J Comp Physiol B (1995) 165: 298–305

ORIGINAL PAPER

T. P. O'Connor

Metabolic characteristics and body composition in house finches: effects of seasonal acclimatization

Accepted: 11 April 1995

Abstract House finches (*Carpodacus mexicanus*) from the introduced population in the eastern United States were examined to assess metabolic characteristics and aspects of body composition associated with seasonal acclimatization. Wild birds were captured during winter (January and February) and late spring (May and June) in southeastern Michigan. Standard metabolic rates did not differ seasonally, but cold-induced "peak" metabolic rate was 28% greater in winter than late spring. The capacity to maintain elevated metabolic rates during cold exposure ("thermogenic endurance") increased significantly from an average of 26.1 to 101.3 min in late spring and winter, respectively. House finches captured in the late afternoon during winter had twice as much stored fat as those during late spring. Both the wet mass and lean dry mass of the pectoralis muscle, a primary shivering effector, were significantly greater during winter. The seasonal changes in peak metabolism and thermogenic endurance demonstrate the existence and magnitude of metabolic seasonal acclimatization in eastern house finches. Increased quantities of stored fat during winter appear to play a role in acclimatization, yet other physiological adjustments such as lipid mobilization and catabolism are also likely to be involved.

Key words Avian fat metabolism · Peak metabolism · Thermogenic endurance · Thermoregulation · Finch, *Carpodacus mexicanus*

T. P. O'Connor[1]
Department of Biology, University of Michigan, Ann Arbor, MI 48109–1048, USA

Present address:
[1] Department of Physiology, School of Medicine, University of California, Los Angeles, CA 90024-1751, USA

Abbreviations *bm* body mass(es) · *MR* metabolic rate(s) · MR_{peak} peak metabolic rate(s) · *SMR* standard metabolic rate(s)

Introduction

The onset of winter presents certain energetically challenging conditions for small birds in seasonal climates. These conditions include not only low temperatures, but also shorter days and the possibility of decreased food supplies that may be covered by snow or ice. The primary means by which small birds meet this energetic challenge is through metabolic adjustments (reviews: Marsh and Dawson 1989a, 1989b; Dawson and Marsh 1989). The most prominent metabolic adjustment observed involves the capacity of many birds to sustain elevated rates of metabolism for longer periods during winter than during other seasons (Dawson and Carey 1976; Dawson et al. 1983a; Swanson 1990). Increased thermogenic endurance is sometimes, but not always, accompanied by increased peak cold-induced MR or "summit" metabolism. Changes in thermogenic endurance and level of summit metabolism provide illustrations of the existence and extent of metabolic seasonal acclimatization, yet the physiological mechanism for this compensatory process remains incompletely understood.

The predominant means by which birds effect thermogenesis in the cold is shivering (West 1965; Hohtola 1982; Hohtola and Stevens 1986). Therefore, physiological adjustments enabling these animals to sustain bouts of shivering for extended periods could be involved in seasonal acclimatization. Because fat is the primary energy substrate utilized by birds during shivering (Carey et al. 1978; Dawson et al. 1983b; Marsh and Dawson 1989a), the mechanism for increased thermogenic endurance (or "shivering endurance") during winter may involve one or more of the

following: (1) increased fat stores, (2) improved ability to mobilize lipids, or (3) increased capacity to catabolize them (Marsh and Dawson 1989a). In this study, the magnitude of seasonal acclimatization will be assessed in house finches (*Carpodacus mexicanus*), and seasonal changes in fat stores will also be examined.

House finches have played a significant role in previous examinations of seasonal acclimatization (Dawson et al. 1983a; Marsh et al. 1984; Root et al. 1991), but the present investigation is the first to examine seasonal acclimatization in free-living house finches from the population introduced into the eastern United States. House finches are native to western North America, from southern Mexico to British Columbia. This range extends over the Rocky Mountains in Colorado to the Great Plains in western Kansas, Nebraska, and Oklahoma (Aldrich and Weske 1978). House finches apparently from southern California were released on Long Island, New York in 1940 and in the ensuing five decades the resultant eastern population has dramatically expanded its range. The birds are now found along the Atlantic Seaboard from New England to South Carolina, and they continue to expand their range westward through the Midwest towards the eastern edge of the house finches' natural western range (Bock and Lepthien 1976; Mundinger and Hope 1982; Root 1988). Because the founders of the eastern population are apparently from southern California stock (Aldrich and Weske 1978), they and their descendants have been exposed to much more severe winter conditions than those under which their ancestors existed. House finches in southern California do not show a seasonal adjustment in thermogenic endurance (Dawson et al. 1983a), and thus physiological differences between these birds and those now in the eastern population could provide valuable information regarding the mechanism of seasonal acclimatization.

This study will address the following questions: (1) Does seasonal acclimatization exist in free-living eastern house finches? (2) If so, what is the magnitude of seasonal acclimatization as determined by measurements of thermogenic endurance and cold-induced peak MR? (3) Are changes in body composition associated with metabolic seasonal acclimatization?

Materials and methods

Animals and collection sites

House finches were captured in Washtenaw County, Michigan, by means of a feeder trap during January and February ("winter") and during May and June ("late spring"). The late spring sampling time was chosen over a summer sample to avoid metabolic determinations during the annual molt of house finches, which occurs between July and October in Washtenaw County [G. Hill, pers. comm.; Stangel (1985)]. During the winter sampling period, sunrise and sundown occurred at ~ 0715 and ~ 1740 hours, respectively. During late spring, sunrise and sundown occurred at ~ 0600 and ~ 2045 hours, respectively.

Standard metabolic rate

All house finches used in determinations of SMR were captured within 3.5 h before sundown and transferred to the laboratory within 1 h of capture. Birds were provided with sunflower seed and water ad libitum from the time of capture until the initiation of metabolic determinations. MR determinations were begun within 60 min prior to sundown on the day of capture. Individuals which lost more than 5% of their bm (including fecal excretions) between capture and initiation of metabolic determinations were not used. After weighing, a house finch was placed in a metabolic chamber which was then positioned in a controlled-temperature cabinet. The temperature in the cabinet was maintained at 32.0 ± 1.0 °C, a temperature within the thermoneutral zone of eastern house finches (Root et al. 1991). Each house finch fasted and rested in the chamber for 4–5 h prior to any data collection. Thus, the SMR values reported are for postabsorptive individuals resting in the inactive phase of their daily cycle. Oxygen consumption was measured in an open-circuit system in which flow-rates were regulated by Brooks thermal mass flowmeters and fractional concentrations of O_2 determined by Ametek S3A oxygen analyzers. These instruments were connected via channels of a 12-bit analog/digital converter to a microcomputer which sampled, and then averaged, 50 signals per min. The full-scale range of the A-D converter was 19–21% O_2. MR was recorded at 1-min intervals for 45 min. Steady-state O_2 consumption was calculated using Eq. 4 from Hill (1972) for upstream flow monitoring and fractional concentrations of O_2 in dry, CO_2-free air. Ascarite and Drierite served as CO_2 absorbent and desiccant, respectively. During SMR determinations, metabolic chambers were ventilated with 800 ml air · min^{-1}. This flow rate maintained fractional O_2 concentrations above 20%, while exposing house finches to wind speeds that were virtually 0 m · s^{-1} (Buttemer et al. 1986; Bakken 1990; Root et al. 1991). The SMR value for a given individual was taken as the minimum 10-min mean within the 45-min test period.

Thermogenic endurance and peak metabolic rate

Birds used in determinations of thermogenic endurance were captured between 1030 and 1330 hours and transferred to the laboratory within 2 h of capture. They were provided with food and water *ad libitum* from the time of capture until the cold resistance tests were initiated. All birds except one were tested on the afternoon of capture, with the exception tested the following day. Again, individuals with a significant change in mass (> 5%) between capture and initiation of tests were not used. After weighing, each house finch was placed in a 1.9-l metabolic chamber which was then connected to the open-circuit respirometry system described above. In order to impose a severe cold stress the controlled-temperature cabinet was maintained at − 10.0 ± 1.0 °C and the chamber was ventilated at 1235 ml · min^{-1} with a "heliox" gas mixture consisting of 21% O_2 and 79% He. The use of a heliox mixture, rather than air, to impose a severe cold stress (Rosenmann and Morrison 1974) has been employed previously with house finches (Marsh et al. 1984). Briefly, the use of heliox increases heat loss from the animal at a given temperature and thereby provides a much more severe cold-stress. In their study of house finches in Colorado, Marsh et al. (1984) estimated that the use of a heliox mixture at 1 °C imposed a cold stress equivalent to that produced by − 50 °C in air.

Instantaneous O_2 consumption was determined according to Eq. 4 of Bartholomew et al. (1981). Average O_2 consumption was calculated over the first 5–7 min of a determination, and the bird was maintained in the chamber as long as it maintained this elevated MR. Once its O_2 consumption fell below two-thirds of this initial

average for three consecutive minutes the bird was retrieved from the chamber and the run was terminated. Such a decline in O_2 consumption invariably indicated that the bird was becoming hypothermic and at risk of dying. Termination of the run and retrieval of the bird at this point resulted in over 95% survival.

Determinations of cold resistance produced two types of data, thermogenic endurance values and peak MR. Thermogenic endurance values consisted of the time, in minutes, that each bird was able to maintain an elevated MR. The cold-induced maximum MR is referred to as MR_{peak} after Dawson et al. (1983a). Given the severity of the imposed cold stress, the MR_{peak} values probably approach "summit" metabolic rates (Giaja 1925) for house finches. However, in the absence of determining the latter by varying the ambient temperature (Swanson 1990; Cooper and Swanson 1994) it is important to distinguish between the two. The reported MR_{peak} value is the maximum 3-min mean instantaneous O_2 consumption recorded during the thermogenic endurance determination.

Body composition

Body composition was determined for birds captured between 1100 and 1940 hours and killed in the field within 15 min of capture by cranial immersion in liquid N_2 or by thoracic compression. While in the field, the right pectoralis muscle was dissected out of each bird, minced, placed in a cryogenic storage tube, and frozen for enzyme activity determinations [see O'Connor (1995) for results of enzyme assays]. Immediately after dissection, the carcasses were sealed in plastic bags, placed in a dry ice cooler in the field, and then stored in a freezer at $-20\,^{\circ}C$ upon return to the laboratory.

Fat content was determined by a method modified from that of Dawson et al. (1983a). Prior to body composition determination, the left pectoralis muscle of each bird was dissected out in order to determine its composition separately. Then the entire digestive tract (from mouth to cloaca) was removed and its contents cleared. The carcass, including digestive tract, was then lyophilized to constant dry mass. The dry carcass was ground into small pieces and placed into a cellulose extraction thimble. The thimble was then placed in a Soxhlet extraction apparatus, where neutral lipids were extracted over 24 h with ethyl ether [Kates (1972), pp 332 and 347). Following the ether extraction, the lean carcass was sequentially air-dried for 1 h, oven dried at 80 °C for 1 h, and finally dried in a desiccator for 2–3 days to constant mass. The difference between bm at capture and dry mass represents total body water. The difference between dry bm and lean dry bm represents the extractable neutral lipid, or fat content. Because the right pectoralis muscle was used for enzyme activity determinations, composition of the left pectoralis muscle was determined separately, and the values of wet mass, dry mass, lean dry mass, fat content, and water content were doubled to account for the missing right pectoralis muscle. Body composition values of the whole bird were then corrected to account for both pectoralis muscles.

Statistics

All means are presented with their corresponding standard errors. Seasonal means were compared using double-tailed Student's *t*-tests as variances were not significantly different. Least squares linear regression was used to evaluate the relationship between time of capture and fat content. Significance is reported at $P < 0.05$. All statistics were computed with SYSTAT 5.0.

Results

Metabolic rates and thermogenic endurance

The mean SMR of house finches captured in winter and late spring was 3.12 ± 0.06 and 3.26 ± 0.07 ml $O_2 \cdot g^{-1} \cdot h^{-1}$, respectively, and these values were not significantly different ($P > 0.13$; Table 1). As with mass-specific SMR, the total (non-mass-specific) SMR did not vary significantly between winter and late spring (Table 1). The winter and late spring values of mass-specific MR_{peak} were 19.81 ± 0.56 and 15.49 ± 0.47 ml $O_2 \cdot g^{-1} \cdot h^{-1}$, respectively (Table 1). Thus, the MR_{peak} during winter was 28% greater than during late spring, a significant increase ($P < 0.001$). The ratio of MR_{peak} to SMR (mass-specific values) was 6.3 in winter and 4.8 in late spring.

A significantly increased capacity to sustain elevated MR was associated with the observed seasonal increase in MR_{peak} during winter. Although considerable variability in thermogenic endurance existed during winter, all but one bird had greater endurance than any of the individuals examined during late spring (Fig. 1). The mean thermogenic endurance during winter and late spring was 101.3 ± 12.1 and 26.1 ± 2.0 min, respectively, and these values differed significantly ($P < 0.001$; Fig. 2).

Body mass and composition

The bm of free-living house finches captured during winter and late spring was 23.49 ± 0.36 g ($n = 24$) and 22.45 ± 0.30 g ($n = 17$), respectively (Table 2). These values were significantly different ($P < 0.001$).

During winter, the fat content of house finches varied throughout the day, increasing significantly through

Table 1 Seasonal changes in metabolic characteristics. See text for definition of terms and methods of determination. Mean values are presented with their respective standard errors. Sample sizes are in parentheses

	Season		
	Winter	Late spring	
Mass-specific SMR (ml $O_2 \cdot g^{-1} \cdot h^{-1}$)	3.12 ± 0.06 (19)	3.26 ± 0.07 (12)	NS
Total SMR (ml $O_2 \cdot h^{-1}$)	70.8 ± 1.2 (19)	71.7 ± 2.6 (12)	NS
Mass-specific MR_{peak} (ml $O_2 \cdot g^{-1} \cdot h^{-1}$)	19.81 ± 0.56 (11)	15.49 ± 0.47 (15)	$P < 0.001$
Total MR_{peak} (ml $O_2 \cdot h^{-1}$)	427.2 ± 9.6 (11)	327.6 ± 9.6 (15)	$P < 0.001$

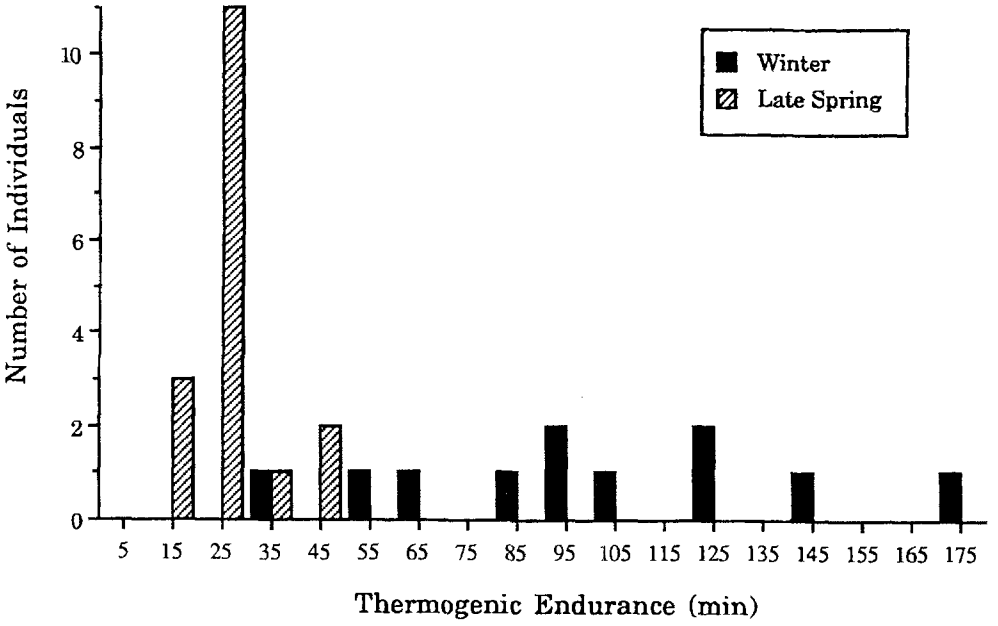

Fig. 1 Histogram representing lengths of time over which house finches could maintain elevated metabolic rates during severe cold-stress. Values on the ordinate represent the number of individuals that showed endurance times of ± 5 min of the value indicated on the *right-hand border of the winter bars*, and the *left-hand border of the late spring bars*. See text for methods and Fig. 2 for mean endurance values of each season

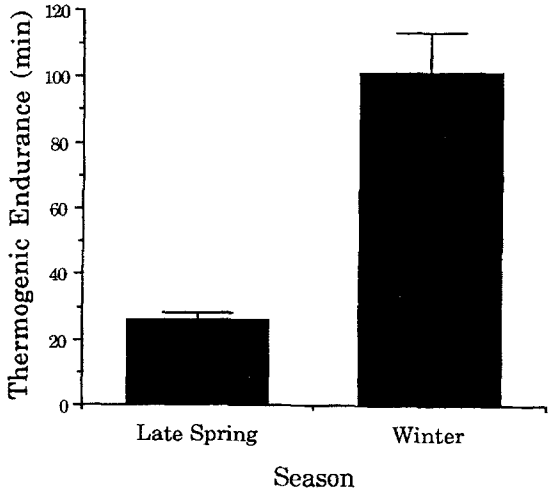

Fig. 2 Seasonal variation in the thermogenic endurance of house finches. Mean values for both winter ($n = 11$) and late spring ($n = 17$) are given with their respective standard errors

the afternoon and early evening as indicated by a regression line with a significant positive slope ($P < 0.001$; Fig. 3). Fat levels during late spring, however, did not vary with time of capture ($P > 0.30$; Fig. 3). The regression equation for fat content as a function of time of capture during winter is:

$$\text{Fat content} = -1.68 + 0.25\ (\text{Time of Capture});$$

$$r^2 = 0.50$$

Stored lipids presumably are the primary energy substrate supporting the overnight fast, so the fat content of the birds as they go to roost, near sundown, is a variable of particular ecological relevance. To facilitate its examination, seasonal comparisons of mean fat levels were restricted to those individuals captured in the late afternoon, within 4 h of sundown. During this period, the fat content in winter was more than double that during late spring (Table 2). Fat content can also

Table 2 Seasonal changes in body composition. Values have been corrected to account for pectoralis nuscles (see Materials and methods). Category C) represents fat content of birds caught within 4 h of sundown in each season. Category E) represents total body water expressed as a percentage of lean mass. Mean values are presented with their corresponding standard errors, and samples sizes are in parentheses. Seasonal values were compared using Student's *t*-test. See text for methods of determination

		Season		
		Winter	Late spring	
A)	Total body mass (g)	23.49 ± 0.36 (24)	22.45 ± 0.30 (17)	$P < 0.001$
B)	Lean dry mass (g)	6.75 ± 0.07 (24)	6.46 ± 0.10 (21)	$P < 0.02$
C)	Fat content (g)	2.37 ± 0.17 (12)	1.12 ± 0.08 (15)	$P < 0.001$
D)	Total body water (g)	14.32 ± 0.20 (24)	14.48 ± 0.26 (19)	NS
E)	D/(A − C)	67.2 ± 0.4% (12)	66.9 ± 0.2% (18)	NS

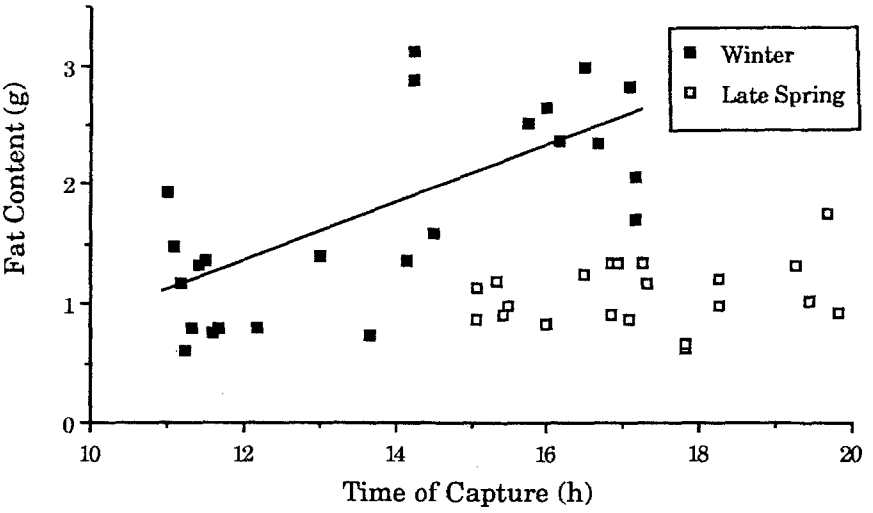

Fig. 3 Daily variation in fat content during winter and late spring. The time values on the abscissa range from 10 a.m. to 8 p.m. The slope of the regression line fitted to the winter data differs significantly from zero ($P < 0.001$), but that for late spring does not ($P > 0.3$). See text for winter regression equation; see also Table 2

Table 3 Seasonal changes in composition of pectoralis muscle. Composition of the left pectoralis was determined and the values were then doubled to account for both pectoralis muscles. Mean values are presented with corresponding standard errors, and samples sizes are in parentheses. Seasonal values were compared using Student's *t*-test. See text for methods of determination

	Season		
	Winter	Late spring	
Wet mass (g)	3.81 ± 0.12 (12)	2.86 ± 0.11 (21)	$P < 0.001$
Lean dry mass (g)	1.34 ± 0.02 (12)	1.12 ± 0.02 (21)	$P < 0.001$
Fat content (g)	0.02 ± 0.01 (12)	0.01 ± 0.01 (21)	NS $P > 0.6$
Water content (g)	2.46 ± 0.12 (12)	1.75 ± 0.10 (21)	$P < 0.001$

be expressed as a percentage of lean mass (lean mass = total mass − fat content). This percentage was 11.2 and 5.3% during winter and late spring, respectively.

The whole-body lean dry mass, which does not vary diurnally, was slightly (4.4%), but significantly ($P < 0.02$), greater during winter than late spring (Table 2). Total body water did not undergo significant seasonal variation ($P > 0.6$; Table 2), averaging 67.2 and 66.9% of lean mass during winter and late spring, respectively.

The wet mass, lean dry mass, and water content of the pectoralis muscle were all significantly greater during winter than late spring (Table 3). However, fat content of the pectoralis muscle was seasonally stable ($P > 0.6$), and quite low (Table 3). The pectoralis muscle fat content averaged 0.5 ± 0.3 and 0.4 ± 0.2% of its lean mass during winter and late spring, respectively. These values did not differ significantly ($P > 0.9$). The respective seasonal values for the fractional water content of this muscle were 64.5 ± 1.1 and 60.3 ± 1.5%, and these also did not differ significantly ($P > 0.6$).

Discussion

Standard metabolic rate

A long-standing view of temperature compensation in small birds, based on early work in the field, has emphasized the lability of MR (Gelineo 1964). Indeed, increased SMR commonly occurs within 1–4 weeks in captive birds transferred from moderate to low temperatures (Gelineo 1964; Arieli et al. 1979). Furthermore, a number of studies have found seasonal shifts in SMR, with metabolic level being higher in winter than late spring or summer (Pohl and West 1973; Weathers and Caccamise 1978; Cooper and Swanson 1994). Recently, Swanson (1991a) reported that SMR of free-living dark-eyed juncos (*Junco hyemalis*) was greater in winter than summer and that this increase was associated with improved cold tolerance (Swanson 1990). Given birds' capacities for regulatory thermogenesis, the adaptive value of increased SMR in the cold is not immediately obvious. In captive birds it may represent an emergency response linked with protection of peripheral tissues from cold injury. Additionally, it might lower the temperature threshold for the onset of shivering. In cases of seasonal lability of SMR, the question of whether such changes are contributing to acclimatization, are a by-product of acclimatization, or are a separate response, remains unresolved (Dawson and Marsh 1989; Root et al. 1991; Dawson and O'Connor 1995).

SMR of free-living house finches from southeastern Michigan was seasonally stable in this study. In fact, seasonal stability of SMR is not uncommon, even for species in which significant metabolic seasonal acclimatization is found. For instance, American goldfinches (*Carduelis tristis*) in Michigan, and house finches in Colorado both have seasonally stable SMR, but increased MR_{peak} and thermogenic endurance

during winter (Dawson and Carey 1976; Dawson et al. 1983a). Thus, although a consistent relationship between SMR and seasonal acclimatization has not emerged, clearly, shifts in SMR are *not* an obligatory component of seasonal acclimatization in birds.

Summit metabolic rate and thermogenic endurance

The mass-specific, cold-induced metabolic expansibility (MR_{peak}/SMR) in eastern house finches was 6.3 in winter and 4.8 in late spring (see Table 1 for metabolic values). Such capacities are typical of passerine birds, which generally show expansibility factors of 4–6 [review: Marsh and Dawson (1989a)]. Interestingly, avian metabolism during locomotion can be as high as 12–14 times resting values, although factors of 5–10 are more typical (Brackenbury 1984). Thus, birds do not appear to use the full aerobic potential of their skeletal muscles in response to cold stress. This may reflect differences in (1) muscle-mass recruited, (2) muscle temperature, or (3) blood flow to the muscles during locomotion and shivering thermogenesis (Marsh and Dawson 1989a).

A great deal of variability exists in seasonal differences in avian MR_{peak}. For instance, winter increases in MR_{peak} for European starlings (*Sturnis vulgaris*), American goldfinches, and evening grosbeaks (*Coccothraustes vespertinus*) average 9, 16, and 18%, respectively (Hart 1962; Dawson and Smith 1986). In these examples, seasonal acclimatization in the form of increased thermogenic endurance occurs, but is not associated with dramatic changes in MR_{peak}. However, a number of studies have found that some passerine birds do have more substantial increases in MR_{peak} associated with increased thermogenic endurance during the winter. Swanson (1990) and Cooper and Swanson (1994) found 28 and 36% increases in MR_{peak} during the winter in dark-eyed juncos and black-capped chickadees (*Parus atricapillus*). The largest winter enhancement of avian MR_{peak} found to date is 43% in house sparrows, *Passer domesticus* (Hart 1962). In the present study, house finch mass-specific and total MR_{peak} increased by 28 and 30%, respectively, between late spring and winter. Increased cold resistance accompanied the elevated MR_{peak} observed during winter.

Evidence thus far obtained suggests that increased MR_{peak} plays a role in the process of seasonal acclimatization in some species but not others. Rather than being a direct mechanism of seasonal acclimatization, increased MR_{peak} may be a by-product of seasonal modifications required for increased endurance. For instance, if increased endurance is associated with elevated total aerobic capacity of muscle and this elevated capacity is achieved by increasing the mass of muscle or the mitochondrial density, then increases in MR_{peak} might be associated with greater endurance. In fact, thermogenic endurance has been linked to MR_{peak} on the basis of a general inverse linkage between endurance and the fraction of maximum MR that is maintained. Thus, if MR_{peak} increases, the endurance at any given absolute MR should rise because this rate is a smaller fraction of the maximum (Marsh and Dawson 1989b). However, whereas increased endurance may be accompanied by elevated MR_{peak} in some cases (such as in this study), dramatic changes in endurance are often achieved with modest adjustments in MR_{peak}.

The results from this study and others cited above clearly demonstrate the existence of a metabolic form of seasonal acclimatization in birds. Yet, the physiological basis of such acclimatization remains incompletely understood. Increased shivering endurance may involve a number of mechanisms, which are not mutually exclusive. For instance, such an increase may be achieved by (1) increased stores of energy substrates, (2) enhanced ability to mobilize energy substrates, or (3) elevated capacities to catabolize such substrates (Dawson et al. 1983b). Material balance and respiratory quotient studies of American goldfinches and house finches indicate that fat is the predominant fuel for the thermogenic shivering response during cold exposure (Carey et al 1978; Dawson et al. 1983a; Marsh and Dawson 1989a). Therefore, seasonal variation in body composition was determined as a first step in examining the mechanism for seasonal acclimatization in house finches.

Body size and composition

The greater bm of eastern house finches in winter compared to late spring is due to seasonal changes in both fat content and lean dry mass (Table 2). Small birds that overwinter in seasonal climates are well known to accumulate greater amounts of fat during winter than summer (King 1972; Blem 1976; Dawson et al. 1983b; Marsh and Dawson 1989a). These reserves presumably (1) support increased overnight energy expenditures resulting from the lower temperatures and longer nights during winter, and (2) supply emergency energy reserves during periods of resource shortage, such as snowfalls and ice storms (Stokkan et al. 1985; Dawson and Marsh 1989b). In addition to seasonal variation in fat content, many small birds have conspicuous daily cycles of body composition during the winter, with fat content increasing over the course of the day and then declining overnight (Helms and Drury 1960; King 1972; Clark 1979; Dawson et al. 1983a; Rogers and Rogers 1990).

In the current study, fat content of house finches increased significantly over the course of the day during winter, but not late spring (Fig. 3). A more complete examination of the diurnal cycle of fat content would obviously necessitate collection of individuals during early morning in both seasons, but the aim here was to assess the patterns of lipid deposition as the birds went

to roost towards the end of the day. When analyses were restricted to those birds captured within 4 h prior to sundown, fat content during winter was more than twice that in late spring (Table 2). The association of elevated fat content with increased thermogenic endurance suggests that the accumulation of energy reserves plays a role in seasonal acclimatization. However, rather than being the exclusive mechanism, increased fat reserves probably represent only one part of a suite of physiological modifications. The evidence for this limited role is two-fold: (1) house finches succumb to cold-stress with significant fat stores remaining, and (2) although fat content is quite variable and considerable seasonal overlap exists, no such seasonal overlap in thermogenic endurance is apparent. An alternative explanation for (1) is that birds may not be able to access all lipid reserves during bouts of shivering thermogenesis and that perhaps they simply draw reserves down to a seasonally uniform minimum. However, evidence contrary to this possibility includes not only (2), but also the observation that birds seem capable of utilizing a greater percentage of their energy reserves during the winter (Carey et al. 1978). It should be noted in connection with (2) that, although there is virtually no seasonal overlap in thermogenic endurance (Fig. 2), the birds used in thermogenic endurance tests were all captured between 1030 and 1330 hours, when considerable seasonal overlap in fat content presumably exists (Fig. 3).

Until recently, physiologists attempting to address the linkage between winter fattening and acclimatization experimentally were limited by the fact that quantitative determinations of lipid reserves necessitated killing the individual. With the increasing applicability of instruments measuring total body electrical conductivity [e.g. EM-SCAN/TOBEC instruments; see Walsberg (1988) and Castro et al. (1990)], temporal variation in body composition of individual birds can be measured. Therefore, one could examine the relationship between fat content and thermogenic endurance, and also the amount of fat depleted during cold-exposure in individuals during different times of the year. Such work should provide important information regarding the role of fat reserves in seasonal acclimatization.

In addition to seasonal changes in fat content, the lean dry mass of eastern house finches was significantly, though modestly (4.4%), greater during winter than late spring (Table 2). House finches in the eastern USA have been described as "partial migrants" because some individuals remain on their breeding grounds throughout the winter, whereas others migrate variable distances during autumn (Gauthreaux 1982; Belthoff and Gauthreaux 1991). Belthoff and Gauthreaux (1991) argued that observations of "partial migration" in eastern house finches may be the result of the capacity of different size individuals to cope with winter conditions. Specifically, they suggested that larger individuals are more resistant to harsh winter conditions than smaller birds, and thus less apt to migrate south. Partial migration per se was not examined in the present study, but the observed seasonal differences in bm and lean dry mass are consistent with the prediction that larger birds overwinter at higher latitudes. Partial migration may be an important ecological response of house finches to winter, but metabolic adjustments clearly represent an important physiological component of acclimatization. If partial migration alone accounted for the seasonal differences in metabolic characteristics, one would expect to see significant overlap in thermogenic endurance between seasons.

Seasonal changes in size of the breast musculature may play a role in metabolic seasonal acclimatization through increased thermogenic capacity. The flight muscles (pectoralis and supracoracoideus) generally represent ca. 15–25% of the adult bm in birds (Hartman 1961), and thus they are thought to play an important role in shivering thermogenesis (Marsh and Dawson 1989a). In the current study, the pectoralis muscle alone represented ca. 20% of house finch bm. In these birds, the 20 and 33% increases in pectoralis lean dry mass and wet mass during winter parallel the 30% increase in MR_{peak} found during this season. Similarly, Swanson (1991b) reported a 28% increase in winter pectoralis muscle mass associated with a 28% increase in winter MR_{peak} of dark-eyed juncos. Such increases in winter muscle masses may result in greater cold tolerance by elevating the capacity for shivering thermogenesis (Swanson 1991b). The role of increased skeletal muscle catabolic capacity in seasonal acclimatization has also been examined by O'Connor (1995). The fact that endogenous fat stores of the pectoralis muscle were seasonally stable and relatively low (70% of the individuals examined had undetectable levels of fat in the pectoralis) indicates that the ability to mobilize fat may be involved in acclimatization, a topic that is also addressed by O'Connor (1995).

Acknowledgements I thank H. Bielac, V. and W.R. Dawson, and A. and T. Jones for access to field sites and for assistance in capturing house finches. I also thank W.R. Dawson and T.L. Root for lab space and equipment and J. Mansfield-Jones for technical assistance and advice. W.R. Dawson, H. Ikuma, T.L. Root, J. Schwartz, P. Webb, and two anonymous reviewers provided useful comments on previous versions of the manuscript. This project was supported by the Frank M. Chapman Fund of The American Museum of Natural History, Hinsdale-Walker Grants from the Museum of Zoology at the University of Michigan, and grants from the Rackham Graduate School and the Department of Biology at the University of Michigan.

The experiments described in this study comply with the "Principles of animal care", publication No. 86–23, revised 1985 of the National Institute of Health and also with the current laws of the United States of America.

References

Aldrich JW, Weske JS (1978) Origin and evolution of the eastern house finch population. Auk 95: 528–536

Arieli A, Berman A, Meltzer A (1979) Cold thermogenesis in summer-acclimatized and cold-acclimated domestic fowl. Comp Biochem Physiol 63C: 7–12

Bakken GS (1990) Estimating the effect of wind on avian metabolic rate with standard operative temperature. Auk 107: 587–594

Bartholomew GA, Vleck D, Vleck CM (1981) Instantaneous measurements of oxygen consumption during pre-flight warm-up and post-flight cooling in sphingid and saturniid moths. J Exp Biol 90: 17–32

Belthoff JR, Gauthreaux SA Jr (1991) Partial migration and differential winter distribution of house finches in the eastern United States. Condor 93: 374–382

Blem CR (1976) Patterns of lipid storage and utilization in birds. Am Zool 16: 671–684

Bock CE, Lepthien LW (1976) Growth in the eastern house finch population, 1962–1971. Am Birds 30: 791–792

Brackenbury J (1984) Physiological responses of birds to flight and running. Biol Rev 59: 559–575

Buttemer WA, Hayworth AM, Weathers WW, Nagy KA (1986) Time-budget estimates of avian energy expenditure: physiological and meteorological considerations. Physiol Zool 59: 131–149

Carey C, Dawson WR, Maxwell LC, Faulkner JA (1978) Seasonal acclimatization to temperature in cardueline finches. II. Changes in body composition and mass in relation to season and acute cold stress. J Comp Physiol 125: 101–113

Castro G, Wunder BA, Knopf FL (1990) Total body electrical conductivity (TOBEC) to estimate total body fat of free-living birds. Condor 92: 496–499

Clark GA (1979) Body weights of birds: a review. Condor 81: 193–202

Cooper SJ, Swanson DL (1994) Seasonal acclimatization in the black-capped chickadee. Condor 96: 638–646

Dawson WR, Carey C (1976) Seasonal acclimatization to temperature in cardueline finches. I. Insulative and metabolic adjustments. J Comp Physiol 112: 317–333

Dawson WR, Marsh RL, Buttemer WA, Carey C (1983a) Seasonal and geographic variation in cold resistance in house finches *Carpodacus mexicanus*. Physiol Zool 56: 353–369

Dawson WR, Marsh RL, Yacoe ME (1983b) Metabolic adjustments of small passerine birds for migration and cold. Am J Physiol 245: R755–R767

Dawson WR, Smith BK (1986) Metabolic acclimatization in the American goldfinch. In: Heller HC et al. (eds) Living in the cold. Physiological and biochemical adaptations. Elsevier, Amsterdam, pp 427–434

Dawson WR, Marsh RL (1989) Seasonal acclimatization to cold and season in birds. In: Bech C, Reinertsen RE (eds) Physiology of cold adaptation in birds. Plenum Press, New York, pp 83–94

Dawson WR, O'Connor TP (1995) Energetic features of avian thermoregulatory responses. In: Carey C (ed) Avian energetics. Chapman and Hall, New York (*In press*)

Gauthreaux SA Jr (1982) The ecology and evolution of avian migration systems. In: Farner DS, King JR (eds) Avian biology, vol 6. Academic Press, New York, pp 93–167

Gelineo S (1964) Organ systems in adaptation: the temperature regulating system. In: Dill DB (ed) Handbook of physiology, section 4. Adaptation to environment, American Physiological Society, Washington, D.C., pp 259–282

Giaja J (1925) Le métabolisme de sommet et le quotient métabolique. Ann Physiol Physiochim Biol 1: 596–627

Hart JS (1962) Seasonal acclimatization in four species of small wild birds. Physiol Zool 35: 224–236

Hartman FA (1961) Locomotor mechanisms of birds. Smithson Misc Collect 143: 1–91

Helms CW, Drury WH (1960) Winter and migratory weight and fat: field studies on some North American buntings. Bird Banding 31: 1–40

Hill RW (1972) Determination of oxygen consumption by use of the paramagnetic oxygen analyzer. J Appl Physiol 33: 261–263

Hohtola E (1982) Thermal and electromyographic correlates of shivering thermogenesis in the pigeon. Comp Biochem Physiol 73A: 159–166

Hohtola E, Stevens ED (1986) The relationship of muscle electrical activity, tremor, and heat production to shivering thermogenesis in Japanese quail. J Exp Biol 125: 119–135

Kates M (1972) Techniques of lipidology: isolation, analysis, and identification of lipids. North Holland, Amsterdam

King JR (1972) Adaptive periodic fat storage by birds. Proc XV Int Ornithol Congr, pp 200–217

Marsh RL, Dawson WR (1989a) Avian adjustments to cold. In: Wang LCH (ed) Advances in comparative and environmental physiology. Springer, Berlin, pp 205–253

Marsh RL, Dawson WR (1989b) Energy substrates and metabolic acclimatization in small birds. In: Bech C, Reinertsen RE (eds) Physiology of cold adaptation in birds. Plenum Press, New York, pp 105–114

Marsh RL, Carey C, Dawson WR (1984) Substrate concentrations and turnover of plasma glucose during cold exposure in seasonally acclimatized house finches, *Carpodacus mexicanus*. J Comp Physiol B 154: 469–476

Mundinger PC, Hope S (1982) Expansion of the winter range of the house finch: 1947–79. Am Birds 36: 347–353

O'Connor TP (1995) Seasonal acclimatization of lipid mobilization and energy metabolism in house finches. Physiol Zool 68 (in press)

Pohl H, West GC (1973) Daily and seasonal variation in metabolic response to cold during rest and forced exercise in the common redpoll. Comp Biochem Physiol 45A: 851–867

Rogers CM, Rogers CJ (1990) Seasonal variation in daily mass amplitude and minimum body mass: a test of a recent model. Ornis Scand 21: 105–114

Root TL (1988) Atlas of wintering North American birds. University of Chicago Press, Chicago

Root TL, O'Connor TP, Dawson WR (1991) Standard metabolic level and insulative characteristics of eastern house finches, *Carpodacus mexicanus*. Physiol Zool 64: 1279–1295

Rosenmann M, Morrison P (1974) Maximum oxygen consumption and heat loss facilitation in small homeotherms by He-O_2. Am J Physiol 226: 490–495

Stangel PW (1985) Incomplete first prebasic molt of Massachusetts house finches. J Field Ornithol 56: 1–8

Stokkan KA, Harvey S, Klandorf H, Blix AS (1985) Endocrine changes associated with fat deposition and mobilization in Svalbard ptarmigan (*Lagopus mutus hyperboreas*). Gen Comp Endocrinol 58: 76–80

Swanson DL (1990) Seasonal variation in cold hardiness and peak rates of cold-induced thermogenesis in the dark-eyed junco (*Junco hyemalis*). Auk 107: 561–566

Swanson DL (1991a) Seasonal adjustments in metabolism and insulation in the dark-eyed junco. Condor 93: 538–545

Swanson DL (1991b) Substrate metabolism under cold stress in seasonally acclimatized dark-eyed juncos. Physiol Zool 64: 1578–1592

Walsberg GE (1988) Evaluation of a nondestructive method for determining fat stores in small birds and mammals. Physiol Zool 61: 153–159

Weathers WW, Caccamise DF (1978) Seasonal acclimatization to temperature in monk parrots. Oecologia (Berlin) 35: 173–183

West GC (1965) Shivering and heat production in wild birds. Physiol Zool 38: 111–120

Communicated by L.-C.-H. Wang