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SEASONAL CHANGES IN FATTY ACID COMPOSITION OF THE WOOD THRUSH¹

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Lipid storage is important for avian reproduction (Drobney 1980, Krapu 1981, Walsberg 1983), migration (Blem 1980, Biebach et al. 1986), and survival (Lima 1986, Blem 1990; but see Kremenetz et al. 1989). In addition to total lipid content, lipid composition is important because the melting points of fatty acids differ, thereby influencing ease of mobilization, use at low temperatures, and net energy produced (Blem 1990). Indeed, lipid composition is essential to an accurate evaluation of avian bioenergetics (Johnston 1970). Lipid composition is particularly important for long-distance migratory birds because small migrants increase reliance on fatty acids during migration (Marsh 1981) and individuals that store fats that have higher energy and are more easily mobilized will be able to travel farther between stopovers during their long migration (Johnston 1970, Yom-Tov and Tietz 1978).

Food sources high in unsaturated, high-energy fats may be important to birds preparing for autumn migration. After the onset of migration, individuals with larger lipid stores and storing lipids high in easily mobilized fats should be better able to survive unpredictable weather and food availability encountered during migration. Clearly, we need to examine the types of lipids important for migrating birds and identify the food items which supply migratory birds with essential fatty acids.

Lipid composition and the factors affecting it have been evaluated infrequently in birds. Examination of seasonal changes in lipid composition and identifica-

tion of important food sources high in essential fatty acids is an important component for improving our understanding of the ecology and evolution of migration in birds. Consequently, we examined lipid composition of breeding and autumn-migrating Wood Thrush. We also examined lipid composition of spicebush (*Lindera benzoin*) fruits and seeds because they are commonly eaten by Wood Thrush preparing for autumn migration.

MATERIALS AND METHODS

We collected 21 Wood Thrush in Washington County, Rhode Island from 16 June to 14 September 1992. Birds were captured in mist-nets, then sacrificed using thoracic compression (AOU 1988). We examined skull pneumatization and plumage to determine age class (Pyle et al. 1987) and carcasses were immediately frozen.

Partially thawed carcasses were plucked and the contents of the crop, esophagus, gizzard, and intestines were removed. Gonads were examined to determine sex of birds and carcasses were weighed to the nearest 0.1 g and freeze-dried for 24 hr to constant mass. Dried samples were homogenized using a Waring blender.

We collected >50 ripe berries from 14 different spicebush plants to quantify lipid content and composition of berries. Spicebush berries are a common food item of Wood Thrush during the autumn (Martin et al. 1951) and are commonly eaten by Wood Thrush during autumn months in Rhode Island (C. Conway, pers. observ.). Spicebush seeds and fruits were separated and frozen separately. Samples were weighed to the nearest 0.1 g, freeze-dried for 24 hr, and homogenized using a Waring blender.

We quantified the fatty-acid composition in Wood Thrushes by extracting fatty acids using a Soxhlet extraction apparatus with chloroform as a solvent, followed by methylation (Kates 1986). We also quantified fatty-acid composition of the seeds and fruits of spicebush berries. Lipids were extracted from 2.0 g aliquot samples in duplicate and reflux time was 12-16 hr.

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TABLE 1. Fatty acid methyl ester composition (%) of breeding ($n = 7$) and autumn migrating ($n = 14$) Wood Thrush from Washington County, Rhode Island, June–September 1992.

Fatty acid methyl ester	Breeding season ^a		Autumn migration ^b		F^c	P
	\bar{x}	SD	\bar{x}	SD		
16:0 ^d	24.0	0.9	15.2	2.0	57.4	0.0001
16:1	4.7	1.1	2.4	1.4	6.1	0.0281
18:0	13.8	2.3	7.6	2.4	12.5	0.0036
18:1	34.4	5.0	61.6	8.2	38.1	0.0001
18:2	12.0	1.7	7.6	0.8	44.9	0.0001
18:3	3.9	0.9	1.3	0.8	10.5	0.0065
20:1	0.3	0.7	0.0	0.0	0.2	0.6423
20:4	3.9	1.6	2.0	1.1	5.4	0.0368
22:5	2.1	1.5	1.8	1.4	0.3	0.5978
22:6	0.9	1.0	0.6	0.8	0.0	0.9660
Ratio of unsaturated : saturated fats	1.65	0.16	3.53	0.91	12.6	0.0035

^a Birds collected between 16 June and 6 August 1992.

^b Birds collected 1–16 September 1992.

^c Main-effects analysis of variance (SAS Institute 1985).

^d Number of carbon atoms : number of double bonds.

Percentage of each fatty acid was determined using the protocol of the National Marine Fisheries Service (National Oceanic and Atmospheric Administration 1988). Percentage lipid content of spicebush was calculated as extracted lipid mass/total wet mass for both seed and fruit samples.

We tested all variables for normality by examining Shapiro-Wilk's W -statistics and normal probability plots (SAS Institute 1985). Distributions of most variables were normal, or nearly so, and unimodal.

We used three-factor main-effects analysis of variance (SAS Institute 1985) to compare fatty acid composition between seasons, sexes, and age classes. Seven birds collected between 16 June and 6 August were considered breeding birds and 14 individuals collected 1–14 September were considered to be autumn migrants preparing for migration.

RESULTS

Carbon 18:1 was the most abundant fatty acid in all Wood Thrush sampled and made up 23–73% of the lipid extracted from each individual (Table 1). Per-

TABLE 2. Fatty acid methyl ester composition (%) of duplicate spicebush seed and fruit samples from Washington County, Rhode Island, June–September 1992.

Fatty acid methyl ester	Seeds		Fruits	
	\bar{x}	SD	\bar{x}	SD
10:0 ^a	45.47	1.35	0.00	0.00
12:0	47.46	0.40	0.89	0.01
14:0	1.83	0.08	1.00	0.02
16:0	0.72	0.01	21.49	0.65
18:1	2.68	0.04	63.88	0.12
18:2	1.83	0.71	11.86	0.53
18:3	0.00	0.00	0.87	0.08
Percentage lipid content ^b	54.54	0.58	58.62	0.53

^a Number of carbon atoms : number of double bonds.

^b Extracted lipid mass/total wet mass.

centages of carbon 18:1 were higher ($P < 0.05$) and carbon 16:0, 18:0, 18:2, and 18:3 were lower ($P < 0.05$) in autumn-migrating birds compared to breeding season birds (Table 1). The ratio of unsaturated : saturated fats was higher ($P = 0.0035$) in autumn-migrating birds compared to breeding birds (Table 1). We failed to find differences ($P > 0.05$) in percentages of all fatty acids and the ratio of unsaturated : saturated fats between sexes or age classes. Percentage of carbon 18:1 was high in spicebush fruits and 10:0 and 12:0 were high in seeds (Table 2).

DISCUSSION

Few studies have identified fatty acid composition of wild birds (Blem 1990, but see Blem 1976). Carbon 18:1 was high in our birds; higher than percentages previously reported for any avian species (Blem 1976, Zar 1977, West and Peyton 1980). Carbon chains of 16 and 18 carbon atoms are the most common fatty acids used in lipid stores in birds (Blem 1990).

The percentage of carbon 18:1 was higher and four other fatty acids was lower in autumn-migrating birds compared to breeding birds. Fatty acid composition can differ seasonally and under different environmental conditions (West and Meng 1968, Barnett 1970, Blem 1973, Yom-Tov and Tietz 1978, Heitmeyer 1985), and birds commonly increase carbon 18:1 over winter (Bower and Helms 1968, Barnett 1970, Blem 1990). Energy content of fatty acids increases with chain length and declines with unsaturation, and 18-chain fatty acids provide relatively great energy content per unit mass (Blem 1990). The composition of dietary fats is one factor that affects the fatty acid composition of depot fats (Bower and Helms 1968; Blem 1976, 1990; Yom-Tov and Tietz 1978; West and Peyton 1980; but see Robel and Klopfenstein 1985). Postbreeding Wood Thrushes increase fat reserves (Johnson et al. 1990) and change their diet (Martin et al. 1951), possibly increasing the amount of high-fat foods, prior to migration. Carbon 18:1 is a relatively high-energy fat with a low melting point (Blem 1990) and common in spicebush (Table 2).

Wood Thrushes switch to a diet dominated by plants in autumn, when spicebush berries become a common item in their diet (Martin et al. 1951, C. Conway, pers. observ.), presumably to store fat in preparation for migration. Indeed, migratory birds, which need to store large amounts of fat, store more carbon 18:1 fatty acid compared to non-migrants (Blem 1976), and we found many spicebush berries and berry skins in the crops and feces of our autumn-migrating birds. Accumulation of easily mobilized, long-chain, low melting point, unsaturated fatty acids may be adaptive for Wood Thrushes prior to a long distance migration where availability and distribution of food resources are unpredictable. The mean ratio of unsaturated : saturated fatty acids in our autumn migrants was extremely high (3.53); ratios of unsaturated : saturated fatty acids greater than 3.0 are rare (Walker 1964, Blem 1976). Additional information on the energy content of depot fat and food among migratory birds may help identify essential food sources for successful migration (Walker 1964). We propose that abundance of local food sources high in carbon 18:1 fatty acid may affect regional distribution and migratory survival of Wood Thrush populations and deserves further study. Future studies should examine the lipid composition of other foods available to birds preparing for migration. More detailed analyses of the lipid composition and energy content of foods available during autumn will facilitate our understanding of the bioenergetics of migration and the factors affecting migratory survival. This information should also help facilitate effective management and conservation of Neotropical migratory birds.

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INTERSPECIFIC BROOD PARASITISM OF MONTEZUMA OROPENDOLAS BY GIANT COWBIRDS: PARASITISM OR MUTUALISM?¹

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Key words: *Montezuma Oropendola*; *Psarocolius*; *Giant Cowbird*; *Scaphidura*; *brood parasitism*; *mutualism*; *colonial nesting*.

Obligate interspecific brood parasitism has evolved independently in several avian families (Hamilton and Orians 1965, Payne 1977). Such parasitism generally has a marked negative effect on host fitness (e.g., Post and Wiley 1976, Davies and Brooke 1988, Power et al. 1989, Scott et al. 1992), and the brood parasite and host are usually viewed as being engaged in a coevolutionary "arms race" (Davies and Brooke 1988, Rothstein 1990, Braa et al. 1992). However, Smith (1968, 1979) described a remarkable and complex interdependence between the parasitic Giant Cowbird (*Scaphidura oryzivora*) and two of its hosts in Panama, the Chestnut-headed Oropendola (*Psarocolius wagleri*) and Yellow-rumped Cacique (*Cacicus cela*). In this system, the hosts could apparently benefit from cowbird "parasitism" in some situations.

Smith found that ectoparasitic botflies (*Philornis* spp.) were a major source of mortality for oropendola and cacique nestlings. Cowbird nestlings removed botfly larvae from their nestmates, such that nests with cowbirds fledged more host young than nests without cowbirds. Indeed, in colonies without any other defense against botfly parasitism (i.e., colonies without hymenoptera nests), oropendolas and caciques allowed cowbirds to enter their nests and did not remove the eggs of cowbirds that were discovered (Smith 1968,

1979). This result contrasts sharply with studies of many other brood parasite-host relationships, where hosts actively defend their nests against brood parasites (e.g., Davies and Brooke 1988, Rothstein 1990), and parasites have evolved many behavioral and developmental tactics to circumvent the defenses of their hosts (e.g., Davies and Brooke 1988, Briskie and Sealy 1990, Braa et al. 1992, Scott et al. 1992).

To determine the factors that allow the interdependence described by Smith (1968, 1979) to arise, it is first necessary to determine the distribution of the phenomenon. Giant Cowbirds parasitize several species of oropendolas and caciques (Orians 1985), many of which have a nesting biology similar to that of the hosts studied by Smith (see Chapman 1929, Skutch 1954, Schäfer 1957, Tashian 1957, Drury 1962, Fraga 1989, Webster 1994). If several of these host populations benefit from and allow cowbirds to lay eggs in their nest, then ecological factors common among them must favor the evolution of this interdependence. Alternatively, giant cowbirds may be parasites to most hosts, such that some feature of the populations Smith studied makes the complex mutualism unique to Panama. These possibilities can be distinguished by determining whether other hosts allow Giant Cowbirds to enter their colonies, or whether they actively defend themselves against cowbird parasitism. Only one published study has directly attempted to answer this question (Robinson 1988).

In this note, I examine the possibility that a similar mutualism exists between Giant Cowbirds and one of their primary hosts in Costa Rica, the Montezuma Oropendola (*Psarocolius montezuma*). To do so, I determined whether Montezuma Oropendolas actively defend themselves against Giant Cowbirds and, if so, whether cowbirds show behaviors that might circumvent this defense. Because it was difficult to examine

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