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INFLUENCE OF DIET ON FATTY-ACID COMPOSITION OF DEPOT FAT IN WESTERN SANDPIPERS (*CALIDRIS MAURI*)

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ABSTRACT.—Western Sandpipers (*Calidris mauri*) have been previously shown to undergo seasonal changes in the fatty acid composition of their fat stores, even though they do not show the marked seasonal variation in diet common to many migratory passerines. We investigated the effect of dietary fatty acid composition on the fatty acid composition of adipose tissue in captive Western Sandpipers by feeding birds experimental diets with different fatty acid composition. In addition, we determined the effect of total percentage of fat content of the diet (5 vs. 10%) on fatty acid composition of depot fat. Birds maintained normal body mass (24–27 g) throughout all experimental treatments. Most adipose fatty acids were sensitive to dietary manipulation to some extent. Changes in fatty acid composition of the diet had the largest effect on adipose tissue composition for the essential polyunsaturated fatty acid linoleate (18:2), whereas it had the least effect for the monounsaturated fatty acid oleate (18:1). The saturated fatty acid palmitate (16:0) demonstrated an intermediate capacity to alter fatty acid composition of adipose tissue. Total amount of fat in the diet did not influence the effect of diet on fatty acid deposition. Results of dietary manipulations in this study suggest that diet does explain some of the variation in fatty acid composition observed during migration in Western Sandpipers, but that certain fatty acids can be modulated independently of diet (probably through *de novo* synthesis, postabsorption modification, or both). *Received 2 February 2002, accepted 17 November 2002.*

RESUMEN.—Se ha demostrado que individuos de la especie *Calidris mauri* sufren cambios estacionales en la composición de ácidos grasos de sus reservas grasas, a pesar de que no muestran la marcada variación estacional en la dieta que exhiben muchas aves paserinas migratorias. Investigamos el efecto de la composición dietaria de ácidos grasos sobre la composición de éstos en el tejido adiposo en *C. mauri*, alimentando aves en cautiverio con dietas experimentales con diferente composición de ácidos grasos. Adicionalmente, determinamos el efecto del porcentaje total del contenido de grasa en la dieta (5 vs. 10%) sobre la composición de ácidos grasos en las reservas adiposas. Las aves mantuvieron un peso corporal normal (24–27 g) a lo largo de todos los tratamientos experimentales. La mayoría de los ácidos grasos adiposos fueron sensibles a la manipulación de la dieta en alguna medida. Los cambios en la composición de ácidos grasos de la dieta tuvieron el efecto más marcado sobre la composición del tejido adiposo para el linoleato (18:2), un ácido graso poli-insaturado esencial, y el efecto menos marcado para el oleato (18:1), un ácido graso monoinsaturado. El palmitato (16:0), un ácido graso saturado, mostró una capacidad intermedia de alterar la composición de ácidos grasos del tejido adiposo. La cantidad total de grasa en la dieta no tuvo influencia sobre el efecto de la dieta en la deposición de ácidos grasos. Los resultados de las manipulaciones de la dieta de este estudio sugieren que ésta sí explica parte de la variación en la composición de ácidos grasos observada durante la migración en *C. mauri*, pero que ciertos ácidos grasos pueden ser modulados independientemente de la dieta (probablemente mediante síntesis *de novo* y/o modificación post-absorción).

FATTY-ACID COMPOSITION of adipose tissue triglycerides has been shown to be a highly variable trait in a variety of animals ranging from mammals and birds to fish and insects (Blem 1976, Roy et al. 1991, Schwalme 1994, Käkelä and Hyvarinen 1996, Banskalieva 1997). Fatty acids can vary between different tissues within the same organism (Käkelä and Hyvarinen 1996, Koopman et al. 1996), or they can change seasonally to perform special functions that may be critical to an animal's survival (Blem 1976,

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Frank 1991). Many migratory birds increase the degree of unsaturation of adipose tissue and so reduce the melting point of their fat stores which may aid in the mobilization of lipids to provide energy for flight (Blem 1976). Several studies, on both migratory and non-migratory species, have shown that this change can be diet-related (Moss and Lough 1968, Morton and Liebman 1974, Austin 1993). Many migratory bird species switch to a more unsaturated diet during migration or premigratory fattening, with unsaturated fatty acids prevalent in the dietary fat being deposited directly into the adipose tissue (Moss and Lough 1968, Bower and Helms 1969, Blem 1976, Austin 1993). Furthermore, in some species at least, birds that were maintained on a natural light cycle and fed a constant diet do not show any fluctuation in fatty-acid composition, confirming that changes in endogenous (*de novo*) lipid synthesis are not involved in seasonal changes in adipose tissue fatty-acid composition (Morton and Liebman 1974, Yom-Tov and Tietz 1978, Conway et al. 1994).

Therefore, it is clearly a common pattern for migratory birds to modify the degree of unsaturation of depot fat through a change in diet (e.g. from seeds to insects). However, not all migratory birds show such clear switches in diet associated with migration. As an example, the Western Sandpiper (*Calidris mauri*) feeds on a more-or-less consistent diet of marine benthic invertebrates in winter, and during spring and fall migration (Wilson 1994). Nevertheless, this species still exhibits marked changes in the fatty-acid composition of its depot fat during the annual migration cycle (Egeler and Williams 2000). Several other studies have also suggested that a direct link between fatty-acid composition and diet may not apply to all species. For example, depot fats of captive Common Redpolls (*Carduelis flammea*) were unaffected by three diets differing in fatty-acid composition even though free-living redpolls exhibit considerable seasonal variation in fatty acids (West and Meng 1968a). That suggests that in this species, environmental factors such as photoperiod and temperature may exert a greater influence on lipid dynamics than dietary factors. Thus, the degree to which diet affects composition of lipid stores appears to vary among different species, even when similar dietary changes are involved.

In this article, we examine the effect of diet on adipose tissue composition in the Western Sandpiper using a controlled, experimental approach. The Western Sandpiper is a migratory, carnivorous bird with a diet naturally low in total fat content and essential fatty acids, and we have previously demonstrated an increased storage of the monounsaturated fatty acid oleate (18:1) in this bird prior to and during migration (Egeler and Williams 2000). Although studies on a closely related species—the Semipalmated Sandpiper (*Caldris pusilla*)—have shown that long-chain polyunsaturated fatty acids (PUFAs) from dietary sources are incorporated into adipose tissue (Napolitano and Ackman 1990), those fatty acids are present in quantities too small to be of energetic importance during migration. Therefore, we investigated whether diet can also affect the proportions of the more abundant C_{16} and C_{18} fatty acids in adipose tissue by feeding captive Western Sandpipers diets that varied in content of those fatty acids. We predicted that the amount of long chain monunsaturated fatty acids in adipose tissue would be less tightly linked to dietary availability than for polyunsaturated fatty acids due to existence of significant *de novo* synthesis, postabsorption modification, or both (e.g. Egeler et al. 2000). In addition, because changes in total lipid content of the diet can affect fatty acid composition (e.g. Beare and Kates 1964, Irie et al. 1990), we determined the effect of the total percentage of fat content of the diet on the fatty-acid composition of depot fat in Western Sandpipers.

METHODS

Animals and diet treatments.—Southward migrating juvenile Western Sandpipers were captured using mist nets during August 1995 at Boundary, British Columbia (49°10′N, 123°05′W). Animal handling protocols conformed with Canadian Committee for Animal Care guidelines, and birds were captured and maintained under permits from Simon Fraser University Animal Care Committee (#529B) and Environment Canada (#10646). Birds were maintained in outdoor aviaries (3 × 6 × 2 m) on a natural light cycle with 1.5 mm Clark's Fry dry trout chow (Moore Clark, Vancouver, Canada; 18% fat, 47% protein, 2% fibre, 9% ash, 17% carbohydrate; energy content 18,206 kJ kg^{-1}) and water provided *ad libitum*. Individuals that maintained unusually low body weights (<20 g) were excluded from the experiment to reduce the risk of mortality due to exposure to a new and untested diet. The same birds were used in two successive sets of diet manipulations.

During June 1996 (experiment 1), birds were fed either a 10% canola oil diet (n = 11), or a control diet (n = 8; unmodified Clark's Fry dry trout chow, see above) for 20 days; after the 20 days, all birds were fed the control diet. Body mass was recorded every two to three days for the first week of the experiment and then a final body mass was recorded on day 20 of the experiment. A ~10 mg sample of fat from the furcular cavity was obtained from each bird during early June prior to experimental diet feeding (pretreatment sample) and after 20 days of feeding on either the canola oil or control diet (posttreatment sample). For birds fed the canola oil diet during experiment 1, a third fat sample was obtained 42 days after refeeding on the control trout chow diet (postrecovery sample). To obtain each fat sample, birds were anesthetized by intramuscular injection with ketamine-rompun (1:1 1μL g^{-1} body weight) and a 2 mm incision was made in the skin overlying the furcular cavity. A small piece of adipose tissue was pulled through the incision with forceps and severed with scissors. The incision was closed with Vetbond (World Precision Instruments, Sarasota, Florida) and the birds were allowed to recover completely from anesthesia before being released back into the aviary.

During September 1996 (experiment 2), birds were fed either a 10% tripalmitin diet (n = 9), 5% tripalmitin diet (n = 8), or a modified control diet (n = 5; in this case a delipidated and relipidated control, see below). Body mass was recorded every two to three days for the first week of the experiment. Experiment 2 was terminated on day 12 when a rat killed all the birds (this prevented a final body mass from being recorded). Fat samples were obtained, as described above, from each bird prior to experimental feeding (pretreatment sample). Posttreatment fat samples were obtained from (banded) carcasses within a few hours of death (at 12 days after diet manipulation). All fat samples were stored at –20°C before analysis for fatty-acid composition.

Diets.—The experimental diets were constructed by removing all lipids from the regular trout chow diet with three consecutive petroleum ether extractions to obtain a delipidated trout chow. Solvent was subsequently removed from the delipidated trout chow in a rotary film evaporator followed by a minimum of 24 h of drying time in air. Fats were then added to the fat-free trout chow by dissolving those fats in chloroform and then adding them to the trout chow. Solvent was again removed from the foods in a rotary film evaporator followed by additional drying in air before feeding. Using that method, we made three diets and a control diet that were equivalent in nutrient content (i.e. macronutrient composition and energy content, see above), but different in fatty-acid composition (Table 1). The experimental diets consisted of, (1) 10% w/w canola oil, (2) 10% w/w tripalmitin–fish oil mixture (60:40, 99% purity; Sigma-Aldrich, Oakville, Canada), and (3) 5% w/w tripalmitin–fish oil mixture. In experiment 2, Moore Clark fish oil (the same oil used by the manufacturer for the original trout chow) was added to the delipidated trout chow at a concentration of 10% w/w and used as the reconstituted control diet. On the basis of observations of food remaining during daily food changes, there were no gross differences in food intake between those different diets (see also mass data below).

TABLE 1. Percentage of fatty-acid composition of lipids extracted from three experimental diets and one control diet fed to Western Sandpipers during captive feeding experiments in 1996 (see text for details of diet preparation and lipid extraction).

Fatty acid	Canola oil[a]	Tripalmitin-fish oil[a]	Tripalmitin-fish oil[b]	Moore Clark fish oil[a]
14:0	2.4	8.0	7.2	16.5
16:0	18.1	65.4	62.0	32.0
16:1	2.2	7.3	7.1	15.3
18:0	9.5	3.8	5.2	5.0
18:1	34.7	7.4	8.7	14.8
18:2	28.8	0.08	1.1	1.0
18:3	1.4	1.1	0.8	1.7
20:0	0.5	0.2	0.2	0.5
20:1	0.1	1.0	0.8	1.5
22:0	1.1	4.9	6.6	11.7
22:1	1.4	0.1	0.2	0.0

[a] 10% fat.
[b] 5% fat.

Fatty-acid composition analysis.—Ten milligrams of each adipose tissue sample were sonicated in methanol and lipids were extracted by a modification of the procedure of Bligh and Dyer (1959). Chloroform, methanol, and water were added to the adipose tissue homogenate to proportions of 1:2:0.8. The resulting single-phase mixture was allowed to stand for 10 min before addition of water and chloroform to result in a new proportion of chloroform:methanol:water of 2:2:1.8. Phase separation was achieved by slow-speed centrifugation (1,000 × g, and the chloroform fraction was evaporated under a stream of nitrogen. Lipids were reconstituted in a small amount of hexane and spotted onto silica gel G 60 thin-layer chromatography plates (Sigma-Aldrich, Canada) that were then developed in a solvent system of hexane:diethyl ether:acetic acid (60:40:1). The triglyceride spot (as identified by its R_f) was removed and extracted with chloroform. After evaporation of the solvent, triglycerides were transmethylated overnight at 50°C with 100 μL of toluene and 1 mL of 1% sulfuric acid in methanol. Methyl esters were then extracted with hexane after addition of 1 mL of water, concentrated under nitrogen, and separated by gas chromatography on a Hewlett-Packard 5890 gas chromatograph fitted with a flame ionization detector using a 30 m × 0.25 mm × 0.25 μm HP-INNOWAX column (VWR-Canlab, Mississauga, Ontario, Canada). Fatty acids

were identified on the basis of retention times of their methyl esters as compared to fatty-acid methyl ester standards (Sigma-Aldrich).

The fatty-acid composition of the experimental diets and the reconstituted control diet was determined by the same lipid extraction and chromatography methods described above for the adipose tissue samples. For the control diet, lipids were extracted from reconstituted trout chow pellets (delipidated and then replipidated with fish oil), and the resulting lipids were analyzed for fatty acid composition. For the experimental diets, lipids were extracted from each relipidated diet and the resulting lipids were analyzed for fatty-acid composition.

Statistical analysis.—For each diet and for each fatty acid, difference in the percentage of the total amount of fatty acids between pretreatment samples and posttreatment samples was calculated for each individual. If the average difference (for all birds on that diet) was significantly different from zero (after Bonferroni adjustment; Rice 1989), then the diet was considered to have had an effect for that fatty acid. A multivariate analysis of variance (MANOVA) was used to test if the differences between pretreatment and posttreatment biopsy samples for each fatty acid varied between the 5% and 10% tripalmitin experimental diets. A univariate repeated measures ANOVA was used to test if the body mass of the birds changed over time on the experiemental and control diets, and pairwise contrasts were used to determine if the mass at various time intervals on the experimental diets differed from pre-treatment values (day 0). All analyses were conducted using SAS (SAS Institute 1990).

RESULTS

The 10% canola oil diet was high in unsaturated fats and consisted primarily of the monunsaturated fatty acid oleate (18:1, 35% of total fatty acids) and the polyunsaturated fatty acid linoleate (18:2, 29% of total fatty acids; Table 1). The 5 and 10% tripalmitin-fish oil diets were high in saturated fats, with tripalmitin (16:0) comprising about 65% of total fat and unsaturated fats constituting only 20% of total fatty acids (Table 1). The control diets (using Moore Clark fish oil) were not associated with any significant changes in fatty acid composition throughout the experimental period ($P > 0.05$). That shows that removal of lipid by solvent extraction (delipidation) and replacement of lipids (relipidation) itself had no effect on dietary fatty-acid composition as determined by changes in depot fatty acids in birds on the two types of control diets; that is, experiments 1 and 2 (cf. experimental diets; see below).

Whereas feeding experiments often employ starvation and refeeding during which energy reserves are depleted and then replenished, the present study did not involve food restriction, that is, birds always had *ad libitum* access to food. During experiment 1, there was no significant change in body mass during the 20-day experimental period for birds on the unmodified control diet or the 10% canola oil diet (Fig. 1A; univariate repeated measures ANOVA, $P > 0.30$ in both cases). For experiment 2, although there was a significant time effect on body mass for both diets (10 % tripalmitin, $F = 6.74$, df = 3 and 5, $P < 0.05$; 5% tripalmitin $F = 19.0$, df = 3 and 5, $P < 0.01$) none of the pair-wise contrasts were significant for any time interval ($P > 0.05$ in all cases). Throughout both experiments, mean body mass remained between 24–27 g, which is normal for migrating Western Sandpipers, and well above lean mass (22 g; Guglielmo 1999).

Feeding birds with a 10% canola oil diet resulted in a large increase in linoleic acid (18:2) content of depot fat, from 3.4% of identified

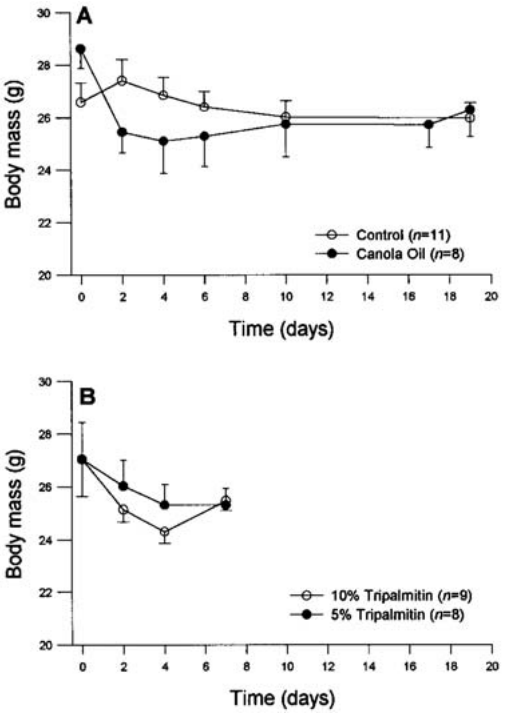

FIG. 1. Body mass of captive Western Sandpipers during 20-day feeding trials for (A) birds fed the control and 10% canola oil diets, and (B) for 5 and 10% tripalmitin diets.

fatty acids to 34.3% (t = 15.3, df = 10, $P < 0.001$; Fig 2). In contrast, although the level of oleic acid (18:1) was more than twice as abundant in the 10% canola oil diet compared to Moore Clark fish oil, no increase in that fatty acid was detected in depot fat of birds fed this diet. The increase in the relative proportion of linoleic acid resulted in a dilution of some of the other fatty acids that consequently decreased in proportion; palmitic acid (16:0) decreased from 33.7 to 21.8% (t = –11.9, df = 10, $P < 0.001$), palmitoleic acid (16:1) from 13.2 to 3.3% (t = –17.7, df = 10, $P < 0.001$), myristic acid (14:0) from 8.2 to 2.8% (t = –8.7, df = 10, $P < 0.001$), and eicosenoic acid (20:1) from 3.0 to 1.4% (t = –7.9, df = 10, $P < 0.001$; Fig. 2). Thus, the increase in linoleic acid was balanced by a decrease in just four fatty acids whereas the proportions of the remaining fatty acids remained constant. Refeeding of the regular trout chow diet after the experimental period on the 10% canola oil diet resulted in the almost complete restoration of the original (pretreatment biopsy) fatty-acid composition of furcular fat. Most notably, the amount of linoleate (18:2) in the postrecovery biopsy fat samples returned to preexperimental proportions, although there was an increase in myristic acid (14:0; t =7.0, df = 10, $P < 0.01$) and a slight decrease in eicosenoic acid (20:1; t = –5.23, df = 10, $P < 0.05$; Fig. 3). There was no significant difference between pretreatment and postrecovery samples for any other fatty acid ($P > 0.05$ in all cases).

Feeding of the 10% tripalmitin-fish oil diet resulted in an increase in the amount of palmitate (16:0) stored in furcular fat, from 33.7 to 44.3% (t = 9.5, df = 8, $P < 0.001$), although palmitate levels in adipose tissue did not ap-

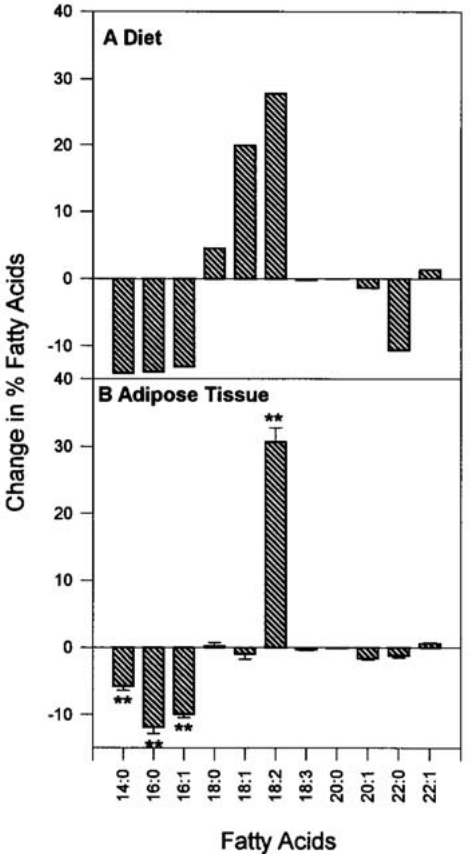

FIG. 2. (A) Difference in fatty-acid composition of extracted lipids from the experimental 10% canola oil diet compared to Moore Clark fish oil used in the control diets, and (B) changes in fatty-acid composition of adipose tissue in captive Western Sandpipers following the 20-day feeding trial on the 10% canola oil diet compared with pretreatment values. Double asterisks indicate those changes in fatty acids that are significantly different from zero (Bonferroni-adjusted t-test, $P < 0.05$) .

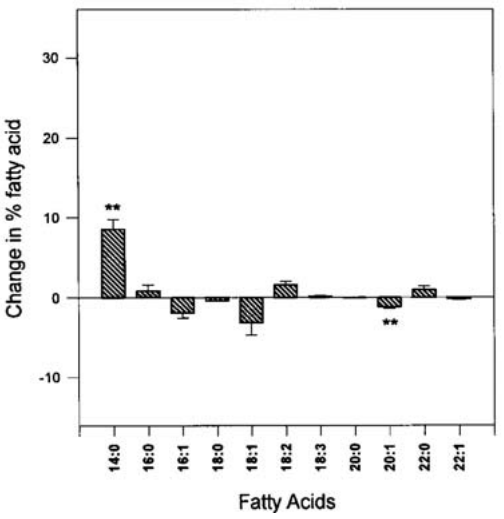

FIG. 3. Changes in fatty-acid composition of adipose tissue in captive Western Sandpipers in the postrecovery sample following return to a control diet (after the 20-day feeding trial on 10% canola oil diet) in comparison with pretreatment values. Double asterisks indicate those changes in fatty acids that are significantly different from zero (Bonferroni-adjusted t-test, $P < 0.05$) .

proach the levels of this fatty acid in the diet (Fig. 4). However, as with the canola oil diet, the increase of one fatty acid was balanced by the decrease in the proportions of only a few of the remaining fatty acids. Palmitoleic acid (16:1) decreased from 11.2 to 6.48% ($t = -8.8$, df = 8, $P < 0.001$), myristic acid (14:0) from 10.0 to 6.7% ($t = -6.3$, df = 8, $P < 0.005$), linoleic acid (18:2) from 4.8 to 3.3% ($t = -6.3$, df = 8, $P < 0.005$), and eicosenoic acid (20:1) from 2.7 to 1.6% ($t = -6.1$, df = 8, $P < 0.005$; Fig. 4).

Changes in adipose tissue fatty acid composition in birds fed with the 5% tripalmitin-fish oil diet were very similar to those for the 10% tripalmitin-fish oil diet (see Fig. 5). Palmitate (16:0) increased from 34.3 to 43.4% ($t = 5.8$, df = 7, $P < 0.005$), whereas palmitoleic acid (16:1) decreased from 11.2 to 5.6% ($t = -8.0$, df = 7, $P < 0.001$), myristic acid (14:0) decreased from 11.1 to 6.2% ($t = 4.1$, df = 7, $P < 0.05$), and stearic acid (18:0) increased from 7.4 to 9.9% ($t = 5.1$, df = 7, $P < 0.02$). The proportions of the remaining fatty acids remained unchanged throughout the experimental period. The changes in fatty-acid composition induced by the 5% tripalmitin-fish oil diet were not significantly different from the changes in fatty-acid composition that resulted from the

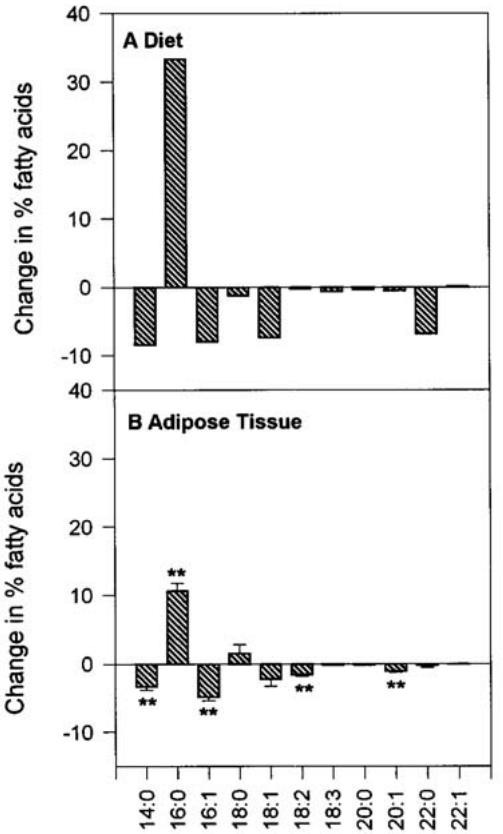

FIG. 4. (A) Difference in fatty-acid composition of extracted lipids from the 10% tripalmitin-fish oil diet compared to Moore Clark fish oil used in the control diets, and (B) changes in fatty-acid composition of adipose tissue in captive Western Sandpipers following a 20-day feeding trial on the 10% tripalmitin diet compared with pretreatment values. Double asterisks indicate those changes in fatty acids that are significantly different from zero (Bonferroni-adjusted *t*-test, $P < 0.05$) .

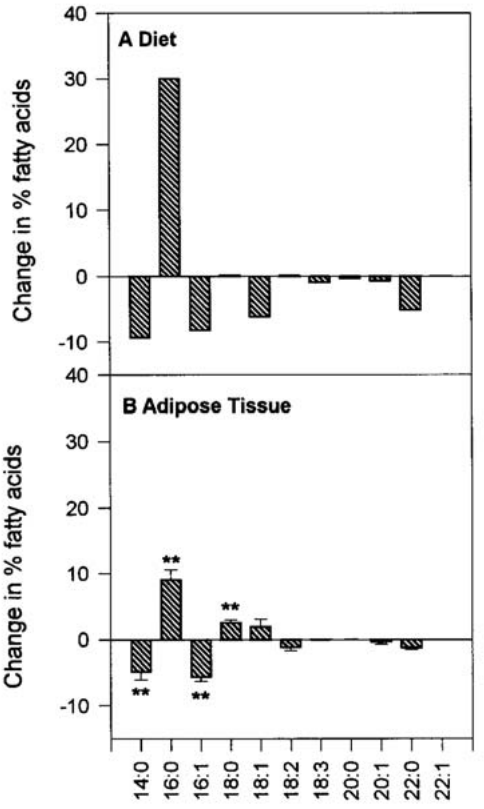

FIG. 5. (A) Difference in fatty-acid composition of extracted lipids from the 5% tripalmitin-fish oil compared to Moore Clark fish oil used in the control diets, and (B) changes in fatty-acid composition of adipose tissue in captive Western Sandpipers following a 20-day feeding trial on the 5% tripalmitin diet compared with pretreatment values. Double asterisks indicate those changes in fatty acids that are significantly different from zero (Bonferroni-adjusted *t*-test, $P < 0.05$) .

10% tripalmitin-fish oil diet with the exception of slightly lower levels of oleate (18:1; $F = 9.5$, df = 2 and 17, $P = 0.02$) with the 10% diet.

Discussion

Manipulation of dietary fatty-acid composition had a marked (and relatively rapid) effect on the fatty-acid profiles of adipose tissue in captive Western Sandpipers. In general, birds showed increased storage of fatty acids that were predominant in the diet with a concurrent decrease in proportions of other fatty acids. However, not all fatty acids in the diet were deposited equally into adipose tissue; that is, the fatty-acid composition of depot fat was not simply a direct reflection of dietary fatty acids. The polyunsaturated fatty acid linoleate (18:2) was incorporated into fat stores until the proportion in adipose tissue exceeded that in the diet. In contrast, palmitate (16:0), although present in very large quantities in the diet, was not incorporated into adipose tissue, and the amount of oleic acid (18:1) in the diet did not affect the proportion of that fatty acid stored in adipose tissue. It therefore appears that, in Western Sandpipers, the effect of dietary fatty acids on adipose tissue composition was greatest for linoleate (18:2) and intermediate for palmitate (16:0), whereas oleate (18:1) levels were not sensitive to diet composition. That suggests that the effect of diet on adipose tissue fatty-acid composition is complex, but that C_{18} essential fatty acids may be preferentially deposited or retained (see also Napolitano and Ackman 1990).

Several previous studies have shown a high congruence between dietary fatty acids and adipose tissue in migratory and wintering birds. For example, Moss and Lough (1968) showed that dietary fatty acids and depot lipids are closely matched in Willow Ptarmigan (*Lagopus lagopus*) and Rock Ptarmigan (*L. mutus*) throughout the year. Similarly, in wintering Canada Geese (*Branta canadensis*) annual differences in depot fat composition corresponded to changes in availability of those fatty acids in the birds' diet between years (Austin 1993). Morton and Liebman (1974) demonstrated that a decrease in linoleic acid (18:2) in the adipose tissues of White-crowned Sparrows (*Zonotrichia leucophrys*) at the onset of vernal migration coincided with a diet switch from seeds high in linoleic acid to insects low in linoleic acid.

Essential fatty acids in adipose tissue can only originate from dietary sources whereas other saturated and monounsaturated fatty acids can originate both from the diet as well as endogenous (*de novo*) synthesis. That predicts that fatty-acid composition of the diet would have the greatest influence on the levels of essential polyunsaturated fatty acids, whereas other fatty acids in the diet may only serve to supplement biosynthesis. Previous studies have reported selective retention of linoleic acid involving the action of monoacylglycerol acyltransferase (an enzyme involved in triglyceride synthesis) in migrating White-throated Sparrows (*Zonotrichia albicollis;* Mostafa et al. 1994) and hibernating marmots (*Marmota flaviventris;* Xia et al. 1993). Although we found evidence for selective uptake of linoleic acid from the diet, that fatty acid was not selectively retained at high levels in adipose tissue in the face of low dietary 18:2: the proportion of linoleate decreased from 35% to ~5% over a period of a few weeks of *ad libitum* feeding of the regular trout chow diet containing low levels of essential fatty acids. That is indicative of rapid fatty-acid turnover and illustrates the dynamic nature of fatty-acid composition of depot fat in Western Sandpipers. Fatty acids can also be enzymatically altered once ingested, which might further complicate any direct effect of diet on adipose tissue composition. For example, palmitate (16:0) can be elongated to stearate (18:0) which can be further desaturated to oleate (18:1). As a consequence, feeding of a high stearate diet to chickens (*Gallus gallus*) has been shown to cause a large increase in stored oleic acid whereas stearic acid levels increased only slightly (Bonanome et al. 1992). The enzyme Δ^9-desaturase plays a key role in modification of the degree of saturation of fatty acids (Bonanome et al. 1992) and activity of that enzyme is correlated with plasma oleate levels (De Antueno et al. 1993). We have previously shown that the level of enzyme activity of Δ^9-desaturase, and fatty acid synthase, increase during migration in Western Sandpipers (Egeler et al. 2000; although not during premigration). That supports the idea that, in this species, *de novo* synthesis of fatty acids—or postdigestion modification of dietary fatty acids—contributes to composition of depot fat and in that way modulates the effect of diet. In the present study, Western Sandpipers also demonstrated a trend towards increasing stearic acid (18:0)

levels with higher dietary levels of palmitate (16:0), possibly caused by microsomal elongation of dietary palmitate to stearate in the liver. The natural diet of Western Sandpipers is low in total fat (~2%, cf. some passerines; Egeler and Williams 2000), and even on our experimental diets approximately 80–90% of dietary caloric intake would have been derived from nonfat sources. That again supports the idea of a key role of endogenous (*de novo*) lipid synthesis in determining adipose tissue fatty-acid composition.

In Western Sandpipers, the level of oleate (18:1) did not increase when birds were fed the canola oil diet with high levels of oleate, and oleate levels did not decrease on the tripalmitin diet with low levels of oleate. That is contrary to findings in poultry. Feeding chickens a diet reduced in oleate (18:1) and supplemented with linoleate (18:2) resulted in increased proportions of linoleate and a reduction in oleate in adipose tissue (Pinchasov and Nir 1992). That suggests that, although in nonmigratory birds oleate (18:1) levels fluctuate with diet, in migratory species like the Western Sandpiper the proportion of that monounsaturated fatty acid might be physiologically regulated to remain around some set point value. The potential importance of oleate during migration has been discussed previously (Egeler and Williams 2000) and it is possible that some migratory birds have evolved a means by which to adjust their fatty-acid composition to aid in mobilization of fuel for flight (but see Heitmeyer and Fredrickson 1990, Conway et al. 1994).

Finally, in this study, effect of dietary fatty-acid composition on adipose tissue composition was very similar regardless of the total fat content of the diet (comparing the 5 and 10% canola oil diets). Other studies in mammals have reported alterations of fatty-acid composition of depot fat associated with changes in fat content of the diet as small as 1 or 2% (Beare and Kates 1964, Irie et al. 1990), suggesting that as fat content of the diet is increased, the importance of endogenous lipogenesis is decreased and body fat composition begins to approach the fatty-acid composition of the diet. That was not the case in Western Sandpipers, for all fatty acids, even with a dietary fat content of 10%. It should be noted that the oils used in our experiments (fish oil and corn oil) are high in polyunsaturated fatty acids that are usually present in low concentrations in mammalian adipose tissues. It thus appears that amounts of essential fatty acids deposited increases with the fat content of the diet whereas the amount of saturated fats deposited is unaffected by fat content of the diet. In other words, the proportions of essential polyunsaturated fatty acids in depot fat are highly sensitive to dietary manipulation, whereas proportions of nonessential fats are not.

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