCA were analyzed using JMP 3.1 for the Macintosh (SAS Institute 1994).

RESULTS

Interspecific blood metabolites.—Blood-metabolite concentrations of newly arrived birds were significantly different among the species independent of fat score (Table 1). In newly arrived birds, free-fatty acid values were highest in Blackcaps and Garden Warblers, and lowest in Redstarts, Nightingales, and Orphean Warblers (Fig. 2). Blackcaps, Garden Warblers, and Lesser Whitethroats had significantly lower uric acid concentrations than redstarts or Orphean Warblers (Fig. 2). Blackcaps, Garden Warblers, and Lesser Whitethroats had higher plasma β-hydroxybutyrate levels than Nightingales, Redstarts, and Thrush-Nightingales (Fig. 2). Glycerol concentrations were not sig-

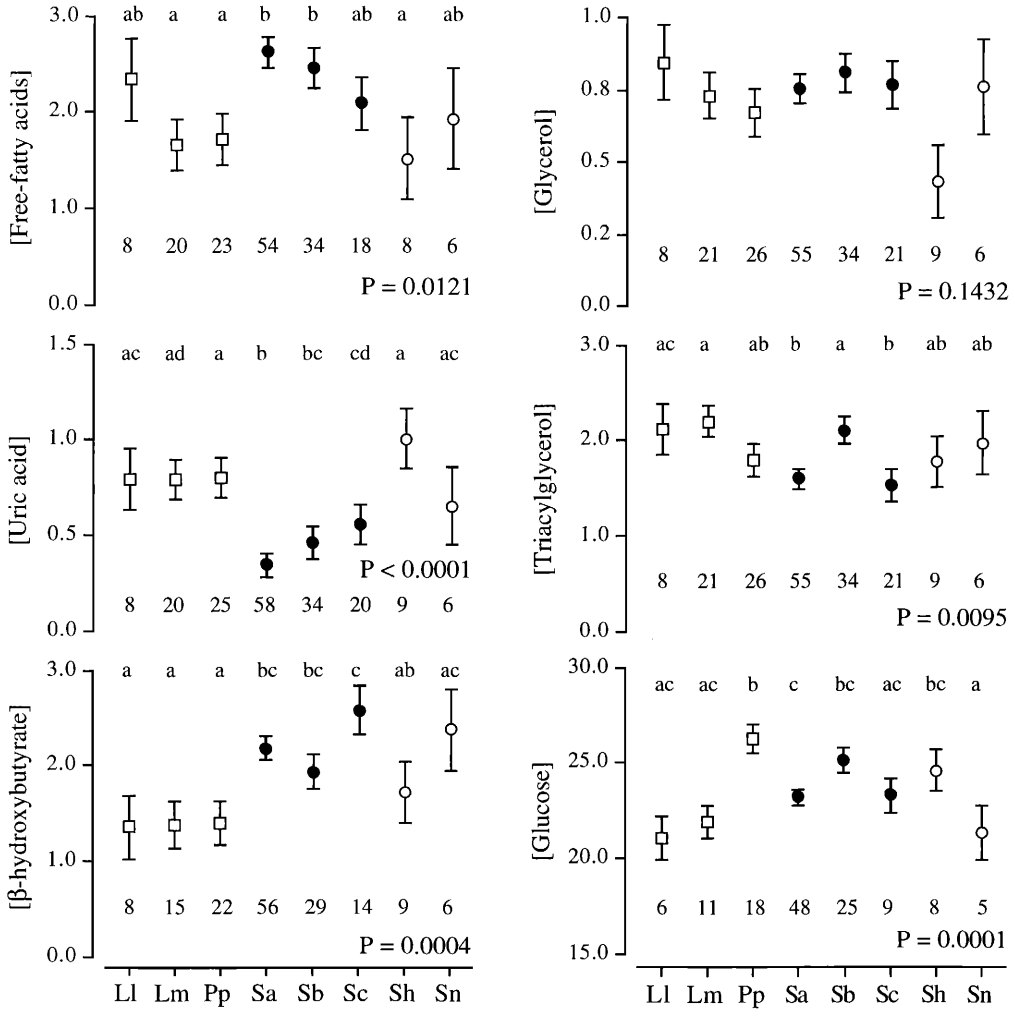

FIG. 2. Blood-plasma concentrations (mmol/L) of free-fatty acids, uric acid, β-hydroxybutyrate, glycerol, triacylglycerol, and glucose significantly vary among migratory species. Least-square means (LSM ± SE) given for turdid chats (squares): Thrush-Nightingales (Ll), Nightingales (Lm), Redstarts (Pp); and sylviid warblers (circles): Blackcaps (Sa), Garden Warblers (Sb), Lesser Whitethroats (Sc), Orphean Warblers (Sh), Barred Warblers (Sn). *P*-values indicate results of species differences in ANCOVA models (Table 1), and different letters indicate significantly different means, by linear contrasts. Sample sizes given below the error bars. Omnivores and insectivores are indicated by filled and empty symbols, respectively.

nificantly different among the species (Fig. 2). Plasma triacylglycerol concentrations in new-arrival Blackcaps and Lesser Whitethroats were lower than those of Garden Warblers, Nightingales, and Thrush-Nightingales (Fig. 2). Redstarts and Garden Warblers had higher levels of plasma glucose than Barred Warblers, Nightingales, or Thrush-Nightingales (Fig. 2).

Principal component analysis (PCA) clarified the complex patterns of interspecific blood metabolites. The first two principal components explained 48% of the variation (Table 2). The first principal component axis (PC1) was positively correlated with concentrations of free-fatty acids and β-hydroxybutyrate and negatively correlated with concentrations of uric acid and triacylglycerol (Table 2). PC1 explained 26% of the total variance. Because PC1 was positively correlated with lipid metabolites and negatively correlated with uric acid, I interpreted PC1 as the "lipolysis–proteolysis axis." PC1 values from Blackcaps, Garden War-

TABLE 2. Results from PCA of blood metabolites for new-arrival migrants. Values indicate correlation coefficients of first (PC1) and second principal component axes (PC2). PC1 was positively correlated with lipid metabolites (B-hydroxybutyrate, free fatty acids), negatively correlated with protein metabolite (uric acid), and interpreted as the "lipolysis–proteolysis axis." PC2 was positively correlated with lipid metabolites (glycerol, triacylglycerol, free-fatty acid), negatively correlated with glucose concentration, and interpreted as the "lipolysis–glycolysis axis."

Metabolite	PC1	PC2
% Explained	26	22
Glycerol	0.12	0.52
Triacylglycerol	−0.42	0.64
Free-fatty acid	0.45	0.50
Uric acid	−0.75	0.13
β-hydroxybutyrate	0.72	0.22
Glucose	−0.03	−0.65

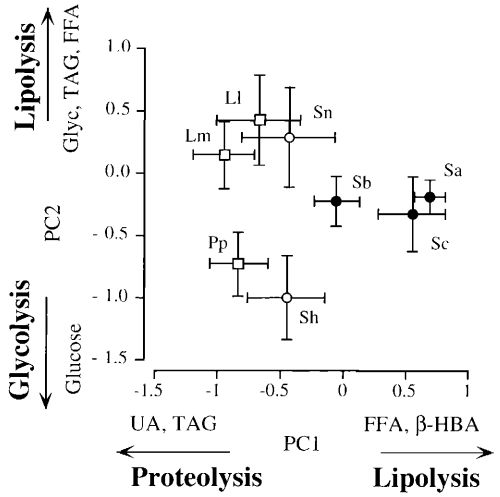

FIG. 3. Protein and lipid oxidation during migration significantly differ among species. The first (PC1) and second (PC2) principal components were interpreted as the "lipolysis–proteolysis" and the "lipolysis–glycolysis" axes, respectively (See Table 2). PC1 values from Blackcaps, Garden Warblers, and Lesser Whitethroats indicated high levels of lipolysis and low levels of proteolysis, but metabolites from Orphean Warblers, Redstarts, Nightingales, Barred Warblers, and Thrush-Nightingales indicated low levels of lipolysis and high levels of proteolysis. Redstarts and Orphean Warblers had significantly lower PC2 values than Nightingales, Thrush-Nightingales, Blackcaps, and Barred Warblers. Values are LSM ± SE. See Figure 2 for explanation of symbols and Table 1 for full ANCOVA models.

TABLE 3. Least square means (LSM ± SE), minimum and maximum visible subcutaneous fat scores for study species. LSM from ANOVA model of species ($F = 5.92$, df = 7 and 183, $P < 0.0001$) controlling for year ($F = 25.9$, df = 1 and 183, $P < 0.0001$). Different letters indicate significantly different means by linear constrasts.

Species	Fat score	Min	Max	*n*
Thrush Nightingale (*Luscinia luscinia*)	2.19 ± 0.3[b]	0.5	3.5	8
Nightingale (*L. megarhynchos*)	1.96 ± 0.19[b]	0.5	3.0	21
Redstart (*P. phoenicurus*)	0.81 ± 0.17[a]	0	2.5	26
Blackcap (*Sylvia atricapilla*)	1.68 ± 0.11[b]	0	4.0	58
Garden Warbler (*S. borin*)	1.25 ± 0.15[a]	0	2.5	34
Lesser Whitethroat (*S. curruca*)	1.81 ± 0.19[b]	0	3.5	21
Orphean Warbler (*S. hortensis*)	2.24 ± 0.30[b]	0	3.0	9
Barred Warbler (*S. nisoria*)	2.21 ± 0.37[b]	2.0	3.0	6

blers, and Lesser Whitethroats indicated high levels of lipolysis and low levels of proteolysis, but metabolites from Orphean Warblers, Redstarts, Nightingales, Barred Warblers, and Thrush-Nightingales indicated low levels of lipolysis and high levels of proteolysis (Fig. 3). The second principal component axis (PC2) was negatively correlated with glucose concentration and positively correlated with glycerol, triacylglycerol, and free-fatty acid concentrations. This axis explained an additional 22% of the overall variance (Table 2). PC2 can be interpreted as the lipolysis–glycolysis axis. Redstarts and Orphean Warblers had significantly lower PC2 values than Nightingales, Thrush-Nightingales, Blackcaps, and Barred Warblers (Fig. 3).

Fat stores.—Although there was a large variation in fat score, only triacylglycerol concentrations were significantly correlated with fat score. Among species, birds covered the entire fat-score range (0–4), and most species also had individuals from all categories (Table 3). Garden Warblers and Redstarts had significantly lower fat scores than any of the other species (Table 3). ANCOVA analyses indicated that fat score covaried with triacylglycerol values regardless of species differences and controlling for year and time after twilight (Table 1). Not surprisingly, PC2 was also positively correlat-

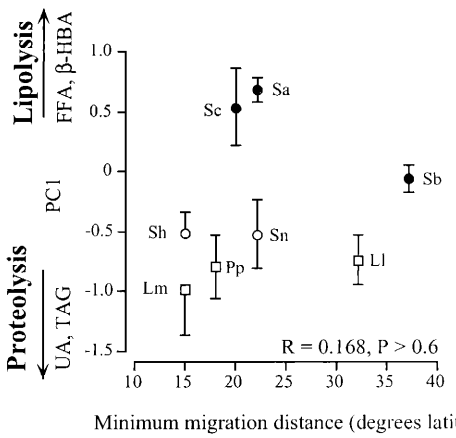

FIG. 4. Minimum migration distance did not explain the variation of lipid and protein use in migrating songbirds. Least-square means (LSM ± SE) of the first principal component (PC1) were not significantly correlated with a species' minimum migration distance (*R* and *P* for pairwise correlations). Migration distance taken from Cramp (1988, 1992). See Figure 2 for explanation of symbols and Table 1 for complete ANCOVA model.

ed with fat score, because PC2 is associated with triacylglycerol concentrations (Table 2). However, the covariance of fat score with glycerol, glucose, free-fatty acids, uric acid, β-hydroxybutyrate and PC1 were not significant (Table 1).

Migration distance.—The wintering ranges of the sylviids and turdids in this study span from north of the equator to the southern tip of Africa, and the breeding ranges begin in the northern Mediterranean and most extend above the Arctic Circle (Fig. 1; Cramp 1988, 1992). The species' means of the first principal component axis (PC1) were not correlated with minimum migration distance of a species (pairwise correlations; Fig. 4). Similarly, none of the individual metabolites or PC2 correlated significantly with minimum migration distance ($P > 0.2$).

Diet.—Diet explained much of the variation in blood metabolite concentrations of newly arrived migrants (Table 4). Fruit-eating omnivores (Blackcaps, Garden Warblers, and Lesser Whitethroats) had significantly higher free-fatty acid and β-hydroxybutyrate, and lower uric acid and triacylglycerol plasma concentrations than insectivores (Orphean Warblers, Redstarts, Barred Warblers, Nightingales, and

TABLE 4. Results from separate ANCOVA models for glycerol, triacylglycerol, free-fatty acid, uric acid, β-hydroxybutyrate, and glucose concentrations, and principal component values in new-arrival passerine migrants. Values were tested for differences between omnivores (*Sylivia atricapilla, S. curruca, S. borin*) and insectivores (*Luscinia luscinia, L. megarhynchos, Phoenicurus phoenicurus, S. hortensis, S. nisoria*), controlling for *Species, Year,* and *Time* (hours after twilight). Significant effects are in bold.

Metabolite	Diet				Species		Year		Time		
	Omnivore[a]	Insectivore[a]	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*n*
Glycerol	0.77 ± 0.04	0.69 ± 0.05	1.4	0.2460	1.2	0.2922	4.2	**0.0423**	1.8	0.1790	180
Triacylglycerol	1.71 ± 0.08	2.00 ± 0.13	4.2	**0.0424**	2.9	**0.0121**	3.4	0.0675	0.3	0.5737	180
Free-fatty acid	2.39 ± 0.13	1.83 ± 0.19	6.7	**0.0107**	0.9	0.5060	3.3	**0.0711**	0.0	0.9090	171
Uric acid	0.46 ± 0.05	0.81 ± 0.07	17.5	**<0.001**	1.0	0.4121	1.5	0.2297	3.0	0.0849	180
β-hydroxybutyrate	2.23 ± 0.12	1.65 ± 0.16	10.6	**0.0014**	1.8	0.1078	0.6	0.4592	4.1	**0.0457**	159
Glucose	23.82 ± 0.43	23.01 ± 0.55	1.8	0.1765	5.8	**<0.0001**	54.5	**<0.0001**	3.7	0.0579	131
PC1	0.49 ± 0.12	−0.50 ± 0.16	33.6	**<0.0001**	2.9	**0.0104**	3.3	0.0721	6.7	**0.0110**	122
PC2	−0.32 ± 0.14	−0.21 ± 0.18	0.3	0.5622	3.6	**0.0025**	17.9	**<0.0001**	0.1	0.7584	122

[a] LSM ± SE of metabolite concentration (mmol/L) and PCA scores.

Thrush-Nightingales). As a result, omnivores had significantly higher means on the lipolysis–proteolysis axis (PC1) than did insectivores (Fig. 2). Glycerol, glucose, and PC2 were not significantly different between the diet groups (Table 4).

Metabolites of newly arrived and recaptured birds.—A five-species subset (Lesser Whitethroat, Nightingale, Redstart, Blackcap, Garden Warbler) of the eight study species were recaptured in large enough numbers to compare blood metabolite concentrations of newly arrived and recaptured birds. Repeated measures on the same bird were not possible, because few birds were sampled both as new arrivals and recaptures. Newly arrived birds had significantly higher glycerol and free-fatty acid, and lower uric acid concentrations than recaptured birds (Table 5). Blood glucose, β-hydroxybutyrate and triacylglycerol levels were not significantly different between new arrival and recaptured birds (Table 5). In addition, blood hematocrit values were significantly lower in recaptured (0.443 ± 0.007) than in new arrival birds (0.492 ± 0.004; $F = 46.1$, df = 1 and 190, $P < 0.0001$), but neither species ($F = 1.9$, df = 4 and 190, $P > 0.1$) nor year ($F = 0.2$, df = 1 and 190, $P > 0.6$) were statistically significant.

DISCUSSION

Blood plasma metabolite concentrations were significantly different among species and indicated clear differences in protein and lipid utilization. Metabolite concentrations in Blackcaps, Garden Warblers, and Lesser Whitethroats were consistent with low levels of proteolysis (low uric acid), and a high degree of lipid oxidation (indicated by high free-fatty acids and β-hydroxybutyrate; Fig. 2). On the other hand, metabolite concentrations of Redstarts, Nightingales, Thrush-Nightingales, Barred Warblers, and Orphean Warblers suggested a higher level of proteolysis and lower lipolysis (Fig. 2). PCA separated species along the lipolysis–proteolysis axis (PC1; Fig. 3). The results were consistent with Blackcaps, Garden Warblers, and Lesser Whitethroats using less protein and more lipids during migration than Redstarts, Orphean Warblers, Barred Warblers, Nightingales, and Thrush-Nightingales.

TABLE 5. Results from separate ANCOVA models for glycerol, triacylglycerol, free-fatty acid, uric acid, β-hydroxybutyrate, and glucose concentrations (mmol/L) in new-arrival and recaptured passerine migrants. Values were tested for differences between new arrival and recaptured individuals (*Type*) controlling for *Species*, *Year*, and *Time* (hours after twilight). Only species with large enough samples to compare new arrival and recaptured birds were used in this analysis (*Luscinia megarhychos, Phoenicurus phoenicurus, Sylvia atricapilla, S. borin,* and *S. curruca*). Significant effects are in bold.

Metabolite	Type				Species		Year		Time		
	New arrival[a]	Recapture[a]	F	P	F	P	F	P	F	P	n
Glycerol	0.73 ± 0.03	0.56 ± 0.06	8.0	**0.0052**	0.3	0.8871	9.5	**0.0023**	0.8	0.3072	212
Triacylglycerol	1.80 ± 0.07	1.60 ± 0.12	2.7	0.1020	3.0	**0.0201**	1.3	0.2623	0.0	0.9305	212
Free-fatty acid	2.09 ± 0.11	1.64 ± 0.20	4.6	**0.0326**	5.7	**0.0002**	1.3	0.2608	0.3	0.5881	201
Uric acid	0.61 ± 0.04	0.76 ± 0.07	4.9	**0.0283**	15.0	**<0.0001**	5.8	**0.0171**	3.7	0.0568	212
β-hydroxybutyrate	1.87 ± 0.09	1.68 ± 0.14	1.6	0.2018	9.2	**<0.0001**	0.0	0.9785	1.9	0.1694	189
Glucose	24.0 ± 0.36	25.0 ± 0.56	3.1	0.0712	7.8	**<0.0001**	79.8	**<0.0001**	3.1	0.0813	154

[a] LSM ± SE of metabolite concentration (mmol/L).

Levels of proteolysis and lipolysis clearly grouped according to diet. Fruit-eating omnivores (Blackcaps, Garden Warblers, and Lesser Whitethroats; Fig. 1) had lower uric acid, and higher free-fatty acid and β-hydroxybutyrate concentrations than insectivores (Orphean Warblers, Redstarts, Barred Warblers, Nightingales, and Thrush-Nightingales; Table 4). Species share a common evolutionary history, and various authors have pointed to the statistical pitfalls of treating species as statistically independent observations (reviewed in Felsenstein 1985, Garland and Carter 1994). However, the blood-metabolite concentrations of the insectivorous Orphean and Barred warblers closely resembled the concentrations of insectivorous turdid chats rather than their omnivorous congeners (Fig. 1). Migratory fuel-use splitting according to dietary preference, rather than phylogenetic relationships, supports the hypothesis that diet was a more important factor in migratory fuel-use than phylogenetic history.

Some individuals labeled as new arrivals may not have been captured when they first arrived at the study site, but several lines of reasoning suggest that blood-metabolite concentrations of new-arrival birds were representative of in-flight concentrations of migrating birds. First, samples were only taken during the period when radar indicated most passerines make landfall (Bruderer and Liechti 1995). Second, only a small minority of the individuals remained at the site for longer than one day. Eighty to 90% of the migrants in 1996 and 1997 were only captured once, and the majority of those birds probably continued migrating the same evening of the day they arrived (L. Gannes unpubl. data). Third, blood metabolites (glycerol, free-fatty acid, uric acid) and hematocrit were significantly different between new-arrival and recaptured birds, suggesting they came from two different "groups" (Table 5). Finally, other work has shown that blood concentrations of glycerol, free-fatty acid, and uric acid were not significantly different between European Robins captured in flight and those captured soon after landing (Jenni-Eiermann and Jenni 1991). In the present study, we included time after twilight as a covariate to control for potential changes in metabolite concentration during the 2 h sampling period.

Diet potentially can affect fuel use in flight by long-term biochemical adaptation to a diet, short-term replenishment of endogenous reserves, or both. The daily nitrogen requirements of frugivorous and nectarivorous birds are lower than omnivores or carnivores (reviewed in Bairlein and Gwinner 1994, Murphy 1996), and changing diet type for a period of days to weeks affects substrate utilization in exercising humans and rats (Hawley et al. 1998, Spriet and Peters 1998). However, proximate mechanisms of dietary adaptation are not well understood, and it remains unclear how diet-induced fuel-use differences might translate into fuel-use differences during migratory flight. Alternatively, dietary intake and composition has a short-term effect, taking hours to days, on an animal's endogenous carbohydrate stores (Hazelwood 1986, Swain 1992a, Spriet and Peters 1998). Because glycogen stores can be depleted quickly during exercise and are replenished independent of lipid reserves, even a highly obese migrant may have very reduced glycogen reserves after a nocturnal flight. Fruit-eating omnivores eating carbohydrate-rich diets (i.e. fruit, nectar) may have larger glycogen reserves at the beginning of a migratory flight than insectivores eating carbohydrate-poor diets, similar to mammals (reviewed in Volek 1997, Hawley et al. 1998, Spriet and Peters 1998). In postabsorptive animals when glycogen stores are reduced, protein becomes the dominant precursor for gluconeogenesis (Maughan et al. 1997). As a result, a bird with large glycogen stores may catabolize less protein to maintain blood glucose levels during migration than a bird with small glycogen reserves. In addition, the two effects probably are not mutually exclusive and could act in concert: enzymatic activity reducing body tissues' glucose requirements, and therefore conserving glycogen reserves and thus body protein. However, without knowing the stopover and feeding history of individual birds, it is impossible to separate long-term dietary adaptation from short-term replenishment of glycogen reserves.

The results from this study are not consistent with the hypothesis that long-distance migrants use fuel differently than short-distance migrants (cf. Jenni-Eiermann and Jenni 1991, Jenni and Jenni-Eiermann 1998). Individual blood-metabolite concentrations and principal component values were not correlated with

minimum migration distances that varied over 20° latitude (~2,200 km; Fig. 4). All the species in the present study winter south of the Sahara, and crossing the Sahara may exert similar selective pressure for differential fuel use regardless of total migration distance. However, the European Robin studied by Jenni-Eiermann and Jenni (1991) winters on the northern edge of the Sahara (Cramp 1988), and used more protein and less lipid than the Garden Warbler that winters in southern Africa (Cramp 1992). As would be predicted from the present study, the European Robin is mainly insectivorous and the Garden Warbler is omnivorous (Berthold 1976, Cramp 1988, 1992; L. Gannes unpubl. data).

Previous authors have hypothesized that species differences in fuel use were mediated by fat reserves: fat birds use more lipid and less protein than thin birds (Jenni-Eiermann and Jenni 1991, Bairlein and Totzke 1992). The results from the present study partially agree. Fat birds had higher triacylglycerol concentrations than lean birds, but none of the other metabolites covaried with fat score (Table 1). It seems that fat migrants increased triacylglycerol mobilization without changing proteolysis or other lipolysis metabolites. Migrating passerines may supply metabolizing cells directly with triacylglycerol, circumventing the potentially rate-limiting albumin-mediated transport of free-fatty acids (Weber 1988, Jenni-Eiermann and Jenni 1992). The present study suggests that fat birds might be able to use the triacylglycerol pathway to a greater degree than lean birds. However, species-level differences in fuel use occur after controlling for differences in fat score (Table 1).

Conclusions.—Spring migrants minimize the time spent on migration, presumably to acquire good breeding territories (Lindström and Alerstam 1992, Klaassen 1996). Over evolutionary time, migrants have "solved" migrational challenges with a suite of morphological and behavioral adaptations (reviewed in Berthold and Terrill 1991, Gwinner 1990, Berthold and Helbig 1991, Bairlein 1991). One such adaptation exhibited by many passerine migrants is switching from a mainly insectivorous diet to a fruit-based diet preceding and during migration (reviewed in Bairlein and Gwinner 1994). Switching to a fruit-dominated diet increases premigrational and en-route rate of mass gain, and may provide important nutrients and fatty acids (reviewed in Bairlein and Gwinner 1994, Parrish 1997). In addition, the present work suggests that the switch from insectivory to fruit-eating omnivory is also associated with decreased catabolism of endogenous body protein.

We might expect a strong selective pressure on insectivores to reduce protein oxidation. Unlike lipid and carbohydrate reserves, protein is stored as functioning tissue. However, birds may preferentially catabolize assimilation organs to avoid catabolizing flight muscles that could impair flying ability (Swain 1992b, Kasperek et al. 1992, Karasov and Pinshow 1998, Biebach 1998). As a result, protein oxidation may lead to decreased performance of absorptive organs (e.g. Biebach 1998, Karasov and Pinshow 1998, Piersma 1998), that could reduce a migrant's ability to refuel en-route. Compared to lipids, protein is a relatively heavy fuel (Schmidt-Nielsen 1990). Protein oxidation actually could reduce the amount of weight birds must carry during long-duration flights (e.g. Piersma and Lindström 1997, Piersma and Gill 1998), perhaps increasing potential flight range. Ultimately, the selective pressures on migrants will be the result of how diet affects total migration duration through proximate factors such as stopover site suitability or availability, stopover duration, and maximum migration distance without refueling. It seems, however, that insectivores and fruit-eating omnivores exhibit different migration strategies, each with an associated suite of morphological and behavioral adaptations to overcome the physical challenges of migration.

ACKNOWLEDGMENTS

This research is dedicated to my grandparents (Jack and Molly Rayman, Miriam and Abe Gannes) who have been a source of inspiration for as long as I can remember. The fieldwork would have been impossible without skilled assistance from Wendy Schelsky, Nathaniel Gerhart, Itai Shani, Nir Sapir, Norm Budnitz, Itamar Giladi, Gilead Michaeli, Kevin Schwartz, and Garr. I thank Berry Pinshow for making facilities available to me at the Mitrani Department of Desert Ecology, Ben-Gurion University, Israel. This manuscript was greatly improved with constructive comments on earlier drafts from Carlos Martínez del Rio, Diane O'Brien, Scott McWilliams, Lila Fishman, William Karasov, Chris Guglielmo, Ulf

Bauchinger, and Herbert Biebach. Insightful comments from two anonymous reviewers improved the clarity of the manuscript. This work was funded by a National Science Foundation Doctoral Dissertation Improvement Grant (# 9623836), a Sigma Xi Grant-In-Aid of Research, and Princeton University funds. The research was conducted with research permits from the Israeli Nature Reserves Authority. This is contribution number 324 of the Mitrani Department for Desert Ecology.

Literature Cited

Bairlein, F. 1991. Recent prospects on trans-Saharan migration of songbirds. Ibis 134:41–46.

Bairlein, F., and E. Gwinner. 1994. Nutritional mechanisms and temporal control of migratory energy accumulation in birds. Annual Review of Nutrition 14:187–215.

Bairlein, F., and U. Totzke. 1992. New aspects on migratory physiology of trans-Saharan passerine migrants. Ornis Scandinavica 23:244–250.

Berthold, P. 1976. The control and significance of animal and vegetable nutrition in omnivorous songbirds. Ardea 64:140–154.

Berthold, P., and A. J. Helbig. 1991. The genetics of bird migration: Stimulus, timing and direction. Ibis 134:35–40.

Berthold, P., and S. B. Terrill. 1991. Recent advances in studies of bird migration. Annual Review of Ecology and Systematics 22:357–378.

Biebach, H. 1996. Energetics of winter and migratory fattening. Pages 280–323 *in* Avian Energetics and Nutritional Ecology (C. Carey, Ed.). Chapman and Hall, New York.

Biebach, H. 1998. Phenotypic organ flexibility in Garden Warblers *Sylvia borin* during long-distance migration. Journal of Avian Biology 29: 529–535.

Blondel, J., F. Catzeflis, and P. Perret. 1996. Molecular phylogeny and the historical biogeography of the warblers of the genus *Sylvia* (Aves). Journal of Evolutionary Biology 9:871–891.

Bruderer, B., and F. Liechti. 1995. Variation in density and height distribution of nocturnal migration in the south of Israel. Israel Journal of Zoology 41:477–487.

Cherel, Y., J. Robin, and Y. Le Maho. 1988. Physiology and biochemistry of long-term fasting birds. Canadian Journal of Zoology 66:159–166.

Cramp, S., Ed. 1988. Handbook of the Birds of Europe the Middle East and North Africa: The Birds of the Western Palearctic: Tyrant Flycatchers to Thrushes. Oxford University Press, Oxford.

Cramp, S., Ed. 1992. Handbook of the Birds of Europe the Middle East and North Africa: The Birds of the Western Palearctic: Warblers. Oxford University Press, Oxford.

Denslow, J. S., D. J. Levey, T. C. Moermond, and B. C. Wentworth. 1987. A synthetic diet for fruit-eating birds. Wilson Bulletin 99:131–134.

Felsenstein, J. 1985. Phylogenies and the comparative method. American Naturalist 125:1–15.

Gannes, L. Z., K. A. Hatch, and B. Pinshow. 2001. How does time since feeding affect the fuels pigeons use during flight? Physiological and Biochemical Zoology 74:1–10.

Garland, T. J., and P. A. Carter. 1994. Evolutionary physiology. Annual Review of Physiology 56: 579–621.

Gwinner, E., Ed. 1990. Bird Migration—Physiology and Ecophysiology. Springer-Verlag, Berlin.

Hawley, J. A., F. Brouns, and A. Jeukendrup. 1998. Strategies to enhance fuel utilisation during exercise. Sports Medicine 25:241–257.

Hazelwood, R. L. 1986. Carbohydrate metabolism. Pages 303–325 *in* Avian Physiology (P. D. Sturkie, Ed.). Springer-Verlag, New York.

Helms, C. W., and W. H. Drury. 1960. Winter and migratory weight and fat field studies on some North American buntings. Bird-Banding 31:1–40.

Hurley, B. F., P. M. Nemeth, W. H. I. Martin, J. M. Hagberg, G. P. Dalsky, and J. O. Holloszy. 1986. Muscle triglyceride utilization during exercise: Effect of training. Journal of Applied Physiology 60:562–567.

Jenni, L., and S. Jenni-Eiermann. 1996. Metabolic responses to diurnal feeding patterns during the postbreeding, moulting and migratory periods in passerine birds. Functional Ecology 10: 73–80.

Jenni, L., and S. Jenni-Eiermann. 1998. Fuel supply and metabolic constraints on migrating birds. Journal of Avian Biology 29:521–528.

Jenni-Eiermann, S., and L. Jenni. 1991. Metabolic responses to flight and fasting in night-migrating passerines. Journal of Comparative Physiology B 161:465–474.

Jenni-Eiermann, S., and L. Jenni. 1992. High plasma triglyceride levels in small birds during migratory flight: A new pathway for fuel supply during endurance locomotion at very high mass-specific metabolic rates. Physiological Zoology 65:112–123.

Jenni-Eiermann, S., and L. Jenni. 1994. Plasma metabolite levels predict individual body-mass changes in a small long-distance migrant, the Garden Warbler. Auk 111:888–899.

Jenni-Eiermann, S., and L. Jenni. 1997. Diurnal variation of metabolic responses to short-term fasting in passerine birds during the postbreeding, molting and migratory period. Condor 99:113–122.

KARASOV, W. H., AND B. PINSHOW. 1998. Changes in lean mass and in organs of nutrient assimilation in a long-distance passerine migrant at a springtime stopover site. Physiological Zoology 71:435–448.

KLAASSEN, M. 1996. Metabolic constraints on long-distance migration in birds. Journal of Experimental Biology 199:57–64.

KLAASSEN, M., A. KVIST, AND Å. LINDSTRÖM. 2000. Flight costs and fuel composition of a bird migrating in a wind tunnel. Condor 102:444–451.

KREMENTZ, D. G., AND G. W. PENDLETON. 1990. Fat scoring: Sources of variability. Condor 92:500–507.

LINDGÅRD, K., K. A. STOKKAN, Y. LE MAHO, AND R. GROSCOLAS. 1992. Protein utilization during starvation in fat and lean Svalbard Ptarmigan (*Lagopus mutus hyperboreus*). Journal of Comparative Physiology B 162:607–613.

LINDSTRÖM, Å., AND T. ALERSTAM. 1992. Optimal fat loads in migrating birds: A test of the time-minimization hypothesis. American Naturalist 140: 477–491.

LINDSTRÖM, Å., AND T. PIERSMA. 1993. Mass changes in migrating birds: The evidence for fat and protein storage re-examined. Ibis 135:70–78.

MARSH, R. L. 1983. Adaptations of the Gray Catbird *Dumetella carolinensis* to long distance migration: Energy stores and substrate concentrations in plasma. Auk 100:170–179.

MARSH, R. L. 1984. Adaptations of the Gray Catbird *Dumetella carolinensis* to long-distance migration: Flight muscle hypertrophy associated with elevated body mass. Physiological Zoology 57: 105–117.

MAUGHAN, R., M. GLEESON, AND P. L. GREENHAFF. 1997. Biochemistry of Exercise and Training. Oxford University Press, Oxford.

MORI, J. G., AND J. C. GEORGE. 1978. Seasonal changes in serum levels of certain metabolites, uric acid and calcium in the migratory Canada Goose (*Branta canadensis*). Comparative Biochemistry and Physiology B 59:263–269.

MURPHY, M. E. 1996. Nutrition and metabolism. Pages 31–60 *in* Avian Energetics and Nutritional Ecology (C. Carey, Ed.). Chapman and Hall, New York.

ODUM, E. P., D. T. ROGERS, AND D. L. HICKS. 1964. Homeostasis of the nonfat components of migrating birds. Science 143:1037–1039.

PARRISH, J. D. 1997. Patterns of frugivory and energetic condition in nearctic landbirds during autumn migration. Condor 99:681–697.

PIERSMA, T. 1998. Phenotypic flexibility during migration: Optimization of organ size contingent on the risks and rewards of fueling and flight? Journal of Avian Biology 29:511–520.

PIERSMA, T., AND R. E. GILL, JR. 1998. Guts don't fly: Small digestive organs in obese Bar-tailed Godwits. Auk 115:196–203.

PIERSMA, T., AND J. JUKEMA. 1990. Budgeting the flight of a long-distance migrant: Changes in nutrient reserve levels of Bar-tailed Godwits at successive spring staging sites. Ardea 78:315–337.

PIERSMA, T., AND Å. LINDSTRÖM. 1997. Rapid reversible changes in organ size as a component of adaptive behaviour. Trends in Ecology and Evolution 12:134–138.

RAMENOFSKY, M. 1990. Fat storage and fat metabolism in relation to migration. Pages 214–231 *in* Bird Migration (E. Gwinner, Ed.). Springer-Verlag, Berlin.

ROBIN, J. P., Y. CHEREL, H. GIRARD, A. GÉLOEN, AND Y. LE MAHO. 1987. Uric acid and urea in relation to protein catabolism in long-term fasting geese. Journal of Comparative Physiology B 157:491–499.

ROGERS, C. M. 1987. Predation risk and fasting capacity: Do wintering birds maintain optimal body mass? Ecology 68:1051–1061.

ROTHE, H.-J., W. BIESEL, AND W. NACHTIGALL. 1987. Pigeon flight in a wind tunnel. Journal of Comparative Physiology B 157:99–109.

SAS INSTITUTE INC. 1994. User's Guide, version 3.1. SAS Institute Inc., Cary, North Carolina.

SCHMIDT-NIELSEN, K. 1990. Animal Physiology: Adaptation and Environment. Cambridge University Press, Cambridge, United Kingdom.

SCHWILCH, R., L. JENNI, AND S. JENNI-EIERMANN. 1996. Metabolic responses of homing pigeons to flight and subsequent recovery. Journal of Comparative Physiology B 166:77–87.

SIBLEY, C. G., AND J. E. AHLQUIST. 1995. Phylogeny and Classification of Birds. Yale University Press, New Haven, Connecticut.

SPENGLER, T. J., P. L. LEBERG, AND W. C. J. BARROW. 1995. Comparison of condition indices in migratory passerines at a stopover site in coastal Louisiana. Condor 97:438–444.

SPRIET, L. L., AND S. J. PETERS. 1998. Influence of diet on the metabolic responses to exercise. Proceedings of the Nutritional Society 57:25–33.

SWAIN, S. D. 1987. Overnight changes in circulating energy substrate concentrations in the Vesper Sparrow (*Pooecetes gramineus*). Comparative Biochemistry and Physiology A 86:439–441.

SWAIN, S. D. 1992a. Energy substrate profiles during fasting in Horned Larks (*Eremophila alpestris*). Physiological Zoology 65:568–582.

SWAIN, S. D. 1992b. Flight muscle catabolism during overnight fasting in a passerine bird, *Eremophila alpestris*. Journal of Comparative Physiology B 162:383–392.

VINCENT, R., AND J. H. BRACKENBURY. 1988. Utilisation of energy substrates in treadmill-exercised domestic fowl (*Gallus gallus domesticus*): Blood

plasma free fatty acids. British Poultry Science 29:469–479.

VOLEK, J. S. 1997. Energy metabolism and high intensity exercise: Dietary concerns for optimal recovery. Strength and Conditioning 19:26–37.

WEBER, J.-M. 1988. Design of exogenous fuel supply systems: Adaptive strategies for endurance locomotion. Canadian Journal of Zoology 66: 1116–1121.

WINGFIELD, J. C., H. SCHWABL AND P. W. MATTOCKS. 1990. Endocrine mechanisms of migration. Pages 232–256 *in* Bird Migration (E. Gwinner, Ed.). Springer-Verlag, Berlin.

Associate Editor: C. Blem