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GEOGRAPHIC VARIATION IN METABOLIC SEASONAL ACCLIMATIZATION IN HOUSE FINCHES[1]

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Abstract. Seasonal acclimatization in small passerine birds is primarily a metabolic process, yet the physiological mechanism is incompletely understood. This study draws on both original and previously published data to examine physiological characteristics associated with seasonal acclimatization in House Finches (Carpodacus mexicanus) from southern California (CA), Colorado (CO), and Michigan (MI). House Finches from MI and CO demonstrate metabolic seasonal acclimatization that is not found in CA birds. The MI and CO birds show seasonal fattening and greater standard metabolic rates than CA individuals. Results from body composition analyses and enzyme activity determinations suggest that seasonal changes in fat stores and catabolic capacity are associated with acclimatization in both CO and MI birds. However, the seasonal patterns of several other physiological parameters reveal differences between MI and CO populations. For instance, the magnitude of winter fattening is much greater in MI than CO birds, and MI House Finches show seasonal changes in peak metabolic rate and lean mass that are absent in CO individuals. These findings indicate that MI birds, in the introduced eastern distribution, and CO birds, in the original western distribution, may employ different physiological mechanisms for seasonal acclimatization. Alternatively, the differences between MI and CO birds may reflect direct or indirect responses to the markedly different altitudes of the locations. The results from this study reinforce the potential dangers of extrapolating findings from single populations to a larger scale in widely distributed species.

Key words: Biogeography; body composition; fat catabolism; House Finch; lipid mobilization; thermoregulation.

INTRODUCTION

House Finches are native to western North America. Their western range extends from northern Mexico to southern British Columbia, through Wyoming and Colorado, to the Great Plains in western Kansas, western Nebraska, western Oklahoma, and central Texas (Aldrich and Weske 1978). Between the turn of the century and 1940, House Finches were transported to the eastern United States and sold as "Hollywood finches" and "red-headed linnets" by pet dealers (Elliott and Arbib 1953). Presumably fearing prosecution for this illegal practice due to the enactment of the Migratory Bird Act, pet store owners released an unknown number of House Finches on Long Island, New York in 1940. This introduction into the eastern United States has provided an unusual natural experiment regarding seasonal acclimatization.

The origin and early expansion of the eastern population from Long Island was documented by Elliott and Arbib (1953). Within the past 25 years, the eastern population has dramatically expanded its range along the Atlantic Seaboard from New England to South Carolina, and continues to expand its range westward throughout the Midwest toward the eastern edge of the western population (Bock and Lepthien 1976, Mundinger and Hope 1982, Root 1988). The 1940 founder group of the eastern population of House Finches is presumed to have originated in southern California, a view supported by morphological analyses of museum specimens (Aldrich and Weske 1978). If this view is correct, then the original members of the eastern population and their descendants have been exposed to more rigorous winter conditions than those under which their southern California ancestors existed (Root et al. 1991).

Seasonal acclimatization in small passerine birds is primarily a metabolic process, resulting in greater resistance to cold temperatures during winter than other seasons (Dawson and Carey 1976, Dawson et al. 1983, Swanson 1990a, O'Connor 1995a). House Finches have played a significant role in previous studies of avian seasonal acclimatization, in part because of the un-

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TABLE 1. Coordinates, elevations, and climatic conditions in the geographic regions examined in this study. The Santa Ana, CA, weather station is within ca. 15 km of the Irvine, CA, field site. The CA House Finches were captured in Riverside (Dawson et al. 1983, 1985) or Irvine (this study). Climatological data represent long-term (>45 y) averages. (Source: U.S. Weather Bureau 1964).

	Ann Arbor, MI	Riverside, CA	Santa Ana, CA	Boulder, CO
Latitude	42°18′N	33°57′N	33°45′N	40°00′N
Longitude	83°43′W	117°23′W	117°52′W	105°16′W
Elevation (m)	274	256	41	1,671
January temperature (°C)				
Average minimum	−8.3	3.2	3.9	−6.4
Average maximum	−0.3	18.8	24.2	7.1
Daily average	−4.6	11.6	13.3	0.3
May temperature (°C)				
Average minimum	8.3	9.6	10.8	6.9
Average maximum	20.3	26.2	24.2	20.7
Daily average	14.4	18.6	17.9	14.8

usual origin of the eastern population. Within the western range of the species, birds in Riverside, California, show no evidence of increased cold resistance during winter, whereas those in Boulder, Colorado, do (Dawson et al. 1983). Thus, seasonal acclimatization exists in some parts of the western distribution, but House Finches on the coastal slope of southern California normally do not show any signs of acclimatization. However, descendents of southern California House Finches in Ann Arbor, Michigan, part of the introduced eastern distribution, do exhibit seasonal acclimatization (O'Connor 1995a). The metabolic seasonal acclimatization found in both Colorado and Michigan house finches involves an enhanced ability to sustain elevated metabolic rates while shivering in response to cold stress (Dawson et al. 1983; O'Connor 1995a). The mechanism for seasonal acclimatization is incompletely understood, but may involve seasonal adjustments in one or more of the following: 1) stores of energy substrates, 2) ability to mobilize such substrates, or 3) capacity to catabolize them (Marsh and Dawson 1989). Evidence supporting each of these possibilities exists for lipid metabolism of eastern House Finches. That is, seasonal adjustments in fat storage, mobilization, and catabolism are associated with acclimatization in House Finches in Michigan (O'Connor 1995a, 1995b).

This study presents original data and draws on results from previous work to examine seasonal and geographic variation in physiological characteristics potentially relevant to acclimatization. This examination involves House Finch populations from the following three locations: 1) Ann Arbor, Michigan (hereafter MI), 2) Riverside and Irvine, two cities in southern California (hereafter CA), and 3) Boulder, Colorado (hereafter CO). These populations differ not only in the extent to which seasonal acclimatization is present, but also in the climatic conditions they face (Table 1). Results from MI House Finches are drawn primarily from previous studies (O'Connor 1995a, 1995b); only the hematocrit data have not been previously reported. Results from Riverside and CO House Finches are from the studies of Dawson et al. (1983, 1985), and those from Irvine birds are original data.

This synthesis will examine variation in metabolic characteristics, body composition, factors associated with lipid mobilization, and catabolic capacity in the MI, CA, and CO populations. The following specific questions will be addressed: 1) In which physiological characteristics do populations that demonstrate seasonal acclimatization (MI and CO) differ from the population that normally does not (CA)?, and 2) Are there differences between MI and CO birds in the physiological characteristics associated with seasonal acclimatization?

METHODS

COLLECTION OF BLOOD AND MUSCLE SAMPLES

House Finches were captured in Irvine, Orange County, CA using a feeder trap. All individuals were caught within 1.5 h after sunrise during January ("winter") or May ("late spring") in 1992

and 1993. After each bird was weighed, a blood sample of ca. 750 μl was drawn by means of cardiac puncture and the bird was then killed by thoracic compression. Approximately 50 μl of the blood sample was transferred to a heparinized microhematocrit tube and the remainder to a microcentrifuge tube containing EDTA (anticoagulant) and leupeptin (protease inhibitor) as previously described (O'Connor 1995b). The blood in the microcentrifuge tube was immediately spun in an International Clinical Centrifuge, whereas the smaller sample in the microhematocrit tube was kept cool and spun within 20 min. After spinning, plasma was collected from the larger blood sample and stored on dry ice in a second microcentrifuge tube, which also contained EDTA and leupeptin. These plasma samples, used for determinations of albumin and glucagon levels, were kept on dry ice until they could be transferred to −70°C. The packed cells were discarded. Hematocrit, used as a measure of blood oxygen capacity, was determined on the small blood sample in the microhematocrit tube and those tubes were then discarded.

While the blood was being centrifuged, the right pectoralis muscle was dissected out, and stored in a cryogenic tube in liquid nitrogen. The elapsed time between bird capture and freezing the dissected muscle was less than 15 minutes, a handling time that does not affect activities of the assayed enzymes (O'Connor and Root 1993). Within one week of collection, both the muscle and the plasma samples were transported to Ann Arbor, Michigan, where they were stored at −70°C until assays were performed. During the time between sample collection and storage at −70°C (including transport time), muscle and plasma samples were maintained in liquid nitrogen and on dry ice, respectively. The storage period at −70°C did not exceed eight months.

Seasonal variation in hematocrit values were also examined in House Finches captured in Washtenaw County, MI during winter and late spring. These individuals were also captured within 1.5 h after sunrise and hematocrit determined in the manner described above. None of the hematocrit values reported have been corrected for plasma possibly trapped in the red cell portion.

EXPERIMENTAL PROTOCOLS

Plasma levels of glucagon, the primarily lipolytic hormone in birds (Hazelwood 1984), and albumin, a potentially limiting lipid transporter molecule (Weber 1988), were determined to assess capacity for lipid mobilization. Plasma concentrations of albumin were measured using a kit from Sigma (St. Louis, Mo.) and glucagon levels were determined using a heterologous, double-antibody radioimmunoassay. Details of both protocols have been described previously (O'Connor 1995*b*).

Activities of citrate synthase (CS; Enzyme Commission 4.1.3.7) and β-hydroxyacyl-CoA dehydrogenase (β-HOAD; E.C. 1.1.1.35) were used as indicators of the total aerobic capacity and capacity for β-oxidation of the pectoralis muscle, respectively (Newsholme and Start 1973, Marsh 1981). Activities were determined according to a protocol described previously (O'Connor 1995b). Briefly, minced muscles were thawed, weighed, and then homogenized in 10 volumes (vol/wt) of 100 mM potassium phosphate buffer with 2 mM ethylenediaminetetraacetic acid (EDTA; pH = 7.3 at 0°C). Homogenates were sonicated with a Branson sonifier for three 15-s intervals separated by 45-s pauses. Enzyme activities were determined spectrophotometrically, under saturating substrate concentrations following Olson's (1990) modifications of the protocols of Srere (1969) and Bass et al. (1969) for CS and β-HOAD, respectively. Duplicate or triplicate assays were performed for each enzyme and the averaged mass-specific results are presented as μmol product $(g \cdot min)^{-1}$.

STATISTICS

Two-way ANOVA was used to examine seasonal, geographical, and interactive differences in hematocrit, enzyme activities, albumin levels, and glucagon titers. Means are presented with their respective standard errors. All statistics were computed using Systat 5.0 and significance was accepted at the 0.05 level.

For geographic comparisons in which only summary statistics were available in the literature, two-tailed *t*-tests of means for a single population were employed to compare mean values. For comparisons among geographic locations, seasonal means at a given location were pooled if they did not differ significantly. Comparisons among three or more means were analyzed by the Tukey-Kramer Method. The statistical procedures used are described by Sokal and Rohlf (1981).

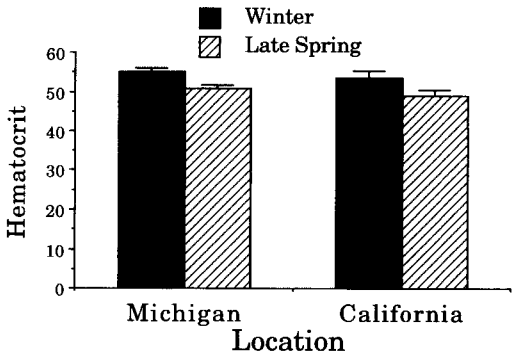

FIGURE 1. Seasonal changes in hematocrit values of House Finches captured in Ann Arbor, MI and Irvine, CA. Means ± SE are presented. Results of statistical analysis are presented in the text.

RESULTS

HEMATOCRIT

Hematocrit values of House Finches captured in MI were 55.1 ± 0.8 (n = 28) and 50.9 ± 0.8 (n = 25) during winter and late spring, respectively. Those of CA House Finches were 53.5 ± 1.8 (n = 11) and 49.0 ± 1.5 (n = 17) during winter and late spring, respectively (Fig. 1). A two-way ANOVA indicated no significant interaction effect ($P > 0.8$) and no significant effect of location ($P > 0.13$). However, hematocrit levels during winter were significantly greater than during late spring at both locations ($P < 0.001$).

PLASMA LEVELS OF ALBUMIN AND GLUCAGON

Plasma albumin concentrations of CA House Finches were 2.05 ± 0.22 and 2.41 ± 0.24 g/dL during winter and late spring, respectively (Table 2). These were combined with previous results from MI individuals (O'Connor 1995b) and analyzed using a two-way ANOVA. There was not a significant interaction effect ($P > 0.25$), nor were significant effects of season ($P > 0.94$) or location ($P > 0.07$) detected.

Glucagon levels of CA House Finches were 1,564 ± 201 and 1,382 ± 124 pg/ml during winter and late spring, respectively (Table 2). Again, these results were combined with previous results from MI individuals (O'Connor 1995b) and analyzed. As was the case for albumin levels, no significant interaction effect ($P > 0.12$), seasonal effect ($P > 0.84$), nor effect of location ($P > 0.07$) was detected.

CATABOLIC CAPACITY

Activity of citrate synthase (CS) in CA House Finch pectoralis muscle was 145.8 ± 4.5 and 136.7 ± 4.5 μmol product $(g \cdot min)^{-1}$ during winter (n = 17) and late spring (n = 18), respectively (Fig. 2). When combined with CS activity determinations from MI individuals (O'Connor 1995b), a two-way ANOVA indicated no significant interaction effect ($P > 0.8$), but significant effects of both season ($P < 0.03$) and geographic location ($P < 0.01$). Pectoralis muscle CS activity was greater in MI than CA House Finches, and greater in winter than late spring at both locations (Fig. 2). The significant seasonal effect ($P < 0.03$) indicated by the two-way ANOVA contrasts with indications of separate t-tests on each population, which suggest that the seasonal variation is not significant in either CA ($P > 0.15$) or MI ($P > 0.08$; O'Connor 1995b). The contrasting P-values presumably are a consequence of the greater total sample size, resulting in increased statistical power, of the two-way ANOVA.

Activity of β-hydroxyacyl-CoA dehydrogenase (β-HOAD) in CA individuals was 12.4 ± 0.8 and 13.2 ± 0.9 μmol product $(g \cdot min)^{-1}$ during winter (n = 15) and late spring (n = 16), respectively. When combined with β-HOAD determinations from MI house finches (O'Connor 1995b), a two-way ANOVA indicated no signif-

TABLE 2. Seasonal variation in plasma levels of albumin and glucagon for House Finches from Michigan (MI) and southern California (CA). For both albumin and glucagon levels, two-way ANOVAs indicated no significant interactions, and no significant effects of either season or location. Sample sizes are in parentheses. Means (±SE) are presented.

	Michigan		California	
	Winter	Late spring	Winter	Late spring
Albumin (g/dl)	3.03 ± 0.27 (20)	2.63 ± 0.32 (15)	2.05 ± 0.22 (6)	2.41 ± 0.24 (13)
Glucagon (pg/ml)	1,598 ± 97 (20)	1,833 ± 135 (16)	1,564 ± 201 (13)	1,382 ± 124 (18)
Reference	O'Connor 1995b		O'Connor, this study	

icant interaction ($P > 0.5$) and no significant seasonal variation ($P > 0.13$), but a significant effect of location ($P < 0.001$). Thus, although mass-specific β-HOAD activity did not vary seasonally in either location, MI values were substantially greater than those of CA individuals (Fig. 2). "Total" (per muscle) enzyme activities were not evaluated because pectoralis masses were not available for CA birds.

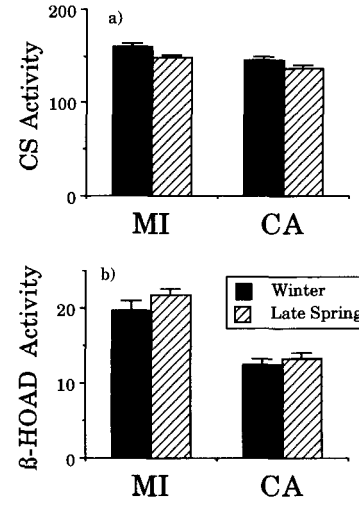

FIGURE 2. Seasonal variation in pectoralis muscle enzyme activities of House Finches from Michigan and southern California. Mass-specific activities of a) citrate synthase (CS) and b) β-hydroxyacyl-CoA dehydrogenase (β-HOAD) are presented as μmol product $(g \cdot min)^{-1}$. Means ± SE values are presented. See text for results of statistical analyses.

DISCUSSION

Winter acclimatization in small passerine birds involves physiological adjustments resulting in greater "thermogenic endurance," the capacity to sustain elevated metabolic rates while shivering (Dawson and Carey 1976, Dawson et al. 1983, O'Connor 1995a). House Finches show considerable geographic variation in the magnitude of seasonal acclimatization (Dawson et al. 1983). The results from this and previous studies (e.g., Dawson et al. 1983; Dawson et al. 1985; O'Connor 1995a, 1995b) provide seasonal comparisons of physiological characteristics that may be involved in seasonal acclimatization.

METABOLIC CHARACTERISTICS

The elevated hematocrit (Hct) levels found in House Finches during winter (Fig. 1) raises the possibility that increased blood oxygen capacity may represent an avian response to cold, through increased oxygen delivery. For instance, American Goldfinches (*Carduelis tristis*) in Ann Arbor, MI, have greater Hct during winter than summer (Carey and Morton 1976), and Rosy Finches (*Leucosticte arcota*) also show a seasonal increase in Hct during winter (Clemens 1990). Dark-eyed Juncos (*Junco hyemalis*) show greater Hct associated with increased cold resistance during winter (Swanson 1990b). However, demonstration of increased arterio-venous differences in blood oxygen concentration accompanying greater Hct would provide more convincing evidence for this possibility. Furthermore, the fact that CA House Finches, which do not seasonally acclimatize (Dawson et al. 1983), show the same response as MI birds tempers this argument.

Seasonal changes in hematocrit may represent a minor physiological adjustment, governed by potential physiological constraints. That is, hematocrit can only be increased to a limited extent before the increased oxygen capacity is offset by circulatory problems due to viscosity effects (Jones and Johansen 1972). This effect was demonstrated in dogs, which showed decreased cardiac output and increased peripheral resistance with increased hematocrit (Murray et al. 1963). A Hct level of 40–41% appeared to be the optimal compromise between oxygen carrying capacity and viscosity-related circulatory problems in dogs under hypoxic stress (Smith and Crowell 1963). Thus, increased Hct may confer thermoregulatory advantages in the cold, but these may be offset by rheological problems.

Standard metabolic rates (SMR) do not vary seasonally in MI (O'Connor 1995a), CA, or CO House Finches (Dawson et al. 1985; Table 3). Such seasonal stability in SMR, as it relates to winter acclimatization, is not surprising given birds' capacities for regulatory thermogenesis. However, a consistent relationship between seasonal acclimatization and SMR has not yet emerged among species that show significantly greater cold resistance during winter. For instance, both House Finches and American Goldfinches (Dawson and Smith 1986) have seasonally stable SMR, but both Dark-eyed Juncos (Swanson 1991) and Black-capped Chickadees, *Parus atricapillus* (Cooper and Swanson 1994), have elevated winter SMR associated with greater cold resistance. In the latter two species, it is

TABLE 3. Metabolic characteristics of House Finches from Michigan (MI), southern California (CA), and Colorado (CO). Body masses are for birds used in SMR determinations. The only significant seasonal difference within each location is the peak metabolic rate of MI birds. See text for comparisons of means among locations. Means (±SE) are presented. Sample sizes are in parentheses.

	Michigan		California		Colorado	
	Winter	Late spring	Winter	Spring	Winter	Spring
Body mass (g)	22.8 ± 0.25 (19)	22.0 ± 0.5 (12)	20.5 ± 0.3 (16)	20.7 ± 0.4 (11)	20.6 ± 0.5 (6)	19.8 ± 0.5 (9)
Standard metabolic rate: SMR ($cm^3 O_2 \cdot g^{-1} \cdot hr^{-1}$)	3.12 ± 0.06 (19)	3.26 ± 0.07 (12)	2.91 ± 0.06 (16)	2.87 ± 0.09 (11)	3.17 ± 0.04 (6)	3.13 ± 0.14 (9)
Peak metabolic rate: MR_{peak} ($cm^3 O_2 \cdot g^{-1} \cdot hr^{-1}$)	19.81 ± 0.56 (11)	15.49 ± 0.47 (15)	16.8 ± 0.4 (13)	15.5 ± 0.4 (9)	20.2 ± 0.4 (11)	19.1 ± 0.4 (6)
MR_{peak}/SMR ratio	6.3	4.8	5.8	5.4	6.4	6.1
Reference(s)	O'Connor 1995a		Dawson et al.1983, 1985		Dawson et al. 1983, 1985	

not clear whether seasonal changes in SMR contribute to acclimatization, are a by-product, or represent a separate response. The stability of SMR in MI and CO populations demonstrates that seasonal adjustments of SMR do not necessarily accompany seasonal acclimatization.

Comparisons among MI, CO, and CA House Finches could reveal whether geographic variation in SMR is associated with observed seasonal acclimatization in this species. Because winter and late spring SMR values do not differ significantly in any of the House Finch populations, seasonal means were pooled for each location. A Tukey-Kramer Test indicated no significant difference between MI and CO populations, but the SMR of CA birds was significantly lower than that of MI and CO house finches ($P < 0.05$). Thus, the two populations that normally demonstrate metabolic seasonal acclimatization show greater SMR than the population that does not.

Possibly the greater SMR of MI and CO birds reflects their capacity for seasonal acclimatization. A number of studies have demonstrated interspecific correlations of SMR with climatic conditions (Dawson and O'Connor 1996), but few studies have addressed the topic on an intraspecific level. Hudson and Kimzey (1966) reported that in North America, House Sparrows (*Passer domesticus*) from warmer climates tended to have lower SMR than those from cooler areas. The results from House Finch populations appear consistent with this pattern. However, no clear explanation has emerged for geographic variation in metabolic level. As is the case for seasonal changes in SMR, geographic variation in SMR may contribute to acclimatization, be a by-product of the capacity for seasonal acclimatization, or be a separate response altogether. Interestingly, Dawson et al. (1983) reported that when CA House Finches were transferred to Michigan in June and maintained in an outdoor aviary, the birds demonstrated seasonal acclimatization involving improved cold resistance the ensuing winter. Thus, the CA birds are capable of acclimatization under certain conditions, but values of SMR are not available for these transplanted individuals. Determinations of SMR before and after transplant experiments could help elucidate the contribution of SMR adjustments to seasonal acclimatization.

Another metabolic characteristic of interest is the cold-induced peak metabolic rate. Avian metabolic rates during flight or running are gen-

erally 5–10 times resting values (Brackenbury 1984). Cold-induced peak metabolic levels (MR_{peak}) tend to be less than those observed during flight or running, and are on the order of 4–7 times resting values (Marsh and Dawson 1989, O'Connor 1995a). Both CA and CO House Finches show seasonally stable MR_{peak} (Dawson et al. 1983), but MI individuals have greater MR_{peak} during winter than late spring (O'Connor 1995a; Table 3). These two studies used different protocols for eliciting MR_{peak}, and therefore, comparisons of absolute values of MR_{peak} among geographic locations probably are not meaningful. Instead, comparisons will focus on the presence or absence of seasonal adjustments in MR_{peak} within each population. The seasonal stability of MR_{peak} in CA House Finches is not surprising, given the absence of metabolic seasonal acclimatization in this population. However, both MI and CO House Finches show seasonal acclimatization, yet the MR_{peak} of the MI population is greater during winter than late spring, whereas that of the CO population is seasonally stable.

BODY COMPOSITION

Seasonal changes in body composition of free-living House Finches captured in the afternoon have been examined in MI (O'Connor 1995a), CA, and CO (Dawson et al. 1983) populations (Table 4). Body mass is seasonally stable in both CA and CO populations, but in MI House Finches, body mass is greater in winter than late spring ($P < 0.001$). For geographic comparisons, winter and spring means were pooled for both CA and CO populations. A Tukey-Kramer Test indicates that body masses of CA and CO birds do not differ significantly, and body mass of MI birds during winter is greater than that of CA or CO birds ($P < 0.05$).

One reason for the greater body mass of MI birds during winter compared to spring, and compared to CA and CO, is the considerable fattening found in MI House Finches during winter. Between late spring and winter, fat content doubles in MI birds. In contrast, the fattening during the same period in CA and CO is 0% and only 18%, respectively (Table 4), and neither of these changes is significant. However, the fat content of CO House Finches during winter was found to be significantly greater than during summer and autumn (Dawson et al. 1983). These results are consistent with the conclusions of previous studies that increased fat content plays some

TABLE 4. Body mass and composition of House Finches from Michigan (MI), southern California (CA), and Colorado (CO). The only significant seasonal differences within each population are the greater body mass, fat content, and lean dry mass of MI birds during winter. See text for comparisons of means among locations. Lean mass was calculated as the difference between total body mass and fat content. Percent water and percent fat are expressed as a percentage of lean mass. All birds used in fat content determinations were captured in the late afternoon. Sample sizes are in parentheses. Means (±SE) are presented. Lean mass, percent fat, and percent water were calaculated from reported means, and therefore are not accompanied by standard error values.

	Michigan		California		Colorado	
	Winter	Late spring	Winter	Spring	Winter	Spring
Total body mass (g)	23.49 ± 0.36 (24)	22.45 ± 0.30 (17)	21.61 ± 0.22 (30)	20.98 ± 0.48 (10)	21.69 ± 0.29 (12)	21.79 ± 0.50 (5)
Lean mass (g)	21.31	21.37	20.35	19.72	20.06	20.41
Fat content (g)	2.18 ± 0.19 (14)	1.08 ± 0.06 (21)	1.26 ± 0.06 (30)	1.26 ± 0.12 (10)	1.63 ± 0.10 (12)	1.38 ± 0.07 (5)
Percent fat (%)	10.2	5.0	6.2	6.4	8.1	6.8
Lean dry mass (g)	6.75 ± 0.07 (24)	6.46 ± 0.10 (21)	6.67 ± 0.07 (30)	6.44 ± 0.13 (10)	6.83 ± 0.11 (12)	6.76 ± 0.22 (5)
Body water (g)	14.32 ± 0.20 (24)	14.48 ± 0.26 (19)	13.68 ± 0.19 (30)	13.28 ± 0.30 (10)	13.23 ± 0.16 (12)	13.65 ± 0.29 (5)
Percent water (%)	67.2	67.8	67.2	67.3	66.0	66.9
Reference	O'Connor 1995a		Dawson et al. 1983		Dawson et al. 1983	

role in seasonal acclimatization (Dawson et al. 1983, O'Connor 1995a).

The dramatic seasonal fattening of MI House Finches appears to contrast with the relatively modest fattening in the CO population. This difference may reflect the relative severity of the winter climates or the marked differences in altitude of the locations (Table 1). Furthermore, the difference in fat content may reflect differences in predictability of climate, reliability of resources, or trade-offs related to flight maneuverability or foraging time (Rogers 1987, Rogers and Smith 1993).

Both lean dry mass and total body water are seasonally stable in CA and CO House Finches (Table 4). Total body water of MI birds is seasonally stable, but lean dry mass is significantly greater during winter than late spring ($P < 0.02$). The only significant difference in lean dry mass among locations is that the pooled CO values are significantly greater than those of the MI population during spring ($P < 0.05$, Tukey-Kramer Test). The modest (4.5%), but significant, seasonal difference in lean dry mass of MI birds is consistent with the suggestion that larger birds may be more tolerant of harsh winter conditions because of their greater cold resistance and ability to fast for longer time periods (Ketterson and Nolan 1976, 1979; Ketterson and King 1977).

Belthoff and Gauthreaux (1991) suggested that such variation in winter tolerance has led to a pattern of partial migration in eastern House Finches during winter, with smaller birds migrating further south and larger ones remaining at winter sites or only migrating small distances. The seasonal difference in lean dry mass of MI birds could be the result of partial migration or temporal variation in body composition of individuals which comprise the local population. Belthoff and Gauthreaux (1991) also suggested that partial migration was a response to winter in eastern House Finches, but not western birds. If so, the significantly reduced lean dry mass of CO birds during summer compared to winter and spring (Dawson et al. 1983) illustrates temporal variation in a presumably resident population.

Total body water of MI House Finches is greater than that of both CA and CO birds ($P < 0.05$, Tukey-Kramer Test), which do not differ significantly. The physiological significance of geographic variation in body water, if any, is not clear. Another way to examine variation in body composition is as the ratio of body water and fat to lean mass (body mass − fat content = lean mass). Total body water modestly varies between 66.0%–67.8% of lean mass, whereas fat content represents 5.0%–10.2% of lean mass (Table 4).

LIPID MOBILIZATION

Lipids are the primary physiological substrate utilized by birds during shivering thermogenesis (Marsh and Dawson 1989). Because the pectoralis (O'Connor 1995a) and presumably other skeletal muscles contain virtually no endogenous lipid stores, factors involved in their mobilization from adipose tissue to shivering muscles may be involved in seasonal acclimatization (O'Connor 1995b). Because free fatty acids (FFA) in the plasma are bound to albumin molecules during transport, the availability of albumin binding sites could limit the rate of FFA mobilization from adipose tissue (Weber 1988). However, in this study there is no evidence of seasonal or geographic variation in levels of albumin in the plasma (Table 2). Therefore, adjustments in albumin concentration do not appear to be involved in house finch seasonal acclimatization.

Mobilization of FFA from adipose tissue involves hormones, and in birds the primary lipolytic hormone is glucagon (Hazelwood 1984). The effects of glucagon in avian systems have been summarized by Dawson et al. (1992). Glucagon levels in free-living MI and CA birds sampled in the early morning did not vary seasonally or geographically in this study (Table 2). However, the ratio of insulin to glucagon levels may be more informative than the glucagon concentration itself (Hazelwood 1984, Dawson et al. 1992) and the enigmatic role of glucagon in avian cold defense has been discussed previously (Dawson et al. 1992, O'Connor 1995b). Clearly, certain hormones and/or hormonal combinations must play prominent roles in avian metabolic seasonal acclimatization. Unfortunately, an understanding of the endocrinology of metabolic acclimatization is still at an early stage (Dawson et al. 1992). Future studies of the role of glucagon and other hormones such as insulin, thyroid hormone, and growth hormone will provide important contributions to the understanding of endocrinological aspects of seasonal acclimatization.

CATABOLIC CAPACITY

The observed seasonal and geographic variation in citrate synthase (CS) activity (Fig. 2) supports the possibility that adjustments in aerobic ca-

pacity are associated with seasonal acclimatization (O'Connor 1995b). As was the case for variability in SMR, it is not clear if these changes contribute to acclimatization, are a by-product, or represent a separate response. The observed seasonal change in CA birds suggests such an adjustment may not be related to acclimatization, but the fact that MI values exceed those of CA birds indicates that aerobic capacity may be related to acclimatization. Both total (per muscle) and mass-specific values for aerobic capacity should be evaluated to address their role more adequately (Marsh 1981, O'Connor 1995b). Unfortunately, pectoralis mass was not measured in CA birds, so total (per muscle) activities are not available for this population.

Mass-specific activities of β-hydroxyacyl-CoA dehydrogenase (β-HOAD) reveal seasonal stability in capacities for β-oxidation of both CA and MI house finches. However, MI values significantly exceed those of CA birds (Fig. 2). In fact, β-HOAD activities of MI House Finches exceed those of CA birds by over 60%, whereas the corresponding difference in CS activities between locations is less than 10%. Thus, MI birds appear to have a greater capacity for β-oxidation than CA individuals during both seasons. In MI House Finches, greater total β-oxidation capacity during winter was associated with acclimatization (O'Connor 1995b), but such calculations were not possible for CA birds, as noted above. However, the geographic variation in β-HOAD activity between MI and CA birds suggests that differences in β-oxidation capacity may be associated with seasonal acclimatization, as appears to be the case for CS activity.

Seasonal comparisons of CS and β-HOAD activities of CO House Finches have been determined previously by Carey et al. (1989). As with values of MR_{peak}, direct comparisons of absolute values from different studies are not made because of potential differences in protocol. Rather, seasonal trends within the CO population are compared to those in MI and CA birds. Carey et al. (1989) reported seasonally stable mass-specific activity of pectoralis muscle CS. This was the same circumstance found in MI House Finches, but, as a result of the seasonal change in pectoralis mass, MI birds had greater total CS activity during winter than spring (O'Connor 1995b), unlike CO birds (Carey et al. 1989). Additionally, mass-specific pectoralis β-HOAD activity of CO House Finches was significantly greater in winter than spring (Carey et al. 1989), but was seasonally stable in both MI and CA populations (Fig. 2). Carey et al. (1989) also provided evidence suggesting that CO House Finch leg muscles initiate shivering activity at lower ambient temperatures than the pectoralis muscle. A comparison of the role of leg muscles in shivering in both CO and MI House Finches would be of interest.

CONCLUSIONS

Seasonal and geographic comparisons of body composition and enzyme activities support suggestions that adjustments in fat stores and catabolic capacity are associated with acclimatization in eastern House Finches. Seasonal patterns of variation in metabolism, body composition, and catabolic capacity differ between CO and MI House Finches. For instance, MI birds show seasonal variation in MR_{peak} and lean dry mass between winter and late spring while CO house finches do not. These results raise the intriguing possibility that the CO population, consisting of native residents of cold winter climates, may be employing a different mechanism for seasonal acclimatization than eastern House Finches, relatively recent introductions to such conditions. However, this suggestion must be tempered by the possibility that the observed differences simply represent variations in magnitude of adjustment among the suite of physiological characteristics related to seasonal acclimatization.

An equally likely explanation for the observed geographic differences is that the MI and CO populations are responding to different climatic and environmental variables. Most notably, the altitude at which CO birds reside is much greater than that of their MI counterparts. The differences in physiological characteristics between the populations could directly reflect adjustments to altitude, or could be the indirect result of the increased climatic variability associated with elevated altitudes. Carey and Morton (1976) correctly noted that the physiological characteristics of montane birds most likely reflect responses to multiple demands of the physical environment. Finally, an additional confounding factor is physiological adjustments related to reproduction. House Finches are in their breeding season during late spring and therefore, some of the seasonal changes in physiology may be associated with reproduction in addition to (or instead of) cold acclimatization (O'Connor 1995b).

As is the case for elucidating avian mechanisms for coping with altitude (Carey and Mor-

ton 1976, Clemens 1990), a more complete understanding of the mechanisms for seasonal acclimatization requires further study. House Finches represent a valuable model for examining physiological mechanisms of seasonal acclimatization because of their pattern of distribution, the variation in historical exposure and response to cold, and the availability of background data on which to build. For example, examination of House Finches from the original western distribution that exhibit seasonal acclimatization but do not reside at elevated altitudes would help distinguish physiological characterics associated with various environments. The magnitude of geographic variation evident in house finch populations reinforces the potential dangers of extrapolating findings from single populations to a larger scale in widely distributed species.

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