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LIVING OFF THE WAX OF THE LAND: BAYBERRIES AND YELLOW-RUMPED WARBLERS

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ABSTRACT.—Yellow-rumped Warblers (*Dendroica coronata*) and Tree Swallows (*Tachycineta bicolor*) are among a small group of birds in temperate North America that regularly eat waxy fruits. During the autumn, winter, and spring, these species feed extensively on fruits of the bayberry (*Myrica* spp.). Covering the pulp of these fruits is a solid, waxy material consisting primarily of saturated long-chain fatty acids. For most animals, saturated fatty acids are poorly assimilated (<50%). Using ^{3}H-glycerol triether as a nonabsorbable fat marker, we determined that Yellow-rumped Warblers are capable of high assimilation efficiences (>80%) of bayberry wax when fed berries recoated with radioactive wax tracers. Efficient fatty-acid assimilation extends to berries coated with cetyl palmitate, a common marine, saturated wax ester (>90%). The fatty-alcohol moiety of the marine wax was assimilated with a much lower efficiency (<50%). A beeswax coating of the berries is assimilated with an efficiency of approximately 50%. Similar assimilation efficiencies of each wax are recorded for Tree Swallows feeding on recoated bayberries. Yellow Warblers (*D. petechia*) rejected recoated bayberries and exhibited little (<5%) lipid assimilation of radiolabeled lipids. Yellow-rumped Warblers possess several gastrointestinal traits that permit efficient saturated-fat assimilation. Among these are an apparent retrograde reflux of intestinal contents to the gizzard, elevated gall-bladder and intestinal bile-salt concentration, and a slow gastrointestinal transit of dietary lipids. These gastrointestinal traits permit efficient assimilation of saturated fatty acids on bayberry fruits and may allow these small passerines to maintain more northerly wintering ranges than closely related species. *Received 24 May 1991, accepted 5 November 1991.*

THE ASSOCIATION between Yellow-rumped Warblers (*Dendroica coronata*) and *Myrica* (bayberry and wax myrtle) is one of the most widely recognized bird-plant associations in North America (Brewer 1840, Hausman 1927, Martin et al. 1951). In fact, until 1983 one form of the Yellow-rumped Warbler was referred to as the Myrtle Warbler (AOU 1983). A similar bird-fruit relationship is found between Tree Swallows (*Tachycineta bicolor*) and *Myrica* (Hausman 1927). During the breeding season Yellow-rumped Warblers and Tree Swallows feed primarily on insects, but during the autumn, winter, and spring their diets include large proportions of fruit, especially bayberry (*Myrica pennsylvanica* Loisel.), wax-myrtle (*M. cerifera* L.) and *M. pussilla* Raf.

In eastern North America, the Yellow-rumped Warbler winters from central Maine and southern Nova Scotia, west to Kansas and Missouri, and south to Panama, which coincides with the entire range of the above *Myrica* species. The Yellow-rumped Warbler is the most northerly wintering wood warbler, and it is very commonly observed over much of its wintering range. The Tree Swallow winters along the coast, occasionally as far north as Massachusetts and south into Central America. In autumn, large flocks (some over 50,000; Stewart and Robbins 1958), move south along the coast and may strip *Myrica* shrubs of all fruits in a matter of minutes (E. Stiles, pers. observ.).

Generally, bayberry is found on dunes, old-fields, and dry hills from Quebec to Louisiana; wax-myrtle typically is found on damp, sandy soils from New Jersey to Florida and Texas (Gleason and Cronquist 1963). Fruits ripen in August through October and persist well into the winter, providing an energy-rich resource for birds residing or wintering in northern and coastal regions of the United States.

Bayberry pulp includes a waxy coating of mono- and diglycerides of myristic, palmitic and stearic fatty acids. Most animals exhibit low assimilation (<50%) of these high-melting-point lipids. For example, with chickens, absorption of these fatty acids decreases monotonically with increasing melting point (Renner and Hill 1961;

Fig. 1). Similar results have been documented in rats feeding on high-melting-point triglycerides (Clifford et al. 1986).

It may be that Yellow-rumped Warblers and Tree Swallows are able to successfully occupy northern regions in winter because they can assimilate efficiently the high-melting-point fatty acids in bayberry wax that few fruit-eating animals can digest. To investigate the capacity of Yellow-rumped Warblers and Tree Swallows to assimilate waxy coatings on bayberries, we removed the natural wax from bayberries and recoated them with radioactively labeled lipids. We included bayberry wax in our coatings, as well as two other naturally-occurring solid waxes known to be eaten by birds—cetyl palmitate and myrcin—the alcohol-insoluble fraction of beeswax. Wax esters, like cetyl palmitate, are major food sources for high-latitude marine animals, especially pelagic seabirds (Roby et al. 1986, Place and Roby 1986, Jackson and Place 1990), and myrcin is consumed and digested by Black-throated Honeyguides (*Indicator indicator*; Diamond and Place 1988). We also measured the rate of bayberry-fruit consumption of captive Yellow-rumped Warblers with fruits available *ad libitum* to assess whether fruit handling might limit ingestion rates. Finally, we characterized in Yellow-rumped Warblers the biliary and pancreatic components known to be essential for efficient lipid assimilation in other species (Carey et al. 1983).

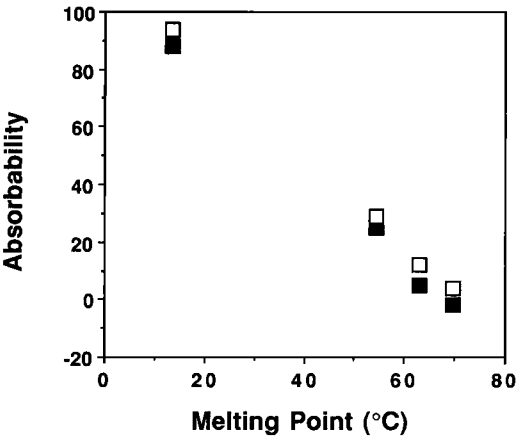

Fig. 1. Absorbability of fatty acids vs. melting points in domestic hens (solid squares) and chicks (open squares; Renner and Hill 1961). Melting points of saturated fatty acids increase with chain length and decrease with degree of unsaturation. Feeding studies performed with unesterified fatty acids. Saturated fatty acids used were myristic, palmitic and stearic acid. Unsaturated homolog of stearic acid (i.e. oleic acid) was assimilated at greater than 85% efficiency.

Materials and Methods

Study species.—Yellow-rumped Warblers and Yellow Warblers (*Dendroica petechia*) were captured with mist nets on 10 March and 7 November 1986 at the Rutgers Ecological Preserve in Piscataway, New Jersey. The Yellow-rumped Warblers had been eating bayberry at the time of capture. Captured birds were held at room temperature in darkened holding cages until initiation of experiments on the same day or the following morning. During the two- to three-day captivity, birds were given water and food regularly (strained peaches and pears baby food mixed with hard-boiled egg). The Tree Swallows used in our study were part of an experimental colony at the Monell Institute.

Bayberry wax removal and recoating.—Bayberries were de-waxed by placing them in a 2:1 mixture of hexane and chloroform at room temperature for 15 min. The berries then were removed and air dried for 24 h. The bayberry wax (24.3% of fruit mass or 54.1% of pulp mass) was recovered by removing the solvent under nitrogen. For fatty-acid methyl ester quantification, an aliquot of extracted wax was hydrolyzed with methanolic HCL, the methyl esters extracted into hexane, and an aliquot of the hexane extract subjected to gas chromatography directly on a Hewlett-Packard model 5890A instrument fitted with a DB-% column (30 × 0.25 mm i.d., 0.25-μm-thick film, J. & W. Scientific Inc., Rancho Cordova, California) and a flame ionization detector at 280°C. The oven temperature was programmed from 50 to 255°C at a heating rate of 18°C min^{-1} up to 125°C (thereafter 4°C min^{-1}). Helium was used as carrier gas with a flow rate of 3.6 ml min^{-1}.

De-waxed bayberries were recoated with radioactively-labeled waxes by placing them in a melt of one of the following materials: (1) bayberry wax containing 9.1 μCi of ^{3}H-GTE/berry and 6.99 μCi of [1-^{14}C] palmitic acid/berry; (2) cetyl palmitate containing 7.33 μCi of ^{3}H-GTE/berry and 5.5 μCi of [1-^{14}C] cetyl palmitate/berry or 4.7 μCi of cetyl [1-^{14}C] palmitate/berry; (3) myrcin (alcohol-insoluble fraction of beeswax) containing 9.1 μCi of ^{3}H-GTE/berry and 8.2 μCi of triacontanol [1-^{14}C] palmitate/berry. Each berry was recoated with 6 to 10 mg of lipid.

Bayberry fruit structure was examined with and without the wax coating with an Hitachi S-450A scanning electron microscope using an accelerating voltage of 10 KV.

Feeding studies.—Twelve Yellow-rumped Warblers were included in the feeding trials with recoated radioactively-labeled bayberries. Five were spring-captured birds (three males and two females), and seven

were fall-captured birds (four males and three females). Sets of three birds were fed each type of recoated bayberry. Only two Tree Swallows were tested (each three times). We also attempted feeding trials with six Yellow Warblers. Two to three recoated bayberries were force fed to each bird. All birds took the feeding without regurgitation except for Yellow Warblers.

After ingestion, each bird was placed on a polyethylene-mesh (¼") platform suspended in an air-tight 7.6-L (2-gallon) Bain Marie polyethylene container (Cole-Palmer). We pumped CO_2-free air through the containers with aquarium pumps attached to soda-lime (indicator grade) scrubbers. The flow rate of air through the containers was adjusted to 1 L min^{-1}. Containers were kept in the dark and maintained at 21 ± 3°C. Respired carbon dioxide was collected by passing the air effluent from each container through NCS (Amersham Corp.) solubilizer (CO_2-trapping efficiency was 88%; Place and Roby 1986). Respired CO_2 was collected in 15-min intervals for up to 4 h post-ingestion. It is especially important with lipid-absorption studies that some measure of metabolism be taken. Lipids can be stored and not utilized. After 3 to 4 h, Yellow-rumped Warblers were killed with an overdose of sodium pentobarbital, or were killed by CO_2 asphyxiation. Accumulated excreta in each container were extracted for lipids by the Bligh and Dyer (1959) technique. We used a nonabsorbable lipid marker, glycerol triether [^{3}H-GTE] to estimate absorption efficiency and transit rate (Morgan and Hofmann 1970, Carlson and Bayley 1972a). An important advantage of this method is that endogenous fecal fat is not measured (Carlson and Bayley 1972b). The percent [^{14}C]-lipid absorbed (L_a) was calculated as:

$$L_a = 100[1 - (t/f)], \quad (1)$$

where t is the ^{3}H/^{14}C in the test meal and f is the ^{3}H/^{14}C in the fecal collection.

To assess the distribution of lipid marker and labeled wax, each bird was dissected into liver, heart, pectoral muscle, gizzard, 1-cm-length intestinal segments, pancreas, gall bladder, and remaining carcass. The contents of each gastrointestinal segment were extruded, and all fractions were stored frozen at −70°C until analyzed. Each body part and the intestinal contents were extracted for lipids by the Bligh and Dyer (1959) technique.

The distribution of label among lipid classes was determined by TLC of the lipid extracts. Aliquots containing equivalent counts were spotted on the pre-absorbent area of channeled silica G plates (Uniplates, Analtech). After development with hexane : diethyl ether : acetic acid (80:20:1), the plate was scanned with a BioScan 100 radiometric scanner. This solvent system resolves wax esters, triacylglycerols, fatty acids, fatty alcohols, 1,3-diacylglycerols, 1,2-diacylglycerols, monoacylglycerols, and complex lipids, in order of decreasing relative mobility (R_f). The carrier gas used in the radiometric scanning was P-10 (90% argon, 10% methane) at a flow rate 0.5 to 1.0 L min^{-1}. The spatial resolution for each scan was set at 4 mm. The distribution of label among the lipid classes was estimated by integration of the counts under each peak after subtraction for background. The overall counting efficiency for ^{14}C averaged 10.5%, while that for ^{3}H averaged 0.5% across the plate. Labeled cetyl oleate, cholesterol oleate, triolein, oleic acid, and cetyl alcohol were used as standards to determine the R_f of these major lipid classes.

Biliary and pancreatic components.—Bile was removed from the gall bladder with a sterile 1-cc tuberculin syringe and placed in a sterile 0.5-ml polyethylene centrifuge tube. Total biliary protein was determined on aliquots using the dye-binding assay of Bradford (1976). Total bile salts were assayed with 3 α-hydroxysteroid dehydrogenase (EC 1.1.150; Coleman et al. 1979). Whole-bile aliquots were analyzed by HPLC on Waters Nova 5 μ Radial packs using a linear gradient (1.2 to 34.0 min, flow rate 2.8 ml min^{-1}) from initial conditions (3.21 mM phosphoric acid, 3.75 mM KOH, and 4.00 mM KH_2PO_4, pH 4.32, 68:32 [v/v] methanol : water) to a final condition (3.21 mM phosphoric acid, 3.75 mM KOH, and 11.00 mM KH_2PO_4, pH 4.32, 68:32 [v/v] methanol : water). Bile salts were detected and quantitated by their absorbance at 204 nm in comparison with standards.

To assay biliary lipids, an aliquot of the bile was spotted on pre-extracted (three times with chloroform : methanol 1:1) and preweighed 3-MM chromatography filter paper. After drying at room temperature for 4 h, the paper was extracted with 5 ml of chloroform : methanol (1:1, v/v). Aliquots of the extract were taken, dried, redissolved in chloroform : methanol (1:1, v/v), and assayed for biliary phospholipid phosphorous (Petitou et al. 1978). Additional samples were spotted on chromarods and developed chloroform : methanol : acetic acid : water (75:25:3:1). Determination of neutral-lipid, phospholipid, and bile-salt mass was by comparison with a standard curve generated for concentrations of cholesterol, oleic acid, triolein, phosphatidyl choline, and taurochenodeoxycholate between 1 and 20 μg. Operating conditions for the Iatroscan TH-10 analyzer (Iatron Laboratories, Tokyo, Japan) were the same as those described by Rigler et al. (1983). Samples were spotted on type S-II chromarods (RSS Incorporated, Costa Mesa, California), which were activated by scanning them twice through a hydrogen flame. Integration was performed by a Hewlett-Packard 3390-A integrator (Avondale, Pennsylvania). Chromarods were developed in equilibrated filter paper-lined glass tanks containing 75 ml of solvent. When multiple systems were used, chromarods were dried according to the method of Harvey and Patton (1981).

Titrametric assays of lipolytic activity were performed using a gum arabic stabilized emulsion of 0.2 M cetyl oleate and 0.1 M triolein. Temperature was maintained at 25°C, and pH maintained at 9.00 using

a pH-stat (TTT80 Radiometer). Purified chicken colipase was added in a five-fold excess and sodium cholate (8 mM) was added to the lipid emulsions.

Materials.—Cholic acid, deoxycholic acid, chenodeoxycholic acid, sodium taurocholate, sodium taurodeoxycholate, sodium taurochenodeoxycholate, cholesterol, tripalmitin, palmitic acid, egg phosphatidylcholine, triglyceride (procedure No. 388), cholesterol (procedure No. 351), and glucose (procedure No. 510) assay kits were purchased from Sigma Chemical (St. Louis, Missouri). Cetyl alcohol and 1-triacontanol were purchased from Aldrich Chemical (Milwaukee, Wisconsin). The A-grade sodium salts of glycochenodeoxycholate, taurodeoxycholate, taurochenodeoxycholate, and taurocholate were purchased from Calbiochem (La Jolla, California). All other chemicals were reagent grade unless specified otherwise. All solvents were either pesticide or HPLC grade. Whatman 3-MM chromatographic filter paper was obtained from VWR Scientific (Philadelphia, Pennsylvania).

We found [1-^{14}C] palmitic acid (5.7 mCi/mmol) from New England Nuclear (Boston, Massachusetts) and tri[1-^{14}C] palmitate (60 mCi/mmol), and [1-^{14}C] cetyl alcohol (24 mCi/mmol) from Amersham (Arlington Heights, Illinois) to have radiopurities greater than 98% by thin-layer chromatography.

Fluors were OCS (Amersham, Arlington Heights, Illinois) and Biosafe II (Research Products International, Mount Prospect, Illinois). All samples were counted on a Beckman LS 3801 scintillation counter with quench corrections for different extracts and tissue types.

Labeled wax esters ([1-^{14}C] cetyl palmitate, cetyl [1-^{14}C] palmitate, and triacontanol [1-^{14}C] palmitate), as well as carrier cetyl and triacontanol palmitate, were synthesized and purified as described by Place and Roby (1986). The cetyl wax esters were dissolved in 250 μl toluene and stored under nitrogen at −20°C. The triacontanol palmitate was stored dry at −20°C. From radiometric scanning, the radiopurity (2.2 mCi/mmol) of each wax ester was 98.7%, with an overall yield of 45 to 75%. Based on TLC/FID using hexane : diethyl ether : formic acid (85:15:0.1), the chemical purity of each wax ester was greater than 98%. The 1-(9 *cis*-Octadecenyl) 2,3-didodecyl glycerol triether was synthesized as described in Morgan and Hofmann (1970). The tritiated triether (^{3}H-GTE) was prepared by reduction with platinum as a catalyst (New England Nuclear, Boston, Massachusetts). Purified ^{3}H-GTE (>98% radiopurity) was obtained by chromatography on a silicic-acid column eluted with hexane/diethyl ether 85:15 (v/v; Roby et al. 1989). The solvent was removed with nitrogen evaporation and the purified triether dissolved in absolute alcohol to a specific activity of 1mCi/ml.

Statistical analysis.—Results are expressed as $\bar{x} \pm$ SE, with n being the number of birds. Comparisons that involve percentages were performed on arcsin-transformed data. We used paired t-tests or Mann-Whitney U-tests for all simple comparisons. All comparisons within each ANOVA were *a priori*. When more than two contrasts were made, probability levels were adjusted by Duncan's new multiple-range test (Steel and Torrie 1960). Differences were considered significant when $P \leq 0.05$.

Results

Bayberry fruit characterization.—The mean diameter of *M. pennsylvanica* fruits used in our study was 3.2 ± 0.05 mm (n = 40). Each bayberry averaged 20 ± 0.8 mg (n = 40) and contained 4.5 ± 0.2 mg of wax (n = 40). The wax coats the outside layer of the fruit (exocarp) and can be removed by organic solvents without disrupting the fruit structure (Fig. 2). The base of each bracteole is loosely attached to the seed and is easily removed by rubbing the fruit.

The waxy coat on a bayberry has an energy density of 39.3 KJ/g as determined by microbomb calorimetry. The wax from the bayberry consisted of mixed mono- and diglycerides of three saturated fatty acids—myristic (14%), palmitic (85%), and stearic (1%) acids—and had a melting point of 42–48°C. The melting points of the other synthetic waxes used in recoating the bayberries were 51.4°C for cetyl palmitate and 62 to 65°C for beeswax.

Feeding trials.—The average mass of the Yellow-rumped Warblers used in our study was 10.9 ± 0.2 g (n = 12), the mean hematocrit was 53.3 ± 3.7 (n = 7), and the average body lipid was 11.2 ± 1.2% of wet weight (n = 6). No bird died during the feeding trials. After 3 to 4 h, each bird had defecated 1.4 ± 0.5 (n = 12) seeds of the 2.4 ± 0.5 (n = 12) bayberries fed. Yellow-rumped Warblers separate the seed and bracteoles (exocarp) in the gizzard when fed bayberries. Partially-denuded bayberries were found in the gizzard. The seed appears to precede the bracteoles during gastrointestinal transit in that bracteoles were frequently found orad to the seed. The bracteoles and seed accumulate in the rectum and are defecated together with urates. Although neither Yellow-rumped Warblers nor Tree Swallows regurgitated forced-fed fruits, all Yellow Warblers regurgitated the fruits immediately upon being placed in the metabolism chambers. We found no statistically significant (<5%) lipid absorption or respired radioactive CO_2 of any wax with Yellow Warblers.

In a separate feeding trial, three Yellow-rumped Warblers were kept in captivity and

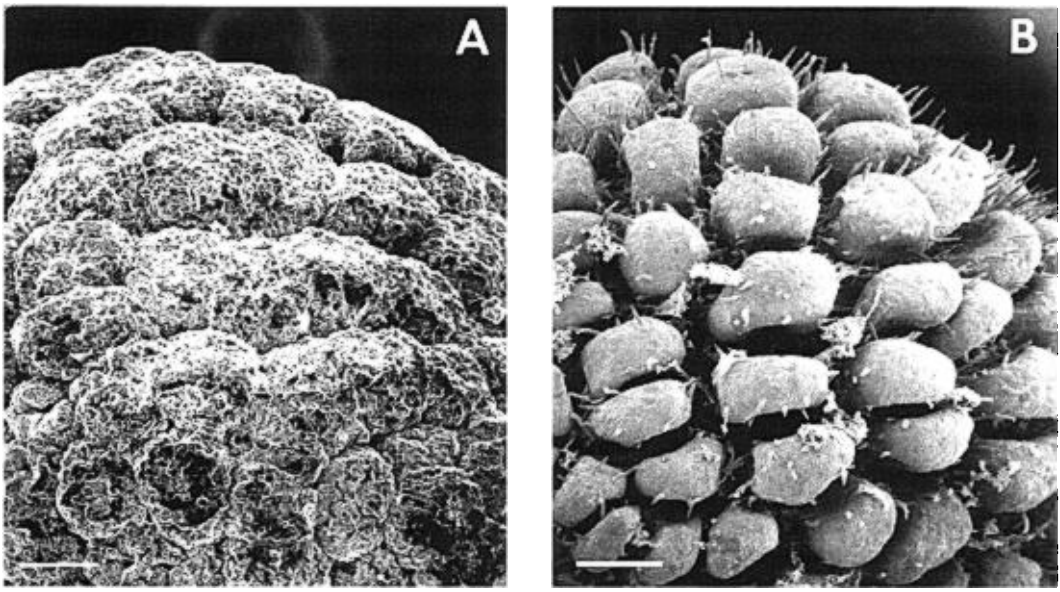

Fig. 2. Scanning-electron micrographs of fruits from bayberries (*Myrica pennsylvanica*) (A) with and (B) without the waxy coat. Fruit of bayberry is a small drupe enveloped by persisting outgrowths of the exocarp (bracteoles) covered with a whitish waxy coating (Lawrence 1951). White bar represents 0.34 mm.

given bayberry fruits with water *ad libitum* to assess the quantity of bayberries they could ingest daily. On average, each bird ate 163 ± 24 bayberries per day. However, each bird lost 1.58 ± 0.28 g of body weight per day during the bayberry feeding trials.

Tracer and marker recovery and distribution.— Within 15 min of ingestion, radiolabeled CO_2 was collected when Yellow-rumped Warblers were fed recoated bayberries (Fig. 3). The highest rates and amount of respired label (40–60% of ingested tracer) as well as the highest assimilation efficiencies ($F = 10.44$, df = 3 and 11, $P = 0.004$) were observed with [1-^{14}C] palmitate in bayberry wax (the natural food) and cetyl [1-^{14}C] palmitate in cetyl palmitate (a marine wax ester). Lower rates of lipid metabolism and assimilation efficiency were observed when birds were fed beeswax or cetyl palmitate labeled in the fatty-alcohol moiety (Fig. 3 and Table 1).

The rate of label respiration reflects the overall rates of assimilation (i.e. hydrolysis, luminal absorption, repacking, transport from the enterocytes and oxidation) for each wax. With bayberry wax and cetyl palmitate, only 15–17% of the radiocarbon (as compared to 33-35% of the nonabsorbable lipid marker, ^{3}H-GTE) was present in the intestinal lumen after 180 min (Fig. 4). The major portion (20–60%) of the nonmetabolized C-14 label was found in adipose tissue in the carcass as triglyceride (>80%), with the pectoral muscle the next highest in label accumulation (5–8%). Only 2 to 4% of the label was found in the liver.

The fatty-alcohol moiety of the marine wax ester was poorly assimilated and metabolized by Yellow-rumped Warblers, despite nearly (>95%) complete hydrolysis of the wax ester in the intestinal lumen. Palmitate, whether as a free fatty acid or as the fatty-acid moiety in a cetyl palmitate, was absorbed with an efficiency of greater than 88%. When esterified to the 30-carbon-long fatty alcohol, triacontanol, the efficiency was reduced to less than 60% and labeled palmitate appeared to reside in the intestinal lumen longer (Fig. 4). However, assimilation of the 16-carbon-length fatty alcohol, hexadecanol (cetyl alcohol), was less than 40%. Overall, we accounted for 96 ± 8.2% of the ingested C-14 tracer in our feeding trials.

No statistically significant differences in excreta ^{3}H-GTE recovery ($F = 1.19$, df = 3 and 11, $P = 0.372$) or in total ^{3}H-GTE recovery ($F = 0.623$, df = 3 and 11, $P = 0.62$) were observed among feeding trials. The overall recovery of the ^{3}H-GTE was 104 ± 6.3% ($n = 12$), and greater than 98% of the recovered tritium label co-chromatographed with pure glycerol triether. Because it

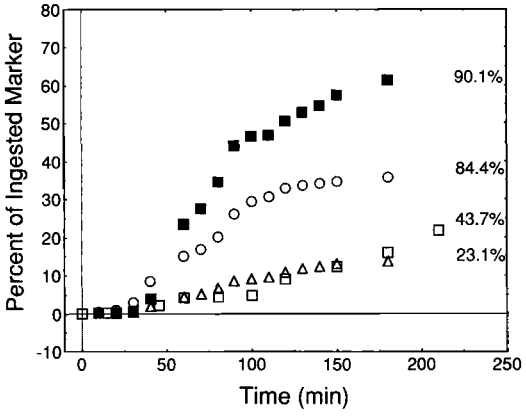

Fig. 3. Representative time courses of respired carbon-14 labeled CO_2 in four Yellow-rumped Warblers fed bayberries coated with four different radiolabeled waxes. Symbols represent percent of ingested label recovered at each time point for the following waxes: cetyl [1-^{14}C] palmitate (solid squares), [1-^{14}C] cetyl palmitate (open squares), [1-^{14}C] palmitate in bayberry wax (open circles), and triacontanol [1-^{14}C] palmitate in beeswax (open triangles). Assimilation efficiency of each bird for the wax coating presented to right of each curve.

was impossible to recoat each berry with an identical quantity of the ^{3}H-GTE marker, the percent recovery is based on the average ^{3}H-GTE found with 10 randomly selected recoated bayberries.

Although we did not set out to measure mean retention time directly in our feeding trials, an estimate can be made from the ^{3}H-GTE marker recovery (Table 1). Excreta in different birds were collected from 180 to 281 min postingestion. If we use each trial as a separate observation in describing the cumulative excretion curve and calculate the mean retention time as described by Warner (1981), we obtain an estimate of 232 min for the mean retention time of the ^{3}H-GTE marker. This estimate is based on force-fed single meals and may overestimate mean retention time in freely-feeding birds.

The assimilation efficiencies recorded for the two Tree Swallows (Table 2) when feeding on recoated bayberries parallels those obtained for Yellow-rumped Warblers. No statistical analysis was performed on these data because of the small sample size.

Bile of Yellow-rumped Warblers.—The bile-salt components in Yellow-rumped Warbler bile were predominantly taurine conjugates of the primary bile salts cholate and chenodeoxycholate (Table 3). Relatively large amounts of taurine and glycine conjugates of ursocholate also were found. Gall-bladder bile-salt concentration in individuals 4 h after feeding was 607 ± 16.2 mM, as determined by HPLC and 598 ± 75 mM, as determined by enzymatic analysis. The phospholipid content (~1.0 mM) was relatively low, while the neutral lipid content (~2 mM) was relatively high compared to mammalian bile (phospholipid 8.1 mM and a trace of neutral lipid in seven mammalian biles; Coleman et al. 1979).

Luminal bile-salt concentrations and distributions of intestinal markers and labels.—The elevated level of bile salts in the gall bladder was reflected in high levels of bile salts in the proximal half of the intestinal lumen (Fig. 5A). After segment 8, the luminal levels dropped below our detection limit. Levels of bile salts approaching 50 mM were found in the gizzard, nearly two segments orad to the biliary and pancreatic ducts. After 4 h postingestion, less than 2% of either label was found in each segment of the intestinal lumen (Fig. 5B). Less than 0.1% of the ^{3}H-GTE marker was recovered from each segment of the intestinal tissue (Fig. 5C), indicative of the marker's low absorption efficiency. The [1-

TABLE 1. Assimilation efficiencies and marker recoveries ($\bar{x}$ ± SD) of fed radiolabeled waxes to Yellow-rumped Warblers (n = 3). Matching letters that follow values represent significant differences ($P < 0.05$, multiple range test).

Carrier lipid	Label	Assimilation efficiency	Percent marker recovery in excreta	Total percent marker recovery
Bayberry wax	[1-^{14}C] palmitate	88.3 ± 3.1^a	63.2 ± 26.7	93.8 ± 9.1
Cetyl palmitate	Cetyl [1-^{14}C] palmitate	88.9 ± 2.5^b	44.8 ± 12.3	98.2 ± 9.1
Cetyl palmitate	[1-^{14}C] Cetyl palmitate	39.7 ± 16.6^{a,b}	47.3 ± 11.8	98.6 ± 9.1
Beeswax	Triacontanol [1-^{14}C] palmitate	56.3 ± 21.9^{a,b}	32.3 ± 27.5	116 ± 10.8

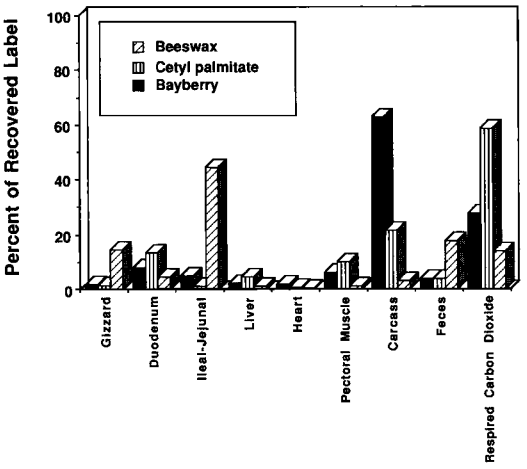

Fig. 4. Distribution of carbon-14 radioactive tracer in respired CO_2, excreta, and tissues. Data presented for three Yellow-rumped Warblers fed different recoated bayberries 180 min postingestion.

C^{14}] palmitate isolated from the intestinal tissue was largely incorporated in triglyceride (>80%), although substantial free fatty acid (>8%) was also recovered.

Similar results were obtained for birds fed cetyl [1-C^{14}] palmitate and triacontanol [1-C^{14}] palmitate. Although in the latter case considerably more unhydrolyzed wax ester could be extracted from the lumen. With birds fed [1-C^{14}] cetyl palmitate, significant levels of free [1-C^{14}] cetyl alcohol could be found in the intestinal lumen. In intestinal tissue, only labeled fatty acid and triglyceride were detected.

Lipolysis by Yellow-rumped Warblers.—Extracts of pancreatic tissue from Yellow-rumped Warblers were capable of hydrolysis of both triglyceride and wax ester emulsions *in vitro*. The specific activity of triglyceride lipolysis was 21 ± 0.3 μmoles min^{-1} mg^{-1} while that for wax ester lipolysis was 2.5 ± 0.5 μmoles min^{-1} mg^{-1}. Hence, under these *in vitro* assay conditions wax esters were hydrolyzed 8.3 ± 2.3 times slower than triglycerides.

TABLE 2. Assimilation efficiency ($\bar{x}$ ± SD) of radiolabeled waxes for two Tree Swallows.

Carrier lipid	Label	Assimilation efficiency
Bayberry wax	[1-^{14}C] palmitate	66.4 ± 0.6
Tripalmitin	Tri [1-^{14}C] palmitin	77.6 ± 0.8
Cetyl palmitate	Cetyl [1-^{14}C] palmitate	79.6 ± 0.8
Cetyl palmitate	[1-^{14}C] Cetyl palmitate	47.8 ± 0.8
Cetyl alcohol	[1-^{14}C] Cetyl alcohol	55.4 ± 1.0
Beeswax	Triacontanol [1-^{14}C] palmitate	18.8 ± 5.3

TABLE 3. Yellow-rumped Warbler gall-bladder bile composition ($\bar{x}$ ± SD, n = 6).

Constituent	Concentration (mM)
Tauroursocholate	20.3 ± 6.66
Taurocholate	181.5 ± 19.3
Taurochenodeoxycholate	341.8 ± 42.2
Taurolithocholate	5.1 ± 0.87
Glycoursocholate	58.5 ± 0.7
Phospholipid	1.18 ± 0.65
Cholesterol + triglyceride + fatty acid	2.6 ± 0.59

DISCUSSION

Frugivory of waxy fruits.—The association of Yellow-rumped Warblers with waxy fruits represents one of the most specialized fruit/frugivore relationships so far reported, similar to those of the Phainopepla (*Phainopepla nitens*) and mistletoe (*Phoradendron californicum*) in the southwestern United States (Walsberg 1975), Cedar Waxwings (*Bombycilla cedrorum*) and mistletoe (*P. serotinum*) in the southeastern United States (Skeate 1985), and Asian flowerpeckers and mistletoes (Docters van Leeuwen 1954). Waxy fruits have been identified as common food items in the diets of Northern Flickers (*Colaptes auratus*), Downy Woodpeckers (*Picoides pubescens*), and other woodpeckers, as well as Tree Swallows and Yellow-rumped Warblers (Martin et al. 1951), yet consumption of large numbers of these fruits by pen-raised Northern Bobwhites (*Colinus virginianus*) has been found to interfere with digestion and may even prove fatal (Martin et al. 1951).

The frugivorous diet of the Yellow-rumped Warblers is not restricted to *Myrica*. In the interior of the United States, where species of *Myrica* are less common, Yellow-rumped Warblers commonly eat poison-ivy fruits (*Toxicodendron radicans*; Ridgeway 1889, Graber and Graber 1979, Graber et al. 1983), another solid and waxy fruit. In fact, the waxy mesocarp of *Toxicodendron* consists primarily of glycerides of palmitic and oleic acids (Brizicky 1963), similar in composition to the waxy pulp of *Myrica* fruits.

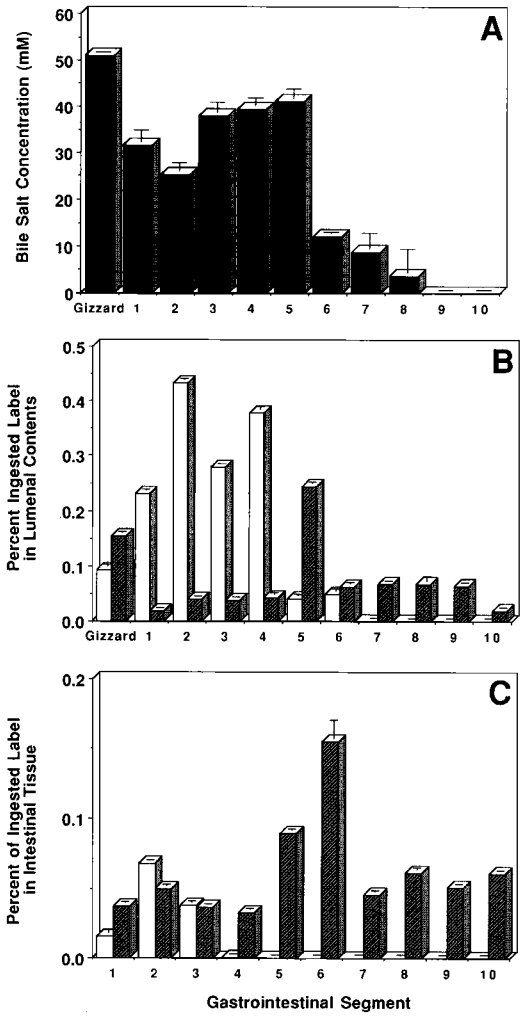

Fig. 5. (A) Concentration and localization of bile salts. ^{3}H-GTE (open bars) and [1-C^{14}] palmitic acid (hatched bars) in (B) luminal contents and (C) tissues in a Yellow-rumped Warbler's gastrointestinal tract 4 h after feeding a recoated bayberry. Each segment number represents 1 cm of intestine, progressing toward the cloaca. Average intestinal length in experimental birds was 10.9 ± 0.27 cm (n = 9). Intact bayberry seeds found in segments 3 and 5 for this individual. Means, with SE indicated.

Of the 21 members of the genus *Dendroica* that breed in the United States and Canada, only the Yellow-rumped, Pine (*D. pinus*), Chestnut-sided (*D. pennsylvanica*), and Bay-breasted (*D. castanea*) warblers have been identified as including fruit as a large part of their diets. Pine Warblers feed on many fruits including poison ivy, bayberry, dogwood, (*Cornus*), wild grape (*Vitis*), Virginia creeper (*Parthenocissus*), and sumac (*Rhus;* Bent 1953, Griscom and Sprunt 1957). This warbler species is second only to the Yellow-rumped Warbler in the northern extent of its wintering range (AOU 1983). The Bay-breasted Warbler rarely is frugivorous within the United States (Martin et al. 1951, Bent 1953), but consumes fruits from 21 plant species in Panama (Greenberg 1981). The Chestnut-sided Warbler eats some fruits on the wintering grounds in Central America (Howe and DeSteven 1979, Greenberg 1979, 1981). Greenberg (1981) found that a major fruit used selectively by Bay-breasted and Chestnut-sided warblers in Panama was from *Lindackeria laurina* (Flacourtiaceae), and he identified the aril as having "a distinctly waxy texture and odor." Skeate (1985) found that 91% of fruit removed from *Myrica cerifera* in hammock communities in central Florida was taken by Yellow-rumped Warblers and that poison ivy was eaten only by Yellow-rumped Warblers and woodpeckers. The Tree Swallow is the only member of North American swallows to eat fruit as a regular part of the diet (Bent 1942). Birds eating waxy fruits represent an unusual association of frugivores as they belong to families or subfamilies of birds that are generally considered highly insectivorous.

Yellow-rumped Warblers feed on bayberries to eat the wax.—The rapid and extensive release of radiolabeled CO_2 for Yellow-rumped Warblers fed bayberries recoated with [1-C^{14}] palmitate is strong evidence supporting a metabolic fuel role for the natural waxy coating on bayberry. Metabolism of dietary fat occurred in birds with greater than 10% body fat, a fat content that agrees closely with prior studies on autumn and spring Yellow-rumped Warblers (Yarborough and Johnson, 1965). With an average coating of 4.5 to 7.3 mg of wax per fruit, we estimate that a Yellow-rumped Warbler eating between 170 and 280 bayberries would meet a 50 Kj/day daily energy expenditure. Our feeding trials indicate that they are capable of eating over 160 fruits per day. However, they lost nearly 1.5 g of body weight per day on a bayberry diet, indicating that for our captive birds the waxy coating was not sufficient for weight maintenance. The loss in body weight also may be attributable to low nitrogen content in the coating or to fat-soluble toxins present in the wax (Levey and Karasov 1989).

Determinants of high lipid digestive efficiency in Yellow-rumped Warblers.—Ingested fat, especial-

ly high-melting-point fatty acids, must be emulsified or solubilized in the stomach prior to the formation of micelles and absorption in the duodenum. Potential emulsifiers that can function in the acid milieu of the stomach include peptic digests of dietary protein, complex polysaccharides and dietary phospholipids. In mammals, some enzymatic hydrolysis of dietary triglycerides occurs in the stomach, resulting in gastric digestion of up to 30% of fats (Carey et al. 1983). It is thought that the monoglycerides formed during this gastric lipolysis of dietary-neutral lipids further aid emulsification.

In seabirds, little gastric lipolysis is found; yet, these birds are highly successful at neutral lipid digestion (Roby et al. 1986, Place and Roby 1986, Place et al. 1989, Jackson and Place 1990, Place 1992). This ability to assimilate nonpolar lipids efficiently may be due to a unique character of the "enterogastric reflex" of birds. In fowl, as in mammals, gastric motility is inhibited by intraduodenal injections of 0.1 N HCl, 1,600 mOsM solutions of NaCl, corn oil, or amino acids, as well as by intraduodenal balloon inflation (Duke and Evanson 1972, Duke et al. 1973). In addition to this inhibition of gastric emptying, the enterogastric reflex in birds includes the occurrence of one or more intestinal refluxes during the period of gastric motility inhibition (Duke et al. 1973, 1989, Duke 1986). In the chick of domestic chickens, this movement appears to be continuous and regular (Sklan et al. 1978), and observations in the domestic turkey (*Meleagris gallopavo*) indicate that antiperistalsis includes the duodenum and possibly the upper jejunum (Duke 1986). Intestinal refluxes occur approximately three times more often in Leach's Storm-Petrels (*Oceanodroma leucorhoa*) than in fowl (Duke et al. 1989), and involve the movement of intestinal contents back to the proventriculus.

Thus, gastric emptying in these birds is closely tied to the receptiveness of the duodenum for additional digesta, and the reflux returns the digesta (both gastric and duodenal) for further processing in the gizzard. In the process, duodenal products like monoglycerides and fatty acids are refluxed to the gizzard along with biliary (bile salts, phospholipids, and triglycerides) and pancreatic products (lipases). Gastric production of lipid emulsifiers is not found in birds; instead, products of normal intestinal lipolysis are refluxed to a highly efficient emulsification mill, the gizzard.

We hypothesize that Yellow-rumped Warblers also may exhibit a gastrointestinal reflux based on our measurements of biliary products found in the gizzard. Bile-salt concentrations exceeding 50 mM are recorded in the gizzard along with lipolysis products of dietary lipids. Direct radiographic observations will be necessary to substantiate this hypothesis, since the accumulation of biliary and intestinal contents in the gizzard may have resulted during euthanasia.

An important corollary with respect to the effectiveness of any biliary reflux is the nature of the bile salts. Because of the acidic nature in the gizzard and the marked pH dependence in the solubility of unconjugated bile salts (Carey et al. 1983), it is important that these natural fatty-acid solubilizers remain in solution and not precipitate in the gizzard. In Yellow-rumped Warblers, because of taurine conjugation, bile salts do not precipitate in the gizzard. Greater than 90% of the bile salts in Yellow-rumped Warbler bile are taurine conjugates (Table 3). Taurine bile-salt conjugates remain soluble at a pH below 1.0 (Carey et al. 1983).

Elevated bile-salt levels were observed also in the proximal lumen of the intestine. The critical micelle concentration of bile salts in the presence of lipolytic products is below 5 mM (Carey et al. 1983). Thus, the bile salts in the intestinal lumen of the Yellow-rumped Warbler are nearly 5 to 10 times above their critical micellar concentration, hence ensuring effective micellar solubilization of lipolytic products and, potentially, establishing a chemical driving force for passive uptake of dietary fatty acids.

The fact that wax esters are hydrolyzed eight times more slowly than triglycerides and pancreatic extracts of Yellow-rumped Warblers may explain the slower rates of metabolism of triacontanol palmitate. However, the fact that the fatty-acid moiety in cetyl palmitate is metabolized as rapidly as the free fatty acid (Fig. 2) indicates that hydrolysis is not a rate-limiting step in lipid absorption of Yellow-rumped Warblers.

One trait observed in seabirds, which appears not present in the two passerines we analyzed, is efficient utilization of long-chain fatty alcohols. Whereas dietary fatty alcohols are efficiently assimilated (>90%; Place and Roby 1986, Jackson and Place 1990, Place 1992) by seabirds, both Yellow-rumped Warblers and Tree Swallows were relatively poor (<50%) at assimilat-

ing long-chain fatty alcohols. This inefficiency in fatty-alcohol assimilation causes few problems for Yellow-rumped Warblers and Tree Swallows, since they rarely ingest large quantities of fatty alcohol in their natural diet (unlike seabirds). However, the findings clearly indicate that the capacity to oxidize fatty alcohols can be modulated independently of the capacity to hydrolyze wax esters.

Many nonwaxy fruits are characterized by a pulp with a dilute solution of sugars, low concentrations of amino acids, and a substantial portion of undigestible seed mass. Accordingly, frugivorous birds feeding on nonwaxy fruits have short digestive retention times (Levey and Karasov 1989, Karasov and Levey 1990). Waxy fruits are characterized by a pulp of increased energy density, because of a high lipid content in the wax. However, a paradox seems to exist, since frugivorous birds typically exhibit short food-retention times (Karasov 1990), yet lipid absorption is positively correlated with retention time (e.g. Jackson and Place 1990). Moreover, the level of dietary fat strongly influences gastrointestinal transit (Mateos and Sell 1981, Mateos et al. 1982). We predict that, for birds feeding on waxy fruits, gastrointestinal retention times would be longer than for birds feeding on nonwaxy fruits. Also, we predict that the gastrointestinal reflux rate would be higher (i.e. more frequent and greater rate) in birds eating waxy fruits than in birds feeding on nonwaxy fruits. While we did not measure mean retention directly in the current study, the estimate we obtain from the ^{3}H-GTE lipid phase marker indicates that mean retention time of bayberry wax in Yellow-rumped Warblers may be fivefold longer than Cedar Waxwings eating wild grapes (Karasov and Levey 1990). We believe a detailed examination of mean retention times in birds feeding on waxy diets may be a useful direction for future studies.

In summary, we find that Yellow-rumped Warblers and Tree Swallows are capable of efficient absorption and metabolism of bayberry wax. Efficient utilization extends to coatings with a marine wax ester, and to a lesser extent with the major wax ester (triacontanol palmitate) in beeswax. Fatty alcohols are less efficiently assimilated than the equivalent-chain-length fatty acid. This unique assimilatory capacity for high-melting-point waxes in Yellow-rumped Warblers is associated with an elevated gallbladder and luminal bile-salt concentration, and an apparent retrograde intestinal reflux to the gizzard. Gastrointestinal mean retention time may also be longer in Yellow-rumped Warblers than expected for other frugivorous birds. Despite these traits, Yellow-rumped Warblers in captivity are not able to maintain constant body weight eating a bayberry diet. Levey and Karasov (1989) concluded that few temperate birds eating nonwaxy fruits could maintain long-term nutrient and energy balance on a diet of solely fruits. Our results with Yellow-rumped Warblers eating the waxy fruits with higher energy density are consistent with their conclusion.

Both Yellow-rumped Warblers and Tree Swallows are facultative in their frugivory, eating insects when available. The gastrointestinal traits we have documented in Yellow-rumped Warblers should enhance lipid absorption overall, whether the lipid is derived from insects or fruits. Whether the traits are constitutive or can be modulated by diet is not known, but we suspect they are constitutive, since both spring and autumn birds displayed similar absorption capacities. We also suspect that these two species, especially Yellow-rumped Warblers, may have an enhanced detoxification machinery for plant secondary compounds. The bile is a major secretory route for detoxified compounds. Yellow-rumped Warblers and Tree Swallows can be added to the list of other birds (Obst 1986, Roby et al. 1986, Place and Roby 1986, Diamond and Place 1988, Jackson and Place 1990) that exhibit a distinctive ability to assimilate otherwise refractory lipids and "live off the wax of the land."

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