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Diet preferences of warblers for specific fatty acids in relation to nutritional requirements and digestive capabilities

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During energy-demanding periods of the annual cycle such as migration or during cold days in winter, birds store fat comprised mostly of 16- or 18-carbon unsaturated fatty acids. In such situations, birds may feed selectively on foods with specific fatty acids that enable efficient fat deposition. We offered wild-caught yellow-rumped warblers *Dendroica coronata* paired choices between semi-synthetic diets that differed only in their fatty acid composition. Warblers strongly preferred diets containing long-chain (18:1; carbon atoms:double bonds) unsaturated, unesterified fatty acids to diets containing long-chain saturated, unesterified fatty acids (18:0) and they preferred diets containing mono-unsaturated fats (18:1) to diets containing poly-unsaturated fats (18:2). The preference for diets containing long-chain unsaturated fatty acids to diets containing long-chain saturated fatty acids was consistent in birds tested one week after capture at 21°C, one month after capture when cold-acclimated (1°C), and six weeks after capture at 21°C. Birds acclimated to a diet with 50% of the fat comprised of unesterified stearic acid (18:0) lost mass and reduced their food intake when we reduced ambient temperature from 21°C to 11°C over three days. We conclude that especially in energy-demanding situations there are limits to the yellow-rumped warblers' ability to assimilate some long-chain saturated fatty acids and that this digestive constraint can explain in part why yellow-rumped warblers prefer diets containing long-chain unsaturated fatty acids to diets containing long-chain saturated fatty acids.

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During migration birds undergo significant changes in body composition (Blem 1976, 1980, 1990, Ramenofsky 1990) and diet (reviewed by Berthold 1996). During periods of fat storage (e.g., during migration or in the cold), birds store large amounts of fats comprised mostly of 16- or 18-carbon unsaturated fatty acids (Blem 1976, Dawson et al. 1983, Blem 1990, Eggler and Williams 2000). Migratory birds deposit these fat stores as a result of eating more food (Blem 1990, Bairlein and Gwinner 1994), and by feeding more selectively on energy profitable prey (Moore and Simm 1985, Wheelright 1988, Whelan and Willson 1994) that may have higher proportions of long-chain unsaturated fatty acids (reviewed by Bairlein and Gwinner 1994, Bairlein and Simons 1995, Berthold 1996). Selectively feeding on long-chain unsaturated fatty acids can be advantageous because such fatty acids may be absorbed and/or metabolized more efficiently than saturated fats into a bird's fat depots (Johnston 1973, Blem 1976, Heitmeyer and Fredrickson 1990, Bairlein and Gwinner 1994, Zurovchak 1997). However, only Bairlein (1991) has directly tested whether birds prefer diets with specific fatty acids. In these pilot studies (sensu Bairlein 1991), he found garden warblers *Sylvia borin* tended to prefer diets with long-chain unsaturated fatty acids compared to diets with either long-chain saturated fatty acids or shorter chain-length unsaturated fatty acids.

In paired-choice experiments where alternative foods are offered on an equal basis, birds may prefer diets with certain nutrient compositions because the preferred food satisfies specific nutrient requirements (i.e., a nutrient preference) or because the alternative food contains certain components that are avoided (i.e., a nutrient avoidance). We know little about nutrient preferences or avoidances of wild birds and how they influence diet selection. Murphy and King (1987) provide one of the few examples of selective feeding by a bird to satisfy specific nutrient requirements. They found that white-crowned sparrows *Zonotrichia leucophrys gambelii* preferentially consumed sulfur amino acids in proportion to the intensity of their molt and the associated demands for sulfur amino acids (Murphy and King 1984a, b, c, 1987). If wild foods of the white-crowned sparrow differ in their sulfur amino acid content while the birds are molting, then the specific appetites of white-crowned sparrows for certain amino acids should explain patterns of their diet selection.

Diet selection and specific nutrient preferences of wild birds may also be determined by digestive constraints. For example, Martinez del Rio et al. (1988) found that bird species that lack the intestinal enzyme to digest sucrose avoid diets containing sucrose. This avoidance can be enhanced through learning (Martinez del Rio et al. 1992) because undigested sucrose in the intestine can cause severe osmotic diarrhea (Sunshine and Kretchmer 1964). In this case, a digestive constraint (lack of sucrase) rather than a specific appetite explains the sugar preferences of many species of birds (Martinez del Rio et al. 1992).

We offered yellow-rumped warblers *Dendroica coronata* paired choices between diets with long-chain unsaturated (18:1; carbon atoms:double bonds), unesterified fatty acids and diets with long-chain saturated (18:0), unesterified fatty acids at three distinct times and conditions: (1) at room temperature (21°C) during their migration period, (2) in the cold (1°C), and (3) at room temperature (21°C) after their migration period. Based on previous evidence that showed garden warblers in premigratory condition preferred diets with mostly unsaturated 18:1 fatty acids over diets with mostly saturated 18:0 fatty acids (Bairlein 1991, Bairlein and Gwinner 1994), we expected yellow-rumped warblers to prefer the unsaturated fatty acids in the two more energy-demanding conditions (i.e. during their migration period and in the cold). However, because they regularly eat fruits high in saturated fats and can assimilate them (Place and Stiles 1992), we expected yellow-rumped warblers to show a less than absolute preference for diets with primarily unsaturated fatty acids especially after their migration period when energy intake and fat deposition are minimal.

Materials and methods

Capture and maintenance of birds

We caught 10 yellow-rumped warblers using mist nets in late September, 1995, as they migrated through Chippewa Falls, WI (45°00′ N, 91°30′ W). All ten birds were then transported to our laboratory at University of Wisconsin at Madison, and placed individually in $60 \times 45 \times 33$ cm cages in a room kept at 21°C with a 12 L:12 D light schedule. All warblers were initially fed a maintenance diet (Diet M, Table 1) that we have previously used to maintain birds in our laboratory for up to one year (Afik and Karasov 1995, McWilliams and Karasov 1998). Diet M simulates an insect diet in nutrient content (Bairlein 1987) with 20% fat, 52% protein, and 10% carbohydrates by dry wt. The fat in Diet M is composed of > 75% unsaturated fatty acids mostly in the form of oleic and linoleic acid (Table 1). Each bird was always offered its food at approximately the same time each day and in equal amounts in two separate dishes, about 20 cm apart. The birds were also given two live waxworms *Galleria mellonella* averaging ca. 0.2 g wet worm^{-1} on top of each food dish to supplement their diet and to ensure they always visited both food dishes.

Preference experiments

We compared the preferences of yellow-rumped warblers for diets with primarily saturated (Diet S) versus unsaturated (Diet U1) fatty acids (Table 1) in three experiments designed to correspond to three different ecological and physiological situations. The fat in Diet S was composed of 87.4% saturated fatty acids and 8.2% unsaturated fatty acids, whereas the fat in Diet U1 was composed of 8.3% saturated fatty acids and 89.2% unsaturated fatty acids. We used unesterified fatty acids for the preference diets (Table 1) instead of the triglyceride form(s) because the unesterified forms are less expensive, do not require enzymatic digestion prior to absorption, and are common in some wild fruits eaten by migratory songbirds (Zurovchak 1997). In the few other wild fruits that have been studied, fatty acids were mostly in the triglyceride form (Zurovchak 1997). We included small amounts of olive oil in all diets (Table 1) to satisfy requirements of birds for essential fatty acid(s) and to provide monoglycerides that promote solubility and hence absorption of the unesterified fatty acids (Scott et al. 1982).

Experiment 1 was conducted one week after capture of the birds and after acclimation to the maintenance diet (Diet M, Table 1) and to 21°C. During this time the birds were in migratory condition as indicated by their restlessness in their cages and high feeding rates (see Results). Experiment 2 was conducted about one month after capture and after acclimation to 1°C. Experiment 3 was conducted one week later than Experiment 2 and after birds were acclimated again to 21°C. We considered the birds post-migratory during Experiment 3 because they no longer exhibited restlessness in their cages and their feeding rates were much lower than when held under similar conditions six weeks earlier in Experiment 1.

Diet M was initially used as the maintenance diet because we had previously used it to successfully maintain yellow-rumped warblers in our laboratory. However, because all birds clearly preferred the diet with unsaturated fatty acids (Diet U1) in Experiment 1 (see Results) and because this diet was also similar to the maintenance diet (Diet M) in having oleic acid as the primary fatty acid (Table 1), we then acclimated the birds to Diet E which contained equivalent proportions of saturated and unsaturated fatty acids (Table 1). We reasoned that if birds continued to show preferences for Diet U1 after being acclimated to Diet E then this would provide stronger evidence for a preference for unsaturated fatty acids and not just a preference for a familiar fatty acid (oleic acid in this case). All birds initially appeared to adjust to Diet E, but when we began to lower ambient temperature (T_a) in preparation for Experiment 2 many birds reduced their food intake and body mass (see Results). Consequently, after only 5 days on Diet E the birds were offered only Diet M and up to 10 waxworms; however, only three of the birds regained mass and ate regularly. The other seven birds eventually died after consuming Diet E.

Once the remaining three birds were maintaining constant mass and were consuming as much of Diet M as before acclimation to Diet E, the T_a was lowered from 11°C to 1°C over 5 days ($-2°C\ d^{-1}$). After three days at 1°C, we conducted Experiment 2, the 6-day cold acclimation preference test using Diet S and Diet U1. We then increased T_a from 1°C to 21°C over 5 days in preparation for Experiment 3. After 1 day at 21°C and now 38 days after capture, we conducted two sets of preference tests: one set of trials compared the bird's preference for Diet S and Diet U1 for 4 days and another set of trials compared Diet S and Diet U2 during the next 6 days. The total fatty acid composition of Diet U2 (93.7% unsaturated, 1.9% saturated) was similar to Diet U1 (above), but the primary unsaturated fatty acid in Diet U2 was linoleic acid whereas in Diet U1 it was oleic acid (Table 1). Thus, if the bird's preference for Diet U1 is quantitatively different from that for Diet U2 then this would suggest that the type of long-chain unsaturated fatty acid is important in diet selection.

During preference testing the birds were simultaneously presented with two dishes, each with equivalent amounts of one of the diets. For each trial we measured daily food intake for 2–4 days and then switched the position of the dishes and measured daily food intake for another 2–4 days. We use the term "trial" to

Table 1. Ingredients (g per 100 g wet weight) and fatty acid (% of total fat) composition of diets.

	Diet M	Diet S	Diet U1	Diet U2	Diet E
Ingredients (g per 100 g wet weight)					
D-Glucose	1.13	1.13	1.13	1.13	1.13
Casein[1]	6.44	6.44	6.44	6.44	6.44
AA mix[2]	0.36	0.36	0.36	0.36	0.36
Vitamins and minerals[3]	0.22	0.22	0.22	0.22	0.22
Salt mix[4]	0.76	0.76	0.76	0.76	0.76
Oleic acid[5]	0	0	2.35	0	1.16
Linoleic acid[6]	0	0	0	2.35	0
Stearic acid[7]	0	2.35	0	0	1.18
Olive Oil	2.61	0.26	0.26	0.26	0.26
Water	87.0	87.0	87.0	87.0	87.0
Agar	1.31	1.31	1.31	1.31	1.31
Calculated fatty acid composition (no. carbon atoms:no. double bonds)[8]					
Oleic acid (18:1)	64.0	6.5	84.8	6.5	45.0
Linoleic acid (18:2)	15.0	1.5	4.2	87.0	2.8
Hexadecenoic acid (16:1)	1.6	0.2	0.2	0.2	0.2
Myristic acid (14:0)	1.2	0.1	0.1	0.1	0.1
Palmitic acid (16:0)	15.6	1.6	4.3	1.6	2.9
Stearic acid (18:0)	2.0	85.7	3.9	0.2	45.0
Unidentified fat	0.6	4.5	2.6	4.5	4.0

[1] Casein (high N) Teklad, US Biochemical Corp. (USB), Cleveland, Ohio.
[2] Amino acid mix (Murphy and King 1982).
[3] AIN-76 Vitamin and Mineral Mix, ICN Biochemicals, Inc.
[4] Salt Mix N Salt mixture, ICN Biomedicals, Inc.
[5] Unesterified (free) fatty acid from Chem. Assoc. of Illinois, Copley, Ohio.
[6] Unesterified (free) fatty acid from US Biochemical Corp. (USB), Cleveland, Ohio.
[7] Unesterified (free) fatty acid from US Biochemical Corp. (USB), Cleveland, Ohio.
[8] Fatty acid composition of olive oil from Scott et al. (1982).

Table 2. Body mass (g), food intake (g wet/day), and dietary preference (% total intake composed of unsaturated diet) of yellow-rumped warblers during pair-wise choice experiments. Shown are means ± SE.

Treatment condition[1]	Diet choices[2]	Body mass (g)	Food intake (g wet d^{-1})		Dietary preference[3]
			Diet U1 or U2	Diet S	
Experiment 1	Diet S vs Diet U1	11.43 ± 0.26	11.92 ± 0.63	1.23 ± 0.16	0.93 ± 0.01
Experiment 2	Diet S vs Diet U1	12.24 ± 0.71	17.37 ± 0.56	0.00 ± 0.00	1.00 ± 0.00
Experiment 3	Diet S vs Diet U1	13.34 ± 0.47	8.52 ± 0.98	0.70 ± 0.71	0.94 ± 0.06
	Diet S vs Diet U2	12.62 ± 0.32	4.73 ± 0.60	1.88 ± 0.59	0.62 ± 0.12
Comparison between three treatment conditions:[4]					
$F_{2,4}$		4.103	31.036		2.352
P-value		0.11	0.004		0.211
Comparison between two diet choices in Experiment 3:[5]					
W_3		8	6		6
P-value		>0.05	<0.05		<0.05

[1] Birds were tested within one week of capture at 21°C (Experiment 1), after acclimation to 1°C (Experiment 2), and after re-acclimation to 21°C and more than 30 days after capture (Experiment 3).
[2] See Table 1 for composition of each diet.
[3] Percent of total intake composed of unsaturated fatty acid diet.
[4] Repeated measures ANOVA comparing body mass, food intake, and dietary preference for Diet U1 vs. Diet S.
[5] Wilcoxon test comparing body mass, food intake, and dietary preference for diets with primarily unsaturated fatty acids (Diet U1 or U2) and diets with primarily saturated fatty acids (Diet S).

describe half an experiment during which the position of the foods was kept constant.

Statistical analysis

We used the chi-squared test to determine whether yellow-rumped warblers were eating disproportionately more of one diet. Expected values in these tests were calculated assuming no diet preference, i.e., 50% of daily intake for each of the two diets. Intake from the last day of a trial was used for this comparison. A low P-value ($P < 0.01$) demonstrated a preference for a certain diet.

We used the Wilcoxon two-sample test (Sokal and Rohlf 1981) to determine if a bird's preference changed when the position of the food was switched from the left to the right side of the cage. We calculated for each individual the average proportion of total food eaten comprised of Diet U1 across days within each trial.

We also used the Wilcoxon test to determine if a bird's preference changed significantly when it was given a choice between Diets S and U1 or Diets S and U2. We calculated for each individual the average proportion of total food eaten comprised of Diet U1 or U2 on the last day of each trial for each of the two preference tests.

We used a repeated measures ANOVA to compare the body mass, gross absolute food intake, and the arc-sine transformed proportion of each diet eaten by individual birds in each of the three experimental conditions. Body mass for each individual was an average across all days and both trials for each of the experimental conditions. Food intake (g wet d^{-1}) for each individual bird was an average across the last day of both trials for each experimental condition. We then used these estimates of food intake to calculate for each individual the proportion of total food eaten comprised of Diet U1. For comparisons across days within the migratory-state preference test, we calculated the proportion of total food eaten comprised of Diet U1 for each individual for each day of an experiment.

Results

Body mass and gross food intake during the experiments

Birds consumed the most total food during the preference experiments when in the cold (Experiment 2: 17.5 ± 0.64 g wet d^{-1}), about 40% less total food during migratory-state (Experiment 1: 10.6 ± 1.03 g wet d^{-1}), and about 50% less total food when in post-migratory condition (Experiment 3: 8.8 ± 0.88 g wet d^{-1}) ($F_{2,4} = 87.9$, $P < 0.0001$). Body mass of the test birds remained relatively constant ($P > 0.05$) during the preference tests (Table 2).

In contrast, body mass and especially food intake of the birds was quite variable when they were fed only Diet E (Fig. 1). All birds increased their food intake by 46% on the first day that Diet E was offered. Mean food intake was 61% less on the second day compared to the first day. Once we began reducing T_a, patterns of body mass and food intake were noticeably different in birds that survived and those that did not (Fig. 1). Seven of the ten birds died within seven days of being offered Diet E; all deaths occurred only after the temperature was reduced. The three surviving birds maintained higher body mass and food intake while eating Diet E; when they were resupplied with Diet M their food intake immediately doubled and their body mass immediately increased by 16%.

Dietary preferences for specific fatty acids

We shortened the length of trials from four days for Experiment 1 to three or two days in later preference experiments based on the daily pattern of preference observed in Experiment 1. In Experiment 1, the average percentage of total intake comprised of the unsaturated diet increased from $87.6 \pm 4.2\%$ (range: 64%–100%, n = 10) on Day 1 to $98.3 \pm 0.6\%$ (range: 89%–100%, n = 10) on each of Days 2–4 ($F_{3,27} = 7.87$, $P = 0.001$). Thus, by the second day of the experiment the bird's preference for the unsaturated diet was consistently strong and stable.

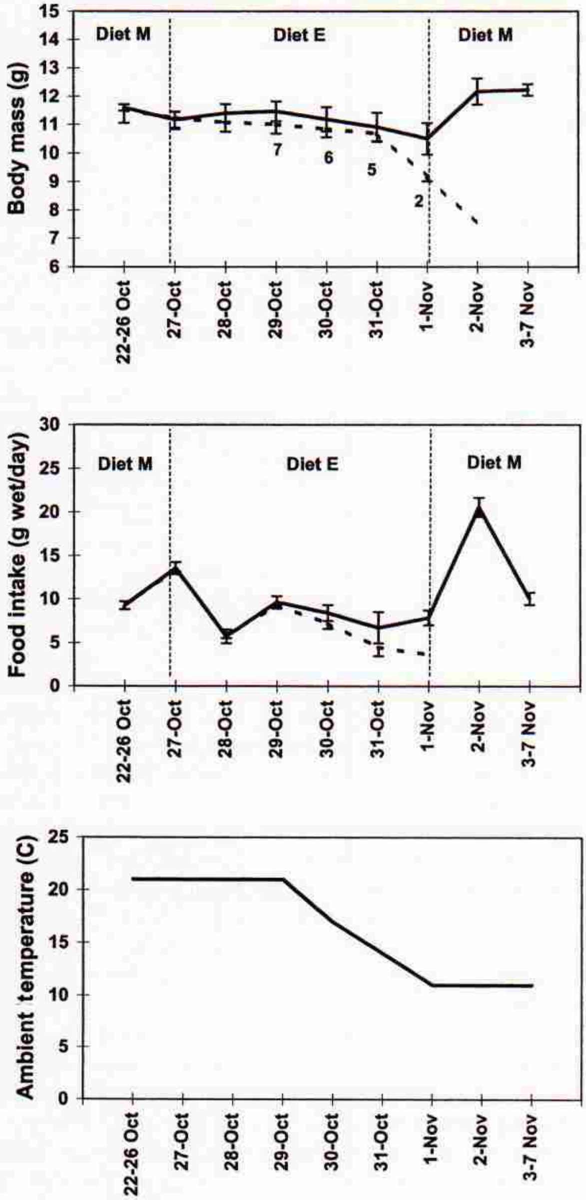

Fig. 1. Body mass (g) and daily food intake (g wet d^{-1}) $\pm$ SE of yellow-rumped warblers while the warblers were provided *ad libitum* amounts of a diet with fat comprised of mostly saturated fatty acids (Diet E) or mostly unsaturated fatty acids (Diet M; see Table 1 for exact composition of these diets). Three birds maintained body mass and food intake while eating Diet E (solid lines). Seven birds reduced their food intake and body mass while eating Diet E after ambient temperature was reduced (hatched lines; numbers below the hatched line in the upper figure are number of birds that ultimately died that were alive on that day).

In Experiment 1, yellow-rumped warblers clearly preferred Diet U1 compared to Diet S ($\chi^2 = 79.6$, $P < 0.001$ with Diet U1 on the right of cage, $\chi^2 = 41.7$, $P < 0.001$ with Diet U1 on the left of cage). However, birds ate proportionately more of Diet U1 when it was placed on the right side of the cage compared to the left side (1.0 ± 0.0 vs. 0.96 ± 0.003, respectively; $W_{10} = 55$, $P < 0.05$). The bird's preference for the unsaturated diet was consistent for all ten birds although data for just the three birds that were tested in all three experimental conditions are included in Table 2.

When the birds were acclimated to the cold (Experiment 2), they clearly preferred Diet U1 over Diet S ($\chi^2 = 26.4$, $P < 0.001$ with Diet U1 on right of cage, $\chi^2 = 26.4$, $P < 0.001$ with Diet U1 on the left of cage) and, in fact, never ate any measurable amount of Diet S (Table 2). Unlike their behavior during Experiment 1, the birds in Experiment 2 showed no preference for either the right or left side of the cage ($W_3 = 9$, $P > 0.05$).

Once the birds were reacclimated to 21°C (Experiment 3), they still clearly preferred Diet U1 over Diet S ($\chi^2 = 13.31$, $P < 0.005$ with Diet U1 on right of cage, $\chi^2 = 13.54$, $P < 0.005$ with Diet U1 on the left of cage). Again, the birds showed no preference for either the right or left side of the cage ($W_3 = 8$, $P > 0.05$).

The three yellow-rumped warblers tested in all three experimental conditions consistently preferred the diet with mostly unsaturated fatty acids (Diet U1) over the diet with mostly saturated fatty acids (Diet S) (see Dietary preferences in Table 2). When in the cold (Experiment 2), the warblers ate only Diet U1 and entirely avoided eating Diet S whereas at room temperature (Experiments 1 and 3) the warblers always ate some Diet S. This stronger preference for the diet with mostly unsaturated fatty acids when in the cold was not statistically significant (Table 2) although the power to detect a difference was low because of small sample size.

To test whether the degree of unsaturation of fatty acids affects the warblers' dietary preferences, we provided the birds a choice between Diet S and Diet U2, a novel diet (Table 1) comprised mostly of linoleic acid (18:2). Warblers consumed significantly less food when presented with Diet U2 compared to Diet U1 along with Diet S (Table 2), but they still demonstrated a preference for the diet with primarily unsaturated fatty acids ($\chi^2 = 9.30$, $P < 0.005$ with U2 diet on right of cage, $\chi^2 = 10.65$, $P < 0.01$ with U2 diet on the left of cage). However, warblers ate proportionately more of Diet S when it was paired with Diet U2 than when it was paired with Diet U1 (Table 2).

Discussion

Preferences for specific fatty acids

Yellow-rumped warblers clearly discriminated between semisynthetic diets differing only in fatty acid composition – in all cases, warblers preferred the two diets with mostly unsaturated, unesterified fatty acids (18:1 or 18:2) over the diet with mostly saturated, unesterified fatty acids (18:0). Furthermore, the warblers ate proportionately more of the diet with mono-unsaturated fatty acids (18:1) than poly-unsaturated fatty acids (18:2) when each was paired with the diet with saturated fatty acids (18:0). The birds responded to altered diet location or diet types within a day suggesting the birds used cues with relatively rapid response times (e.g., taste, smell) when making their choices.

Only Bairlein (Bairlein 1991, reviewed in Bairlein and Gwinner 1994, Bairlein and Simons 1995) and Zurovchak (1997) have studied such preferences for specific fatty acids in wild birds. Bairlein (1991) and Zurovchak (1997) offered garden warblers and wood thrushes *Hylocichla mustelina* and American robins *Turdus migratorius*, respectively, paired choices between diets that were similar in gross lipid content but had different fatty acid compositions. Like yellow-rumped warblers in our study, garden warblers and wood thrushes and robins preferred diets with mostly 18-carbon unsaturated fatty acids over the diets with mostly 18-carbon saturated fatty acid. Since we used purified fatty acids rather than oils that have many differences in their fatty acid composition (e.g., olive oil, sunflower oil, linseed oil (Bairlein 1991, Zurovchak 1997)), our work along with two of Bairlein's pilot experiments (sensu Bairlein 1991) demonstrates that at least two species of migratory songbird can discriminate between diets that differ only in certain long-chain fatty acids.

Negative effects of ingesting saturated fats

At first glance, one might suppose that the yellow-rumped warblers preferred the diet with mostly unsaturated fatty acids (Diet U1) over the diet with mostly saturated fatty acids (Diet S) simply because the fatty acid composition of Diet U1 was similar to the maintenance diet (Diet M). However, our failed attempt at acclimating the birds to Diet E which contained more stearic acid (18:0) is not consistent with such a simple explanation and suggests instead that the bird's diet choice is determined in part by an avoidance of stearic acid.

When we forced the birds to eat Diet E that contained more saturated fats (especially more unesterified stearic acid (18:0)) than the maintenance diet (Diet M, Table 1), we observed patterns of food intake and body mass that suggest there is a limit to the warblers' ability to efficiently assimilate some saturated fats. When unesterified stearic acid (18:0) comprised 50% of the fat in the diet (9% of diet's dry weight) all birds maintained or only slightly declined in body mass until we began reducing ambient temperature (from 22°C to 11°C). As temperature declined and energy requirements increased, body mass and food intake of all birds declined but the seven birds that ultimately did not survive quickly decreased food intake and lost body mass. When we resupplied the birds with Diet M, which was similar to Diet E except Diet M had more unsaturated fatty acids than Diet E (Table 1), the three surviving birds immediately increased food intake and body mass and these birds were then successfully acclimated to much lower temperatures.

The negative effects of ingesting saturated fats that we observed in yellow-rumped warblers are surprising for at least two reasons. First, Bairlein reports successfully feeding garden warblers diets containing "pure stearic (18:0) fatty acid lipids" for weeks with apparently no ill effects (unpublished data presented in Bairlein and Gwinner 1994). In fact, these garden warblers refattened faster when fed the pure stearic diet compared to when fed a pure palmitic (16:0) diet (Bairlein and Gwinner 1994). Second, yellow-rumped warblers are exceptional among passerines in regularly feeding on bayberry fruit which has a waxy coat comprised entirely of saturated fatty acids (myristic (14%), palmitic (85%), stearic (1%)) (Place and Stiles 1992). In 4-h feeding trials, yellow-rumped warblers efficiently assimilated (> 80%) ^{14}C-labelled palmitic acid (16:0) in this bayberry wax thus demonstrating that digestion of saturated fatty acids in the natural waxy coating on bayberry may play an important metabolic role as fuel for these birds (Place and Stiles 1992).

However, despite their impressive abilities to digest some saturated fatty acids, yellow-rumped warblers supplied with *ad libitum* bayberry fruit and water were unable to maintain body mass (losing 1.58 g day^{-1} or 14.5% of average body mass) (Place and Stiles 1992). This result along with our own suggests that yellow-rumped warblers can assimilate some saturated fatty acids but they may have difficulty relying on them for metabolic fuel, especially if energy requirements and food intake increase.

For most animals, the assimilation of fatty acids decreases with chain length and increases with degree of unsaturation (Renner and Hill 1961a, b, Clifford et al. 1986, Place 1996). Chickens, for example, assimilate unesterified oleic acid (18:1) at greater than 85%

efficiency, stearic acid (18:0) at only 4% efficiency, palmitic acid (16:0) at 12% efficiency, and myristic acid (14:0) at 29% efficiency (Scott et al. 1982). Chickens assimilate nonpolar saturated fatty acids like stearic acid more efficiently (> 40%) if the saturated fatty acids are consumed with unsaturated fatty acids that facilitate the absorption of the saturated fatty acids by forming micelles (Scott et al. 1982, Zubay 1983). Although we did not measure assimilation efficiency in our study, the feces of many birds on Diet E were sticky and firm suggesting the birds may have been suffering from steatorrhoea caused by incomplete digestion of unesterified saturated fatty acids (Larbier and Leclercq 1994, Place 1996) even though at least 50% of the dietary fat was composed of unsaturated fatty acids.

Diet preferences, nutrient requirements, and digestive constraints

Studies of fatty acid nutrition in wild birds have focused mainly on the fatty acid composition of birds themselves (typically just their fat depots (e.g., Landau 1970)) especially during migration (reviewed by Blem 1976, 1980, 1990). The focus on fat depots during migration is justified because lipids provide a relatively light-weight, energy-rich source of fuel. As in most migratory birds, the fat depots of warblers are comprised mainly of 16:0, 18:1, and 18:2 fatty acids with 18:0 fatty acids comprising usually < 5% of fatty acids (Blem 1976, 1990). Blem (1980, 1990) found few consistent patterns in fatty acid composition of birds between migratory and non-migratory periods and concluded that the composition of fat depots was primarily caused by diet and not migratory state. If other migratory passerines are like yellow-rumped warblers and show a strong preference for long-chain unsaturated fatty acids (18:1, 18:2) over long-chain saturated fatty acids (18:0), then it is not surprising that the occurrence of 18:0 fatty acid in fat depots is so uniformly low.

The dietary preferences we observed for specific fatty acids are also consistent with the hypothesis that digestive constraints in part determine dietary preferences. In energy-demanding conditions like in the cold or during migration, warblers may eat proportionately less food containing certain saturated fats so that gross intake of saturated fats stays below possibly pathological levels. Just as the inability to digest sucrose influences sugar preferences in some passerine birds (Martinez del Rio et al. 1988, 1992), our results along with those from studies of poultry (reviewed by Scott et al. 1982) and other birds (reviewed by Place 1996) suggest that an inability to efficiently assimilate long-chain saturated fatty acids like stearic acid influences fatty acid preferences in birds. An important unresolved question is whether the warbler's preference for diets with mostly long-chain unsaturated, unesterified fatty acids is similar if the dietary fatty acids are in their common triglyceride form.

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