



The Auk 122(2):544–557, 2005
© The American Ornithologists' Union, 2005.
Printed in USA.

FAT-DEPOSITION STRATEGIES AMONG HIGH-LATITUDE PASSERINE MIGRANTS

ANNA-MARIE BENSON^{1,3} AND KEVIN WINKER²

¹*Alaska Bird Observatory, P.O. Box 80505, Fairbanks, Alaska 99708, USA; and*

²*University of Alaska Museum, 907 Yukon Drive, Fairbanks, Alaska 99775, USA*

ABSTRACT.—We studied fat stores in passerine migrants at a high-latitude site in Fairbanks, Alaska (64°50'N, 147°50'W). We examined fat-deposition strategies during the final (spring) and initial (autumn) stages of long-distance migration, 1992–1998, to (1) improve understanding of geographic fat-deposition patterns by adding a high-latitude perspective; (2) determine whether there are age-related differences in fat-deposition strategies in autumn; and (3) test the “spring fatter” hypothesis of seasonal fat-deposition, which suggests that migrants should carry more fat in spring when they near their breeding areas than in autumn when they depart. Our analyses examined factors affecting daily fat scores during migration and compared between-season differences in fat stores among a total of 18,685 individuals of 16 migrant species. In autumn, adults had higher visible subcutaneous fat scores than immatures in 11 of 16 species. However, in all but two species, those differences were attributable to the effects of overnight low temperature, day length, and time of day, rather than age, probably because of later departures by adults. Fat scores were higher in autumn than in spring in 6 of 16 species, and body-condition indices were higher in autumn in 5 of 16 species. Only one species showed higher fat scores in spring, but that difference was not reflected in a seasonal comparison of body-condition indices. No species arrived with high fat loads in spring, and generally low fat levels in autumn suggest that high-latitude passerine migrants in North America are paying most of the energetic costs of long-distance migration with resources obtained en route to their wintering grounds. Among passerine migrants near these high-latitude breeding grounds, seasonal fat-deposition strategies appear to be responding to energetic needs at the level of daily maintenance, rather than to hypothesized insurance needs in spring or to the forthcoming needs of a long-distance migration in autumn. *Received 16 October 2003, accepted 10 November 2004.*

Key words: birds, energetics, migration, Nearctic–Neotropic migrants, stopover ecology, subarctic stopover sites.

Stratégies de Constitution de Réserves de Graisse chez des Passereaux Migrants à des Hautes Latitudes

RÉSUMÉ.—Nous avons étudié les réserves de graisse chez des passereaux migrants sur un site situé à une haute latitude à Fairbanks, Alaska (64°50'N, 147°50'W). Nous avons étudié les stratégies de constitution de réserves de graisse lors des haltes finales (printemps) et initiales (automne) survenant au cours de longues migrations entre 1992 et 1998. Les objectifs de cette étude étaient (1) d'améliorer la compréhension des patrons géographiques pour la constitution de réserves de graisse en considérant la perspective d'une étude à haute latitude; (2) de déterminer s'il y a des différences dans les stratégies de constitution de réserves de graisse en fonction de l'âge au cours de l'automne; et (3) de tester l'hypothèse “spring fatter” (“plus gras au printemps”).

³E-mail: acbenson@gci.net

de constitution de réserves de graisse saisonnières. Cette hypothèse suggère que les migrateurs devraient posséder plus de graisse au printemps, quand ils sont proches de leurs aires de reproduction, que pendant l'automne quand ils partent. Nos analyses ont examiné les facteurs qui affectent les réserves journalières en graisse au cours de la migration et comparé les différences inter-saisonnières en réserves de graisse parmi un total de 18 685 individus appartenant à 16 espèces migratrices. À l'automne, les adultes avaient des réserves apparentes de graisse plus importantes que les immatures chez 11 des 16 espèces étudiées. Néanmoins, pour toutes les autres espèces (sauf deux), ces différences étaient attribuables aux effets de la basse température au cours de la nuit, de la longueur du jour, et le moment de la journée, plutôt que l'âge, probablement en raison du départ plus tardif des adultes. Les dépôts de graisse étaient plus importants à l'automne pour 5 des 16 espèces. Seule une espèce a montré des dépôts de graisse plus importants au printemps, mais cette différence n'a pas été retrouvée dans une comparaison saisonnière des indices de conditions corporelles. Aucune espèce n'est arrivée avec des réserves de graisse élevées au printemps. Généralement, les faibles niveaux de graisse à l'automne suggèrent que les passereaux migrants à de hautes latitudes en Amérique du Nord assument la plupart des coûts énergétiques encourus au cours des longues migrations grâce à des ressources obtenues lors de leur voyage vers les aires d'hivernage. Parmi les passereaux migrants vers les aires de nidification situées à ces hautes latitudes, les stratégies saisonnières de constitution de réserves de graisse semblent répondre aux besoins énergétiques requis par la demande journalière, plutôt qu'aux besoins complémentaires et hypothétiques au printemps et lors de la longue migration automnale.

LONG-DISTANCE MIGRATION is energetically expensive (Berthold 1975, Blem 1990). During migration, metabolic rates for some passerines can be 6–8× the normal resting rate (Hussell 1969). Those energetic demands are satisfied by fat deposited before and during the migratory period (e.g. Nisbet et al. 1963, Mueller and Berger 1966, Berthold 1975, Cherry 1982, Blem 1990). Although fat deposition has been documented at stopover sites, continental patterns of fat deposition in Nearctic–Neotropical migrants are not well understood. Understanding the geographic and temporal patterns of migratory fat-deposition could elucidate broad patterns of migration strategies and the selective pressures associated with continental migration systems.

Fattening strategies employed during migration vary among species in rate of fat deposition and in amount of fat stored. Strategies may be influenced by body size, foraging habits, season, distances between breeding and nonbreeding ranges, and stopover location in relation to each end of the migratory journey (King et al. 1963; Winker et al. 1992a, b; Winker 1995; Berthold 1996; Sandberg 1996; Pilastro and Spina 1997; Farmer and Wiens 1999; Katti and Price 1999). Independently of migration, fat stores of passerines can also vary in response to daily

environmental variables, including temperature and photoperiod (Lehikoinen 1987, Lehikoinen and Hakala 1988, Bednekoff et al. 1994, Bednekoff and Krebs 1995). During migration, many passerines increase fat stores during daylight hours at stopover sites (Cherry 1982, Blem 1990, Winker et al. 1992b, Winker 1995, Morris et al. 1996, Dunn 2002, Jones et al. 2002). Seasonal differences in fat reserves are partly endogenously programmed in circannual patterns (Gwinner 1990). For example, some migrants undergo hyperphagia, the principal mechanism of premigratory fattening, at predictable times in the annual cycle (Berthold 1975).

Here, we examine fat-deposition strategies among passerine migrants just before arrival on and just after departure from high-latitude breeding areas. Our purposes are threefold:

(1) To gain a better understanding of geographic patterns of fat deposition among Nearctic–Neotropical migrants by adding a high-latitude perspective. The fat loads that migrants carry at high latitudes can illuminate how resources are used on and near the breeding grounds to pay the energetic costs of long-distance migration.

(2) To determine whether there are age-related differences in fat-deposition strategies among

high-latitude migrants in autumn. In that season, adults tend to depart the breeding grounds later than immatures, probably because of the more extensive prebasic molt that adults undergo at that time (Benson and Winker 2001).

(3) To test the "spring fatter" hypothesis of seasonal fat-deposition, developed from studies at lower latitudes (Winker et al. 1992a, Sandberg 1996, Sandberg and Moore 1996). That hypothesis suggests that migrants should carry more fat in spring when they near their breeding areas than in autumn when they leave those same areas, because in spring, passerine migrants are usually approaching a temporal barrier of resource availability. Given time, resources on their breeding areas will become predictably available. Until resource availability becomes certain, however, carrying extra fat onto the breeding grounds to prevent starvation or to potentially gain reproductive benefits (e.g. through territory defense, gonadal development, or accelerated initiation of breeding) would seem to be advantageous. Fat stores in passerines can provide enough energy to maintain birds during mornings when food is scant (Kettersen and Nolan 1978) and have been estimated to ensure survival for up to four days (Blem 1976). In contrast, autumn migrants are departing their breeding areas, having just completed their prebasic molt (also energetically costly), and they are headed generally southward into areas of longer growing seasons and presumably greater resource predictability.

Given those seasonally different energetic scenarios, and that there are costs to carrying fat (Witter and Cuthill 1993, Sandberg and Moore 1996), the "spring fatter" hypothesis has intuitive appeal. Higher fat stores in spring as compared with other seasons have been documented at many locations in Canada and the United States (King et al. 1963, Biermann and Sealy 1984, Winker et al. 1992a, Dunn 2002). Passerines are also known to arrive at some high-latitude breeding ranges with high fat levels (Sandberg 1996, Fransson and Jakobsson 1998). Testing the "spring fatter" hypothesis requires the study of populations near breeding grounds that lie at the beginning and end of long-distance migrations, far from physical (as opposed to temporal) ecological barriers to migration, such as oceans and deserts, and which themselves require larger fat stores for successful passage.

METHODS

Study area.—The present research is part of the most intensive standardized mist-netting study ever conducted in subarctic North America. Mist nets were operated by the Alaska Bird Observatory at Creamer's Field Migration Station (CFMS), in Fairbanks, Alaska (64°50'N, 147°50'W), ~10 km from the confluence of the Chena and Tanana rivers, at 130 m elevation. The Tanana Valley is a well-documented migration corridor (Kessel 1984, Cooper and Ritchie 1995, McIntyre and Ambrose 1999). Encompassing ~20 ha, CFMS provides a good representation of the common habitat types that occur within the boreal forest of interior Alaska.

Data collection.—A standardized netting protocol was used at CFMS from 1992 to 1998, employing an array of 22–50 standard mist nets (30-mm mesh, 2.6 × 12 m). Nets were arranged in a north–south direction, perpendicular to the migration corridor through the Tanana Valley. During spring migration (25 April–15 June), nets were operated daily from 0600 to 1300 hours (Alaska Daylight Savings Time). During autumn migration (15 July–30 September), net-opening times varied with sunrise (e.g. 0600 hours on 15 July and 0730 hours on 30 September), and nets were closed seven hours later. Sampling at the end of each season (10–15 June and 25–30 September) occurred every other day. Birds were banded with U.S. federal bands, and data were collected to determine age (autumn only, using degree of skull ossification), body mass, wing length (chord), and breeding condition (spring only). During autumn, an estimate of the proportion of juvenal plumage on each immature was recorded.

We used ordinally scored subcutaneous fat deposits as an indicator of total body fat, employing an eight-class scoring system modified from Helms and Drury (1960): 0 = no fat observed on furculum or abdomen; 1 = trace of fat on furculum and abdomen; 2 = thin layer of fat on furculum and abdomen; 3 = half of furculum fat-filled, and fat covering most of abdomen; 4 = fat on furculum level with clavicles and slightly mounded on abdomen; 5 = fat slightly bulging on furculum and well mounded on abdomen; 6 = fat greatly bulging in furculum and mounded on abdomen; 7 = large fat pads from furculum and abdomen meet. Using fat-score data is a fairly reliable method for

indexing total body fat of passerines if observer bias is limited (Krementz and Pendleton 1990; Rogers 1991, 2003). We minimized observer bias by intensively training field staff on thousands of birds. Although no formal measures of observer bias were recorded, staff frequently compared fat-score estimates to ensure consistency. Additionally, ~75% of the data were collected by three individuals whose tenure at the bird observatory overlapped by at least two years each, further enhancing standardization.

Data analysis.—To ensure independence of records, we used only initial captures of birds. Because our autumn netting period began before the initiation of autumn migration in most species, we excluded individuals that were identifiable at first capture as non-migrants (i.e. females with incubation patches and first-year birds with >30% of their bodies in juvenal plumage; Benson and Winker 2001). We also excluded all individuals that were molting flight feathers and birds recaptured >7 days after their first capture. Several species breed at our study site and are captured throughout summer banding: Swainson's Thrush, American Robin, Orange-crowned Warbler, Yellow-rumped Warbler, Yellow Warbler, Savannah Sparrow, Lincoln's Sparrow, White-crowned Sparrow, and Dark-eyed Junco (scientific names are given in Table 1). For these species, we defined a species-specific migration window, whereby we removed the last 5% of captures during spring migration and the first 5% during autumn migration (Table 1). That date-defined migration window was not applied to species that do not breed at our study site, because of the rapid onset and intense nature of migration at high latitudes. That is, birds captured early in our netting period during autumn or late in the netting period during spring with no evidence of breeding or molting could be migrants. Further, for each species, ≥95% of individuals in the analysis fell into clear distributional peaks for each migration season. Although there is potential for a few "floaters" (birds that are not migrating or breeding) in our data set, their removal would not greatly affect our results, and their inclusion in both seasons might indeed balance the potential effects of inadvertent inclusion.

Because fat-score data are ordinal, we used Mann-Whitney *U*-tests to examine differences in fat levels between spring and autumn and,

in autumn, between adults and immatures. Although the median is the appropriate measure of central tendency for fat-score data (Hailman 1965), the mean is also presented for comparisons with other studies that reported only means.

In addition to using ordinal fat scores, we calculated an index of body condition using mass (in grams) divided by wing chord (in millimeters). Because factors other than season could affect fat deposition (e.g. temperature, night length, time of capture), a parametric measure (ratio of mass to wing) was required to determine how each factor affected mass gain at this site. In wood warblers, when body mass is standardized for body size, it is a reasonable predictor of an individual's fat content (Rogers and Odum 1964). Because recent studies indicate that fat stores may vary independently of mass gain (e.g. Katti and Price 1999, Piersma et al. 1999, McWilliams and Karasov 2001), we examined the relationship between fat score and body-condition index in autumn (when sample sizes were sufficiently large). The strong positive relationship found in all 16 species (Table 1) legitimizes use of the condition index as a correlate of fat for those populations, and we therefore use both measures in our analyses.

Analysis of covariance (ANCOVA) was used to examine age-related differences in body condition; age was used as a main factor, and time of capture, night length, and daily low temperature (°C) were incorporated as covariates. That is, low temperature on the date the bird was captured (usually the night before), night length on the date the bird was captured (data from the Alaska Climate Research Center; see Acknowledgments), and time of day when the bird was captured were recorded for each individual. We did not include Julian date as a covariate, because it is highly correlated with night length at this location ($r = 0.99$, $P < 0.0001$ during autumn); therefore, the effects of night length could be used as a surrogate for Julian date. For species with significant age-related differences in body condition, we tested for year effects using ANCOVA with year and age as main factors and time of day, daily low temperature, and night length as covariates.

Seasonal differences in body-condition indices were evaluated using ANCOVA with season as the main factor and time of capture, daily low temperature, and night length as covariates. For

TABLE 1. Migration distance, timing of migration, and relationship between fat score and body condition index (ratio of mass to wing chord) of passerine migrants in Fairbanks, Alaska (1992–1998).

Species	Distance ^a	Spring				Autumn				Fat score and body condition ^d
		Median ^b		Window ^c		Median ^b		Window ^c		
		Adults	Immatures	Adults	Immatures	Adults	Immatures	Adults	Immatures	
Alder Flycatcher (<i>Empidonax alhorum</i>)	L	161	167	209	222	196	204	372	0.195	
Ruby-crowned Kinglet (<i>Regulus calendula</i>)	S	130	143	253	245	226	204	671	0.116	
Gray-cheeked Thrush (<i>Catharus minimus</i>)	L	144	159	242	239	225	211	205	0.277	
Swainson's Thrush (<i>C. ustulatus</i>)	L	145	155	240	232	229	221	642	0.457	
American Robin (<i>Turdus migratorius</i>)	S	137	163	266	249	248	225	229	0.511	
Orange-crowned Warbler (<i>Vermivora celata</i>)	L	143	156	245	237	229	217	2,604	0.279	
Yellow-rumped Warbler (<i>Dendroica coronata</i>)	L	136	152	244	234	227	222	3,432	0.261	
Yellow Warbler (<i>D. petechia</i>)	L	151	157	235	227	205	206	553	0.446	
Blackpoll Warbler (<i>D. striata</i>)	L	142	160	236	231	223	209	286	0.382	
Wilson's Warbler (<i>Wilsonia pusilla</i>)	L	144	162	242	229	222	199	699	0.269	
American Tree Sparrow (<i>Spizella arborea</i>)	S	131	153	257	256	236	224	2,557	0.587	
Savannah Sparrow (<i>Passerculus sandwichensis</i>)	L	143	156	235	231	222	209	440	0.275	
Fox Sparrow (<i>Passerella iliaca</i>)	S	131	147	247	244	228	213	272	0.441	
Lincoln's Sparrow (<i>Melospiza lincolni</i>)	L	139	153	235	229	209	204	1,023	0.172	
White-crowned Sparrow (<i>Zonotrichia leucophrys</i>)	S	135	150	240	230	229	210	359	0.295	
Dark-eyed Junco (<i>Junco hyemalis</i>)	S	135	151	256	246	238	227	1,994	0.394	

^a Abbreviations: L = Nearctic–Neotropical migrant, S = Nearctic–Nearctic migrant.

^b Median Julian dates of passage (Benson and Winker 2001).

^c Migration window (last day of spring migration and first day of autumn migration).

^d Comparison between body condition index and fat score using Pearson product-moment correlation coefficient. All $P < 0.003$.

species with significant differences in body condition between seasons, we determined whether those differences were attributable to year effects by using season and year as main factors and time of day, daily low temperature, and night length as covariates in ANCOVA models. Year of capture was not included as a main factor for all species, because we did not have sufficient sample sizes in all years. All analyses were conducted using SPSS (Chicago, Illinois), and each of those tests was conducted on 16 species. The overall rate of making any Type I error (rejection of a true null hypothesis) can be controlled by applying the Dunn-Sidak correction to maintain an overall, study-wide $\alpha = 0.05$ (Sokal and Rohlf 1995). Using that method, P -values less than 0.0032 are considered significant. That is a conservative approach for independent tests, however, increasing the likelihood of making Type II errors (accepting a false null hypothesis) on individual tests (Sokal and Rohlf 1995). Because we are testing broad hypotheses among multiple species, we chose the conservative approach in general interpretation, but we report individual tests at both levels of α (0.05 for individual independent tests and 0.003 for the overall, study-wide error) to enable species-level comparisons with future studies.

RESULTS

Age-related differences in autumn.—Both fat-score and body-condition data were used to examine possible differences in fat loads between adults and immatures in the autumn sample. At the species level, adults of all species had significantly higher mean fat scores than immatures, and that pattern prevailed study-wide, with 11 of 16 species having $P < 0.003$ (Table 2). Immatures did not have higher fat scores in any species examined, unless $P < 0.05$ is considered significant, in which case, fat scores of immatures were higher than those of adults in Alder Flycatchers (Table 2).

When time of capture, night length, and overnight low temperature were included in ANCOVA models, age-class differences in body condition (mass/wing) were mostly nonsignificant, with $P < 0.003$ occurring in only two species (or 4 at $\alpha = 0.05$; Table 3). In Swainson's Thrushes and Yellow-rumped Warblers, adults possessed higher condition indices when covariates were held constant (Table 3). The ANCOVAs showed no interaction between age and year in Swainson's Thrushes ($F = 2.03$, $df = 6$ and 588, $P = 0.07$) or in Yellow-rumped Warblers ($F = 0.14$, $df = 6$ and 3,324, $P = 0.98$), which suggests that the age-related differences did not

TABLE 2. Differences in fat scores between adults and immatures during autumn migration (15 July to 30 September) at Creamer's Field Migration Station in Fairbanks, Alaska (1992–1998).

Species	Adults			Immatures			Z ^a
	<i>n</i>	Mean $\pm$ SE	Median	<i>n</i>	Mean $\pm$ SE	Median	
Alder Flycatcher	72	0.38 $\pm$ 0.59	0	300	0.52 $\pm$ 0.71	0	2.39*
Ruby-crowned Kinglet	84	1.49 $\pm$ 1.35	1	584	0.84 $\pm$ 0.93	1	4.26**
Gray-cheeked Thrush	41	1.68 $\pm$ 1.04	2	163	1.26 $\pm$ 0.95	1	2.30*
Swainson's Thrush	73	1.85 $\pm$ 1.09	2	569	0.93 $\pm$ 0.96	1	6.93**
American Robin	63	2.78 $\pm$ 1.59	3	166	1.37 $\pm$ 1.50	1	5.95**
Orange-crowned Warbler	410	1.62 $\pm$ 1.40	2	2,194	0.85 $\pm$ 0.99	1	10.68**
Yellow-rumped Warbler	241	1.45 $\pm$ 1.41	1	3,191	0.41 $\pm$ 0.70	0	13.88**
Yellow Warbler	65	1.64 $\pm$ 1.52	1	488	0.79 $\pm$ 1.07	0	4.54**
Blackpoll Warbler	32	1.56 $\pm$ 1.22	1	254	0.85 $\pm$ 0.94	1	3.29**
Wilson's Warbler	73	2.15 $\pm$ 1.36	2	609	1.00 $\pm$ 0.99	1	7.05**
American Tree Sparrow	391	2.44 $\pm$ 1.41	3	2,159	1.82 $\pm$ 1.42	2	7.73**
Savannah Sparrow	23	1.00 $\pm$ 1.13	1	417	0.86 $\pm$ 1.07	0	0.68
Fox Sparrow	32	1.45 $\pm$ 1.04	1	184	1.13 $\pm$ 1.12	1	2.25*
Lincoln's Sparrow	46	1.61 $\pm$ 1.54	1	977	1.01 $\pm$ 1.17	1	2.69*
White-crowned Sparrow	30	2.13 $\pm$ 1.14	2	329	0.75 $\pm$ 0.99	0	6.26**
Dark-eyed Junco	166	1.92 $\pm$ 1.53	2	1,828	0.95 $\pm$ 1.09	1	8.55**

^a Z values from Mann-Whitney *U*-test.

* $P < 0.05$, ** $P < 0.003$.

TABLE 3. Body condition (ratio of mass to wing chord) of adults and immatures during autumn migration (15 July to 20 September) at Creamer's Field Migration Station in Fairbanks, Alaska (1992–1998). ANCOVA models were used with age class as the main factor and time of day (time), daily low temperature, and night length on the date prior to capture as covariates.

Species	Body condition indices				Covariates					
	Adults		Immatures		Time		Low temperature		Night length	
	<i>n</i>	Mean	<i>n</i>	Mean	<i>b</i>	<i>F</i>	<i>b</i>	<i>F</i>	<i>b</i>	<i>F</i>
Alder Flycatcher	72	0.181	300	0.182	0.001	6.21	0.000	8.11*	0.003	27.22
Ruby-crowned Kinglet	84	0.115	584	0.115	0.001	55.86**	0.000	0.48	0.000	4.05*
Gray-cheeked Thrush	41	0.317	163	0.313	-0.001	0.28	0.000	0.1	0.003	1.50
Swainson's Thrush	73	0.319	569	0.304	0.001	11.17**	0.000	2.29	0.004	19.71**
American Robin	63	0.663	166	0.637	0.001	2.72	0.001	2.37	0.016	10.93**
Orange-crowned Warbler	410	0.159	2,194	0.158	0.001	165.85**	0.000	13.43**	0.001	54.93**
Yellow-rumped Warbler	241	0.181	3,194	0.176	0.001	105.58**	0.000	28.73	0.003	188.96**
Yellow Warbler	65	0.159	488	0.156	0.001	28.90**	0.000	2.145	0.003	62.20**
Blackpoll Warbler	32	0.174	254	0.169	0.001	14.67**	0.000	0.079	0.002	7.80*
Wilson's Warbler	73	0.140	609	0.137	0.001	43.45**	0.000	0.23	0.001	18.04**
American Tree Sparrow	391	0.240	2,159	0.240	0.002	129.32**	0.000	5.01*	0.007	466.20**
Savannah Sparrow	23	0.244	417	0.241	0.000	0.65	0.001	14.48**	0.003	24.13**
Fox Sparrow	32	0.426	184	0.419	0.002	3.50	0.000	9.29**	0.005	9.29**
Lincoln's Sparrow	46	0.268	977	0.263	0.001	15.19**	0.000	1.08	0.001	4.12*
White-crowned Sparrow	30	0.336	229	0.327	0.002	10.21**	0.000	0.36	0.001	0.09
Dark-eyed Junco	166	0.249	1,828	0.248	0.001	45.61**	0.000	1.66	-0.001	116.57**

* $P < 0.05$, ** $P < 0.003$ (significance level with Bonferroni adjustments).

vary among years. Time of capture had a significant positive effect on body condition in 11 of 16 species during autumn (Table 3). Negative effects were not found in any species. Overnight low temperature had a significant effect on body condition in just 4 of 16 species (or 6 at $\alpha = 0.05$), but night length affected body condition in 10 of 16 species (or 13 at $\alpha = 0.05$; Table 3). In sum, most age-related differences among autumn birds were accounted for by the environmental variables prevailing at time of capture.

Between-season differences.—Comparisons of fat scores (adults only) showed that 6 of 16 species had significantly higher fat loads in autumn than in spring (or 10 species at $P < 0.05$; Table 4). Ruby-crowned Kinglet was the only species with significantly higher fat loads in spring than in autumn (Table 4). Median fat scores for all species were low, ranging from 0 (no fat visible) to 3 (half of furculum filled with fat; Table 4).

When time, overnight temperature, and night length were included as covariates in ANCOVAs, five species (again, in adults only) showed higher body condition in autumn than in spring: Swainson's Thrush, American Robin, Orange-crowned Warbler, Yellow-rumped Warbler, and Fox Sparrow (Table 5). Two more species, Gray-cheeked Thrush and Yellow Warbler, showed the same pattern at $\alpha = 0.05$ (Table 4). Our ANCOVA

tests for interaction between season and year with time, temperature, and night length held constant showed no significant interaction (after Dunn-Sidak corrections) for any of the following species: Swainson's Thrush ($F = 2.76$, $df = 6$ and 262 , $P = 0.02$), American Robin ($F = 1.31$, $df = 6$ and 234 , $P = 0.26$), Orange-crowned Warbler ($F = 5.74$, $df = 6$ and 630 , $P = 0.06$), Yellow-rumped Warbler ($F = 1.45$, $df = 6$ and 141 , $P = 0.199$), and Fox Sparrow ($F = 0.54$, $df = 6$ and 73 , $P = 0.81$). Thus, no species had higher body-condition indices in spring when covariates were held constant.

We also present results for seasonal differences in body condition when immatures are included in the autumn sample (Table 6). Inclusion of immatures in analyses, though making our study more directly comparable to those in other regions that have not separated age groups, introduces additional variation that produces different species-level results. The larger sample sizes of immatures increases power to detect small differences in body-condition indices and is the most likely explanation for differing results. When immatures are included in these analyses, Alder Flycatcher, Wilson's Warbler, and Savannah Sparrow show higher spring condition indices; whereas Orange-crowned Warbler, Yellow-rumped Warbler, Yellow Warbler, and

TABLE 4. Differences in fat scores between spring and autumn (adults only) in passerine migrants at Creamer's Field Migration Station in Fairbanks, Alaska (1992–1998).

Species	Spring			Autumn			Z ^a
	<i>n</i>	Mean $\pm$ SE	Median	<i>n</i>	Mean $\pm$ SE	Median	
Alder Flycatcher	39	0.15 $\pm$ 0.43	0	72	0.38 $\pm$ 0.59	0	2.68*
Ruby-crowned Kinglet	46	2.30 $\pm$ 1.53	2	84	1.49 $\pm$ 1.35	1	2.81**
Gray-cheeked Thrush	98	1.04 $\pm$ 0.88	1	41	1.68 $\pm$ 1.04	2	3.33**
Swainson's Thrush	250	1.02 $\pm$ 0.85	1	73	1.85 $\pm$ 1.09	2	5.96**
American Robin	180	0.53 $\pm$ 0.64	0	63	2.77 $\pm$ 1.59	3	10.13**
Orange-crowned Warbler	220	1.30 $\pm$ 1.33	1	410	1.62 $\pm$ 1.40	2	2.73*
Yellow-rumped Warbler	489	1.26 $\pm$ 1.22	1	241	1.45 $\pm$ 1.41	1	1.40
Yellow Warbler	124	0.75 $\pm$ 0.96	0	65	1.65 $\pm$ 1.52	1	3.93**
Blackpoll Warbler	46	1.37 $\pm$ 1.06	1	32	1.56 $\pm$ 1.22	1	0.73
Wilson's Warbler	225	1.42 $\pm$ 1.23	1	73	2.15 $\pm$ 1.36	2	3.94**
American Tree Sparrow	83	2.19 $\pm$ 1.16	2	391	2.44 $\pm$ 1.41	3	2.56*
Savannah Sparrow	166	1.11 $\pm$ 1.13	1	23	1.06 $\pm$ 1.12	1	0.47
Fox Sparrow	45	1.33 $\pm$ 1.26	1	57	1.46 $\pm$ 1.04	1	2.25*
Lincoln's Sparrow	61	1.11 $\pm$ 1.24	1	46	1.61 $\pm$ 1.54	1	1.64
White-crowned Sparrow	81	1.29 $\pm$ 1.26	1	30	2.13 $\pm$ 1.14	2	3.26**
Dark-eyed Junco	194	1.68 $\pm$ 1.43	2	166	1.92 $\pm$ 1.53	2	1.26

^a Z values from Mann-Whitney U-test.

* $P < 0.05$, ** $P < 0.003$.

TABLE 5. Differences in adult body condition (ratio of mass to wing chord) between spring (25 April to 15 June) and autumn migration (15 July to 20 September) at Creamer's Field Migration Station in Fairbanks, Alaska (1992–1998). ANCOVA models were used with age class as main factors and time of capture (time), daily low temperature, and night length on the date of capture as covariables.

Species	Season				Covariates					
	Spring		Autumn		Time of capture		Low temperature		Night length	
	<i>n</i>	Mean	<i>n</i>	Mean	<i>b</i>	<i>F</i>	<i>b</i>	<i>F</i>	<i>b</i>	<i>F</i>
Alder Flycatcher	39	0.186	72	0.181	0.000	0.08	-0.001	9.12**	-0.001	1.55
Ruby-crowned Kinglet	46	0.117	84	0.115	0.001	5.20	0.000	2.24	0.000	1.18
Gray-cheeked Thrush	98	0.290	41	0.317	0.002	3.92	0.001	2.85	0.005	46.06**
Swainson's Thrush	250	0.286	73	0.319	0.001	4.37*	0.001	3.38	0.000	0.07**
American Robin	180	0.587	63	0.613	0.001	0.59	0.000	0.20	-0.007	3.93***
Orange-crowned Warbler	234	0.155	437	0.159	0.001	68.40**	0.001	0.40	0.001	26.09**
Yellow-rumped Warbler	489	0.176	241	0.181	0.001	10.23**	0.000	4.05	0.003	30.79**
Yellow Warbler	124	0.156	65	0.159	0.001	9.80**	0.000	0.14	0.002	9.50**
Blackpoll Warbler	62	0.168	32	0.174	0.002	12.45**	0.001	4.64*	0.001	4.86*
Wilson's Warbler	225	0.138	70	0.140	0.002	62.26**	0.000	0.44	0.000	0.00
American Tree Sparrow	83	0.228	389	0.240	0.002	44.37**	-0.001	12.47**	0.000	6.16*
Savannah Sparrow	166	0.241	23	0.243	0.001	4.18*	0.000	0.02	0.001	0.86
Fox Sparrow	45	0.397	57	0.426	0.002	4.09*	0.001	1.56	0.005	24.26**
Lincoln's Sparrow	61	0.261	46	0.268	0.001	0.81	0.000	1.37	0.001	0.07
White-crowned Sparrow	81	0.329	30	0.336	0.002	3.87*	0.000	0.07	0.007	6.35*
Dark-eyed Junco	194	0.241	166	0.249	0.001	6.76*	0.000	0.48	-0.001	12.65**

* $P < 0.05$, ** $P < 0.003$ (significance level with Bonferroni adjustments).

TABLE 6. Differences in body condition (ratio of mass to wing chord) between spring (25 April to 15 June) and autumn migration (15 July to 20 September) at Creamer's Field Migration Station in Fairbanks, Alaska (1992–1998). ANCOVA models were used with season as main factors and time of capture (time), daily low temperature, and night length on the date of capture as covariates. This table includes adults and immatures in the autumn sample, unlike Table 5.

Species	Season				Covariates						
	Spring		Autumn		Time		Overnight low		Night length		
	n	Mean	n	Mean	F	b	F	b	F	b	F
Alder Flycatcher	39	0.186	372	0.182	25.74**	0.001	5.76*	-0.001	37.19**	0.001	2.79
Ruby-crowned Kinglet	46	0.117	668	0.115	5.52*	0.001	50.44**	0.000	6.73*	0.000	0.13
Gray-cheeked Thrush	98	0.290	204	0.313	3.06	0.000	0.01	0.000	1.02	0.005	48.49**
Swainson's Thrush	256	0.286	642	0.306	1.90	0.001	18.78**	0.000	1.05	0.005	23.63**
American Robin	180	0.587	229	0.644	2.13	0.001	0.89	0.000	0.07	0.005	2.80
Orange-crowned Warbler	220	0.155	2,604	0.158	10.97**	0.001	178.74**	0.000	7.76*	0.004	53.10**
Yellow-rumped Warbler	489	0.176	3,432	0.177	78.01**	0.001	102.13**	0.000	7.45*	0.003	168.57**
Yellow Warbler	134	0.156	553	0.156	45.97**	0.001	39.84**	0.000	3.75	0.003	63.93**
Blackpoll Warbler	62	0.168	286	0.170	6.55*	0.001	24.54**	0.000	0.73	0.001	6.33*
Wilson's Warbler	225	0.138	682	0.137	13.53**	0.001	86.98**	0.000	10.76**	0.000	0.58
American Tree Sparrow	83	0.228	2,550	0.239	119.86**	0.002	174.15**	0.000	9.13**	0.002	108.58**
Savannah Sparrow	166	0.242	440	0.241	14.74**	0.001	4.45*	0.000	5.920*	0.003	17.85**
Fox Sparrow	45	0.397	241	0.421	1.52	0.002	5.55*	0.000	0.596	0.005	30.20**
Lincoln's Sparrow	61	0.261	1,023	0.263	0.44	0.001	16.65**	0.000	0.664	0.001	4.20*
White-crowned Sparrow	81	0.329	359	0.327	2.20	0.002	11.80**	0.000	0.360	0.002	1.92
Dark-eyed Junco	194	0.241	1,994	0.248	6.58*	0.001	45.22**	0.000	1.210	-0.001	111.31**

* $P < 0.05$, ** $P < 0.003$ (significance level with Bonferroni adjustments).

American Tree Sparrow have higher autumn condition indices.

Analysis of adults only (which possess fewer complicating variables present in autumn, such as molt and foraging inexperience; Table 5) enable us to address more cleanly the role of ambient environmental factors in relation to fat deposition, and we therefore focus on adult-only results below.

DISCUSSION

Most species examined at our study site carried relatively low fat loads upon arrival in interior Alaska in spring (Table 2). King et al. (1965) found similar results in an intensive study of White-crowned Sparrows in central Alaska. Those findings are contrary to results from the subarctic of Scandinavia, which showed that some migrants arrived with high fat levels in spring (Sandberg 1996, Fransson and Jakobsson 1998). King et al. (1965) suggested that White-crowned Sparrows may not restore the fat depleted during the final migratory flight in spring, and that perhaps the tendency to maintain increased reserves diminishes as migration progresses in spring in northwestern North America.

Although hyperphagia is well documented during and prior to migration (Berthold 1975), it is not known whether it persists until birds reach their breeding grounds. Our data suggest that, in interior Alaska, passerines tend to follow the pattern that King et al. (1965) described for the White-crowned Sparrow, and that Dunn (2002) described for several species at different locations in Canada: migrants are depositing only the fat they need for migration and daily energetic requirements; little or no "insurance" fat is being deposited; and there is a correspondingly lower potential demand placed on resources at stopover sites used just before arrival on breeding grounds. Another consideration, however, is that the amount of energy stored during spring migration is dependent on resource availability along the migration route—a bird cannot store fat for insurance if food is not readily available. Perhaps stopover sites during the final stages of spring migration to interior Alaska do not provide sufficient resources to enable fat deposition beyond what is necessary to fuel the final stages of migration.

A similar situation prevailed in autumn. The

generally low levels of fat carried by migrants at that time of year (Table 2) suggest that they must be paying most of the energetic costs of their long-distance migrations with resources obtained en route to their wintering grounds.

Age-related differences in autumn fattening.—Adults had significantly higher fat stores than immatures in 11 of 16 species. Our results are similar to those of many previous studies that have documented adults that were heavier than immature birds at migratory stopover sites (Morris et al. 1996, Woodrey and Moore 1997, Jones et al. 2002). However, at our study site, adults departed significantly later than immatures in many of those species (Benson and Winker 2001), and higher fat loads in adults could be attributed to longer nights and colder temperatures later in the season in all but two species (Table 3). Adult Swainson's Thrushes and Yellow-rumped Warblers had higher mean body-condition indices than immatures in autumn, and the differences could not be explained by daily environmental variables. Thus, although most species do not show age-related differences in autumn fattening, some do. We cannot determine whether that reflects genuine species-level variation in autumn fat-deposition strategies between age classes or simply superior performance in adults of some species because of experience.

"Spring fatter" hypothesis.—Only 1 of the 16 species in our study showed higher relative fat loads in spring than in autumn (Ruby-crowned Kinglet), and that difference was not reflected in the between-season comparison of body condition (Tables 4 and 5). In a direct comparison of fat loads alone, the opposite situation appeared to prevail: many species seemed to carry heavier fat loads in autumn. However, when environmental variables prevailing at time of capture were analyzed as covariates, those differences disappeared in all but five species. King et al. (1965) interpreted an increase in fat deposition among White-crowned Sparrows prior to migration from central Alaska as premigratory fattening; however, he did not evaluate the influence of daily variables known to affect fat storage. Lower overnight temperatures and increased night length in autumn accounted for most of the autumnal increase in fat and body condition that we observed. We could not examine variance in food availability, but that factor may also influence fat stores (Lima 1986, Houston

and McNamara 1993, Pravosudov and Grubb 1997), and it could not be ruled out as a possible mechanism for the higher autumn fat stores found among 5 of the 16 species. Thus, again, although this may indicate some species-level variation in fat-deposition strategies among migrants at this latitude, local factors alone could be responsible for that variation.

The hypothesis that migrants should carry higher levels of fat onto their breeding grounds in spring for insurance against unpredictable resources or to possibly increase reproductive success is not valid for the species studied at this site, which clearly suggests that the hypothesized benefits of such fat deposition are outweighed by the costs (whether temporal or energetic). It also suggests that, as King et al. (1965) alluded, hyperphagia may not persist during the final stages of high-latitude migration in spring in northwestern North America. Just as importantly, however, the species examined did not have high fat levels in either season. At this latitude, most of the variation in passerine fat-deposition between seasons and between age classes in autumn appears to be explained by environmental variables prevailing when capture occurred: time of day, overnight low temperatures, and night length. Our results indicate that passerine migrants near their high-latitude breeding grounds in Alaska have fat-deposition strategies similar to those of many species at stopover sites across Canada (Dunn 2002). Seasonal fat-deposition strategies appear to be responding to energetic needs at the level of daily maintenance, rather than to hypothesized insurance needs in spring or to the forthcoming needs of a long-distance migration in autumn.

ACKNOWLEDGMENTS

We thank the many volunteers, interns, and staff who have made contributions to the data collection process at the Alaska Bird Observatory (ABO); N. D. DeWitt, T. H. Pogson, and S. K. Springer, in particular, banded thousands of birds here. Members of ABO funded this research, together with large contributions from ABR Inc. Environmental Research and Services, Alaska Department of Fish and Game, ARCO Alaska, the Bureau of Land Management, Exxon Company USA, the Skaggs Foundation, and the U.S. Fish and Wildlife Service. A.-M.B. also thanks the Wilson Ornithological Society for the Paul A. Stewart Award. E. C. Murphy

and E. A. Rexstad offered statistical advice and improved the manuscript with their insightful comments. Thanks to M. Katti, E. Dunn, and two anonymous reviewers for helpful reviews. The Alaska Climate Research Center data we used is available at climate.gi.alaska.edu/FaiData/Fai0592.html.

LITERATURE CITED

- BEDNEKOFF, P. A., H. BIEBACH, AND J. R. KREBS. 1994. Great Tit fat reserves under unpredictable temperatures. *Journal of Avian Biology* 25:156–160.
- BEDNEKOFF, P. A., AND J. R. KREBS. 1995. Great Tit fat reserves: Effects of changing an unpredictable feeding day length. *Functional Ecology* 9:457–462.
- BENSON, A.-M., AND K. WINKER. 2001. Timing of breeding range occupancy among high-latitude passerine migrants. *Auk* 118:513–519.
- BERTHOLD, P. 1975. Migration: Control and metabolic physiology. Pages 77–128 in *Avian Biology*, no. 5 (D. S. Farner and J. R. King, Eds.). Academic Press, New York.
- BERTHOLD, P. 1996. *Control of Bird Migration*. Chapman and Hall, London.
- BIERMANN, G. C., AND S. G. SEALY. 1984. Seasonal dynamics of body mass of insectivorous passerines breeding on the forested dune ridge, Delta Marsh, Manitoba. *Canadian Journal of Zoology* 63:1675–1682.
- BLEM, C. R. 1976. Patterns of lipid storage and utilization in birds. *American Zoologist* 16:671–684.
- BLEM, C. R. 1990. Avian energy storage. Pages 59–113 in *Current Ornithology*, no. 7 (D. M. Power, Ed.). Plenum Press, New York.
- CHERRY, J. D. 1982. Fat deposition and length of stopover of migrant White-crowned Sparrows. *Auk* 99:725–732.
- COOPER, B. A., AND R. J. RITCHIE. 1995. The altitude of bird migration in east-central Alaska: A radar and visual study. *Journal of Field Ornithology* 66:590–608.
- DUNN, E. H. 2002. A cross-Canada comparison of mass change in birds during migration stopover. *Wilson Bulletin* 114:368–379.
- FARMER, A. H., AND J. A. WIENS. 1999. Models and reality: Time-energy trade-offs in Pectoral Sandpiper (*Calidris melanotos*) migration. *Ecology* 80:2566–2580.
- FRANSSON, T., AND S. JAKOBSSON. 1998. Fat storage

- in male Willow Warblers in spring: Do residents arrive lean or fat? *Auk* 115:759–763.
- GWINNER, E. 1990. Circannual rhythms in bird migration: Control of patterns and interactions with photoperiod. *In* *Bird Migration: Physiology and Ecophysiology* (E. Gwinner, Ed.). Springer-Verlag, Berlin.
- HAILMAN, J. P. 1965. Notes on quantitative treatments of subcutaneous lipid data. *Bird-Banding* 36:14–20.
- HELMS, C. W., AND W. H. DRURY, JR. 1960. Winter and migratory weight and fat field studies on some North American buntings. *Bird-Banding* 31:1–40.
- HOUSTON, A. I., AND J. M. McNAMARA. 1993. A theoretical investigation of the fat reserves and mortality levels of small birds in winter. *Ornis Scandinavica* 24:205–219.
- HUSSELL, D. J. T. 1969. Weight loss of birds during nocturnal migration. *Auk* 86:75–83.
- JONES, J., C. M. FRANCIS, M. DREW, S. FULLER, AND M. W. S. NG. 2002. Age-related differences in body mass and rates of mass gain of passerines during autumn migratory stopover. *Condor* 104:49–58.
- KATTI, M., AND T. PRICE. 1999. Annual variation in fat storage by a migrant warbler overwintering in the Indian tropics. *Journal of Animal Ecology* 68:815–823.
- KESSEL, B. 1984. Migration of Sandhill Cranes, *Grus canadensis*, in east-central Alaska, with routes through Alaska and western Canada. *Canadian Field-Naturalist* 98:279–282.
- KETTERSON, E. D., AND V. NOLAN, JR. 1978. Overnight weight loss in Dark-eyed Juncos (*Junco hyemalis*). *Auk* 95:755–758.
- KING, J. R., S. BARKER, AND D. S. FARNER. 1963. A comparison of energy reserves during autumnal and vernal migratory periods in the White-crowned Sparrow, *Zonotrichia leucophrys gambelii*. *Ecology* 44:513–521.
- KING, J. R., D. S. FARNER, AND M. L. MORTON. 1965. The lipid reserves of White-crowned Sparrows on the breeding ground in central Alaska. *Auk* 82:236–252.
- KREMENTZ, D. G., AND G. W. PENDLETON. 1990. Fat scoring: Sources of variability. *Condor* 92:500–507.
- LEHIKONEN, E. 1987. Seasonality of the daily weight cycle in wintering passerines and its consequences. *Ornis Scandinavica* 18: 216–226.
- LEHIKONEN, E., AND J. HAKALA. 1988. Variation in weight of migratory Dippers (*Cinclus cinclus*) in their Finnish winter quarters. *Bird Study* 35:101–108.
- LIMA, S. L. 1986. Predation risk and unpredictable feeding conditions: Determinants of body mass in birds. *Ecology* 67:377–385.
- McINTYRE, C. L., AND R. E. AMBROSE. 1999. Raptor migration in autumn through the Upper Tanana River Valley, Alaska. *Western Birds* 30:33–38.
- McWILLIAMS, S. R., AND W. H. KARASOV. 2001. Phenotypic flexibility in digestive system structure and function in migratory birds and its ecological significance. *Comparative Biochemistry and Physiology* 128:579–593.
- MORRIS, S. R., D. W. HOLMES, AND M. E. RICHMOND. 1996. A ten-year study of the stopover patterns of migratory passerines during fall migration on Appledore Island, Maine. *Condor* 98:395–409.
- MUELLER, H. C., AND D. D. BERGER. 1966. Analyses of weight and fat variations in transient Swainson's Thrushes. *Bird-Banding* 37:83–112.
- NISBET, I. C. T., W. H. DRURY, JR., AND J. BAIRD. 1963. Weight loss during migration. Part I: Deposition and consumption of fat in the Blackpoll Warbler *Dendroica striata*. *Bird-Banding* 34:107–139.
- PIERSMA, T., G. A. GUDMUNDSSON, AND K. LILLIENDAHL. 1999. Rapid changes in the size of different functional organ and muscle groups during refueling in a long-distance migrating shorebird. *Physiological and Biochemical Zoology* 72:405–415.
- PILASTRO, A., AND F. SPINA. 1997. Ecological and morphological correlates of residual fat reserves in passerine migrants at their spring arrival in southern Europe. *Journal of Avian Biology* 28:309–318.
- PRAVOSUDOV, V. V., AND T. C. GRUBB, JR. 1997. Management of fat reserves and food caches in Tufted Titmice (*Parus bicolor*) in relation to unpredictable food supply. *Behavioral Ecology* 8:332–339.
- ROGERS, C. M. 1991. An evaluation of the method of estimating body fat in birds by quantifying visible subcutaneous fat. *Journal of Field Ornithology* 62:349–356.
- ROGERS, C. M. 2003. New and continuing issues with using visible fat classes to estimate fat stores of birds. *Journal of Avian Biology* 34: 129–133.

- ROGERS, D. T., JR., AND E. P. ODUM. 1964. Effect of age, sex, and level of fat deposition on major body components in some wood warblers. *Auk* 81:505–513.
- SANDBERG, R. 1996. Fat reserves of migrating passerines at arrival on the breeding grounds in Swedish Lapland. *Ibis* 138:514–524.
- SANDBERG, R., AND F. R. MOORE. 1996. Fat stores and arrival on the breeding grounds: Reproductive consequences for passerine migrants. *Oikos* 77:577–581.
- SOKAL, R. R., AND F. J. ROHLF. 1995. *Biometry*, 3rd ed. W. H. Freeman, New York.
- WINKER, K. 1995. Autumn stopover on the Isthmus of Tehuantepec by woodland Nearctic–Neotropic migrants. *Auk* 112:690–700.
- WINKER, K., D. W. WARNER, AND A. R. WEISBROD. 1992a. The Northern Waterthrush and Swainson's Thrush as transients at a temperate inland stopover site. Pages 384–402 in *Ecology and Conservation of Neotropical Migrant Landbirds* (J. M. Hagan III and D. W. Johnston, Eds.). Smithsonian Institution Press, Washington, D.C.
- WINKER, K., D. W. WARNER, AND A. R. WEISBROD. 1992b. Daily mass gains among woodland migrants at an inland stopover site. *Auk* 109:853–862.
- WITTER, M. S., AND I. C. CUTHILL. 1993. The ecological costs of avian fat storage. *Philosophical Transactions of the Royal Society of London, Series B* 340:73–92.
- WOODREY, M. S., AND F. R. MOORE. 1997. Age-related differences in the stopover of fall landbird migrants on the coast of Alabama. *Auk* 114:695–707.

Associate Editor: S. G. Sealy