A STUDY OF FASTING IN TREE SPARROWS (*SPIZELLA ARBOREA*) AND DARK-EYED JUNCOS (*JUNCO HYEMALIS*): ECOLOGICAL IMPLICATIONS

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ABSTRACT.—Despite similarities in winter distribution, habitat selection, and food choice, Dark-eyed Juncos (*Junco hyemalis*) and Tree Sparrows (*Spizella arborea*) differ in the extent to which they store fat during winter, with juncos accumulating greater stores. Anticipating that Tree Sparrows might have some means of conserving energy during fasting and thus suffer no disadvantage when weather prevents feeding, we compared the species for weight loss, body temperature, and locomotor activity during fasting and noted relative fasting endurance. Because both species exhibit geographic variation in sex ratio during winter, we also made sexual comparisons, anticipating that males would be able to fast longer than females. The species responded similarly to fasting by (a) lowering body temperature, especially at night, and (b) becoming hyperactive, progressively more so as fasting time increased. Tree Sparrows did not exhibit these responses to a greater degree (although they became hyperactive sooner) and were not able to fast as long as juncos. No sexual differences in fasting ability were observed. Because the species-specific difference in tendency toward fat accumulation cannot be attributed to differences in energy expenditure while fasting, at least in the laboratory, other explanations are considered. *Received 22 June 1981, accepted 21 September 1981.*

TREE Sparrows and Dark-eyed Juncos that winter in the northern half of the eastern United States have similar ground-feeding habits and overlapping diets and sometimes forage together in mixed flocks (West 1967, Bent 1968, Willson 1971, Pulliam and Enders 1971, Coulter pers. comm.). Their ability to meet energy requirements is surely severely tested during winter at times when cold is intense, nights are long, and snow covers food for prolonged periods or storms prevent feeding. Like many other species that winter in the north-temperate zone, juncos and Tree Sparrows increase deposits of body fat in winter (Helms et al. 1967, Helms and Smythe 1969), a response that is commonly accepted as an adaptation to provide energy during forced fasting (e.g. King 1972, Ketterson and King 1977). In both species, the sexes tend to separate by latitude in winter, with females settling in milder climates (Ketterson and Nolan 1976, 1979, unpubl. data), a behavior that could be related in part to sexual differences in the ability to withstand severe weather. Yet despite the similarities of these two small sparrows and despite the fact that populations wintering at the same location encounter identical weather, the two species differ in the reserves of energy stored as fat. Juncos have been reported to store fat in an amount that is 12–17% of their mean wet winter weight (Helms et al. 1967); by comparison, the figure for Tree Sparrows is only 5–12% (Helms and Smythe 1969). This difference led us to test experimentally the prediction that Tree Sparrows either (1) cannot endure fasting for as long as juncos, or (2) compensate for their reduced energy stores by conserving energy in ways not used by juncos.

Fasting endurance is determined by the ratio of energy stored to the rate of energy utilized, and, because per-gram metabolic rate is negatively correlated with body size, fasting endurance is theoretically affected by body size (Calder 1974). Thus, larger species, or larger size classes within a species, might be expected to be able to fast longer than smaller ones if the individuals being compared store fat in similar proportion to their body weight. Because juncos are somewhat larger than Tree Sparrows, they might therefore be expected to show greater fasting endurance, even in the absence of their disproportionate fat stores already mentioned. Further, both species are

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The Auk 99: 299–308. April 1982

sexually dimorphic in size, and as no significant sexual differences in fat stores (as a percentage of body weight) have been observed (Helms et al. 1967, Helms and Smythe 1969), fasting endurance in both species might also be greater in the larger sex, the male.

Decreases in body temperature are for birds a common means of saving energy during fasting (Baldwin and Kendeigh 1932, Biebach 1977, deGraw and Snelling pers. comm., Ketterson and King 1977). Hyperactivity, presumably the result of hunger, is also typical of fasted, caged birds and in the field would lead to more active searching for food (Wagner 1937, Eyster 1954, Merkel 1966, deGraw and Snelling pers. comm., Ketterson and King 1977). The extent to which hyperactivity incurs an energy cost is not known, because heat generated by exercise may fully or partially substitute for thermoregulatory costs, depending on the level of activity, air temperature, and perhaps nutritional state (Ketterson and King 1977, Paladino 1979). These considerations suggested that Tree Sparrows could employ marked body temperature lability to save energy during fasting but might or might not conserve energy by diminished locomotor activity. In any case, a difference between the two species in locomotor response to fasting would call for further investigation.

In the work reported here, we first determined that juncos and Tree Sparrows at Bloomington, Indiana conformed to the general pattern of greater fat storage by juncos and then investigated the following questions:

1. Did fasting endurance of the two species differ?
2. Regardless of the answer to 1, did fasting Tree Sparrows develop hyperactivity to a greater or lesser extent than fasting juncos or exhibit greater or less lability in body temperature?
3. Recalling the sexual difference in distribution in each species in winter, did fasting affect the sexes differently in either or both species?

These questions were investigated using newly caught birds (as in Kendeigh 1945, Biebach 1977) rather than captive birds (as in Ivacic and Labisky 1973, deGraw and Snelling pers. comm., Ketterson and King 1977). Evidence that captive birds differ from wild birds in fat deposition and cold acclimatization (Kendeigh 1949, Hart 1962, King and Farner 1966, Helms and Smythe 1969) suggests that studies of fasting in birds newly taken from the wild may yield more reliable results.

We note here (and discuss below) that the ability to fast is only one factor that might affect winter survival and that carrying excess fat may have its costs (Helms and Smythe 1969). Evidence that winter fat levels may sometimes be regulated below maximum capacity is provided by reports that some bird species are fatter preceding migration than during midwinter (Linsdale and Sumner 1934, Baumgartner 1938, Wolfson 1945, Odum 1949, King et al. 1963, King 1972) and by the observation that juncos of equal body dimensions are fatter in winter at northern than at southern latitudes (Ketterson and Nolan unpubl. data). Thus, a final objective of this paper is to consider circumstances that might select against maximal fat storage.

METHODS

Ten Tree Sparrows and 18 juncos were confined in a windless room at 8–10°C on a 10L:14D photoperiod and deprived of food until death seemed imminent (as defined below). Body temperature (T_b) of some birds and weights of all were taken every 4 h [or sometimes 8 h, because recordings (hereafter RT, recording time) at 0330 were irregular], while locomotor activity was monitored continuously. Controls were birds treated similarly except that they were given unlimited access to a mixture of turkey starter mash, millet, ground eggs, beef, and carrots. All birds were provided with water and were caged individually so that none could see any other bird.

Some controls did not eat and lost weight at the same rate as experimentals, a response to captivity that we have occasionally observed in various other seed-eating fringillids. To eliminate the confounding effects of data from such individuals, we have omitted their weights, T_b's, and activity from all calculations. Controls, therefore, included only individuals whose percentage weight loss, if any, was at least 20% less than that of the experimental bird of the same species that exhibited the smallest percentage weight loss. All controls, so defined, gained weight at least once between successive RTs, indicating that they were eating. Seven Tree Sparrows and 14 juncos satisfied the criteria for inclusion as controls, and 3 Tree Sparrows and 8 juncos did not. We now think that had the birds not been visually isolated, this loss of data could have been avoided.

Six experiments were conducted between 13 January and 15 February 1981. On the day each was to begin, we captured as many juncos and Tree Sparrows as possible (extremes 4 and 16) between 1450

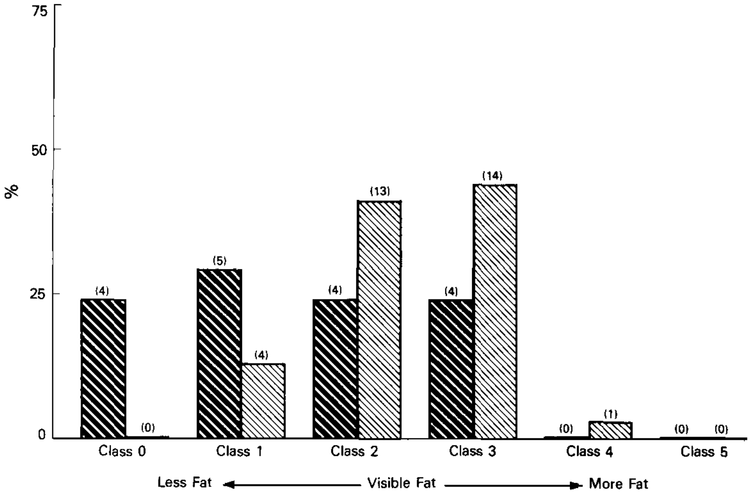

Fig. 1. Percentage of juncos and Tree Sparrows according to fat class at capture. Sample sizes as indicated in parentheses include both the experimental subjects and those controls that satisifed criteria for inclusion (see text). Light bars = Dark-eyed Juncos, dark bars = Tree Sparrows.

and 1830. These we weighed immediately in the field (Pesola spring balance, 50-g capacity, nearest 0.1 g) and transported to the laboratory, where we measured the flattened wing and classed for fat according to a modified version of the scale described by Helms and Drury (1960). Juncos we sexed at the time of capture using the criteria of Ketterson and Nolan (1976), whereas Tree Sparrows were sexed by laparotomy after the completion of all experiments. Experiments were conducted too late in the year to permit us to age subjects. Birds destined to be fasted or fed were assigned to these classes randomly.

Each bird was weighed again 4 h after capture when the gut may be assumed to have been empty (Kontongiannis 1967), and this weight we designate as "initial weight." Birds were transferred to the cold room between 2045 and 2215. Each was placed in a small cage (22 cm × 26 cm × 28 cm) equipped with a single perch attached to a microswitch; each hop on the perch was recorded on an Esterline-Angus event recorder. In order to minimize the effects of disturbance, T_b measurements were made on only a subset of subjects (maximum, 10) in each experiment; subjects were taken from the cold room one at a time in a prescribed order and a Schultheis quick-responding thermometer was inserted into the cloaca for 30 s (nearest 0.1°C). In the first experiment, an experimental bird's T_b was measured first, then a control bird's, then an experimental's; in the second experiment, a control bird was measured first.

TABLE 1. Comparisons of fasted Dark-eyed Juncos and Tree Sparrows in a 10°C cold room, sexes pooled.

Measurement	Juncos (n = 18)[a]	Tree Sparrows (n = 10)[a]	t	P
Wing length (mm)[b]	79.7 ± 0.72	75.8 ± 0.84	3.34	<0.01
Initial weight (g)[c]	20.78 ± 0.39	18.27 ± 0.32	4.36	<0.001
Final weight (g)[d]	15.63 ± 0.22	14.74 ± 0.25	2.54	<0.05
Weight loss (g)[e]	5.16 ± 0.24	3.44 ± 0.19	3.52	<0.01
Percentage weight loss[f]	24.5 ± 1.25	17.6 ± 0.90	3.18	<0.01
Rate of loss (g/h)[g]	0.120 ± 0.004	0.120 ± 0.008	0.07	n.s.
Fasting endurance (h)[h]	43.19 ± 2.79	29.51 ± 2.02	3.38	<0.01

[a] Mean ± 1 SE.
[b] Flattened wing.
[c] Four h after capture (i.e. gut contents voided).
[d] At time bird believed to be within 4 h of death.
[e] (Initial weight − final weight).
[f] (Weight loss/initial weight) × 100.
[g] (Weight loss/h endured).
[h] Number of hours elapsed between time initial weight taken (i.e. 4 h after capture) and termination of experiment (see text).

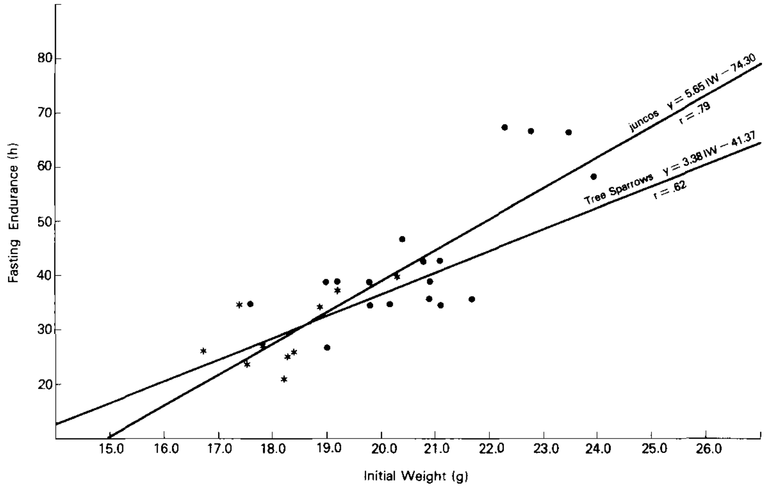

Fig. 2. Relationship between initial weight and fasting endurance for Tree Sparrows (*) and juncos (●). In regression equations, Y stands for fasting endurance and IW for initial weight (see text).

The alternation of experimentals and controls and the order in which the first subject was selected was continued for the remainder of the experiments. When T_b measurement was completed, body weights of all individuals in the experiment were taken as before and recorded.

For experimental birds, the experiment was terminated at the RT when death appeared imminent using the standards of Ketterson and King (1977). For controls, the experiment was terminated when the last experimental was removed. Ketterson and King (1977) report that death could be expected within 4 h in White-crowned Sparrows (*Zonotrichia leucophrys gambelii*) that erected the feathers of the head, breast, and back, were very lethargic, held the eyes partly closed, and sometimes refused food when presented. Fasted juncos and Tree Sparrows behaved similarly and also tucked the head into the scapular feathers when severely stressed. Tree Sparrows showed all signs of stress to a greater degree than juncos. The application of the foregoing subjective standard to determine when death was approaching introduces some error into our results, but we believe that it is similar for the two species. Equal efforts were made to restore experimental birds at the end of experiments (they were warmed and supplied with food, including hand feeding of glucose and water), but two juncos (11%) and four (40%) Tree Sparrows died within 24 h after removal from their cages. Fasting endurance was calculated as the number of hours elapsed between the time the bird's gut could be assumed empty (4 h after capture) and the time that death was judged imminent.

To summarize activity data, we selected blocks of time 1.5 h in length from each 4-h interval between RTs, specifically, the 1.5-h block beginning 2.5 h before the next RT. Blocks are assumed to have been representative of the 4-h intervals. Because caged birds develop idiosyncratic patterns of movement that may only occasionally include landing on the perch, within each 1.5-h block we counted only the number of 30-s intervals in which the individual activated its perch. Thus, activity scores could range between 180 and 0. Occasionally a perch would stick or a pen would fail to write; consequently, the number of individuals comprising a sample sometimes varied among RTs.

RESULTS

Fat class.—As predicted from the findings of Helms and Drury (1960), Helms et al. (1967), and Helms and Smythe (1969), juncos showed more visible fat when captured than did Tree Sparrows (Fig. 1). The actual values of the fat classes reported here are lower than those of Helms and Drury (1960), but we believe that this is due to a difference in application of the 0–5 scale and not to a difference in fat. In any case, the difference between the species is comparable.

Fasting endurance and weight loss.—The mean duration of fasting of the experimental juncos was 43 h and the extremes 34 h and 67 h; mean weight loss was 25% of initial weight and the extremes 19% and 36% (Table 1). In contrast, mean fasting endurance of the Tree Sparrows was 30 h and the extremes 21 h and 40 h; mean

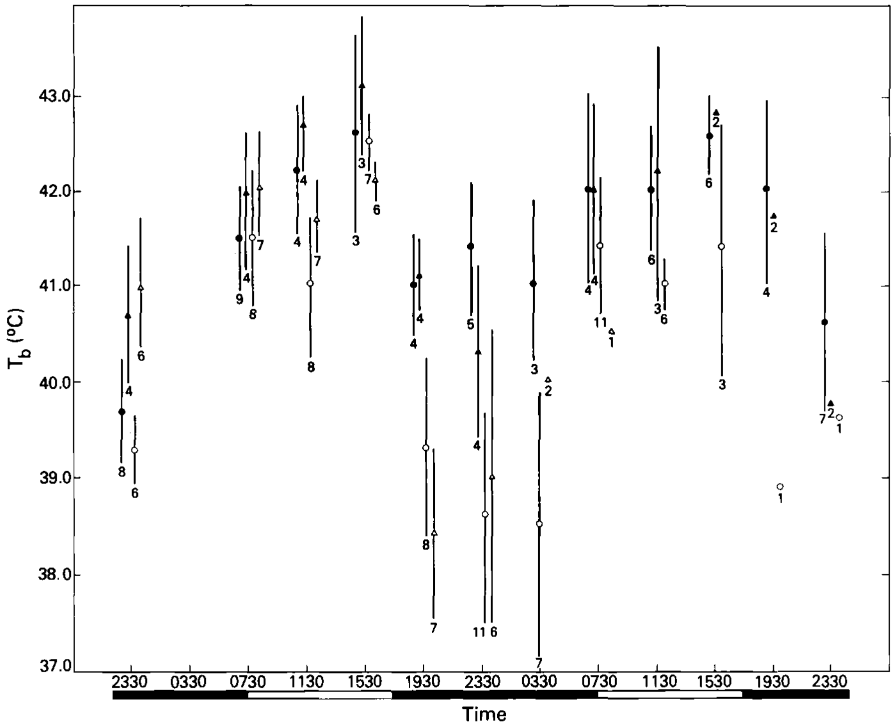

Fig. 3. Mean body temperature of fasted (○) and fed (●) juncos and fasted (△) and fed (▲) Tree Sparrows kept in a 10°C cold room. Vertical lines represent ±2 SE. Sample size is indicated below the line. Open horizontal bars indicate daylight hours; closed bars indicate dark hours.

weight loss was 18% and the extremes 14% and 24% (Table 1).

The mean rate of weight loss per hour was identical in the two species. In each species, initial weight significantly predicted fasting endurance: in the juncos, fasting endurance = 5.65 (initial weight) − 74.30, $r^2 = 0.62$; in Tree Sparrows, fasting endurance = 3.38 (initial weight) − 41.37, $r^2 = 0.39$ (Fig. 2). The difference in the slope of the lines suggests that in juncos a given weight change reflects a greater increase or decrease in fasting endurance than in Tree Sparrows, but the difference was not significant (in juncos, $s_b = 1.11$, in Tree Sparrows, $s_b = 1.73$ where s_b is the standard error of the regression coefficient).

Body temperature.—Control juncos and Tree Sparrows had very similar T_b's. Differences were recorded at 2330 on nights 1 and 2 (Fig. 3, Table 2), but the differences were inconsistent. In one case, the mean for Tree Sparrows was greater; in the other, the mean for juncos was greater.

When the effects of fasting first became apparent (after 0730 on the first day of fasting), fasted birds of both species tended to drop their temperatures below those of controls, and the differences were greater at night (Fig. 3, Table 2, experimental vs. control body temperatures differed significantly in both species except juncos, 1530 day 1, 0730 and 1530 day 2; Tree Sparrows 2330 night 2, one-tailed Mann-Whitney *U*-tests).

Fasted birds showed no species-specific difference in the extent to which T_b dropped: T_b's differed significantly only at 1530 on day 1 when the mean for fasted Tree Sparrows was below that of fasted juncos. (For some unknown reason, juncos had lower body temperatures than Tree Sparrows at 2330 night 1, before the effects of prolonged fasting could have set in.)

The extreme T_b's recorded in fasted juncos were 35.2°C and 43.4°C; the comparable figures for control juncos were 38.9°C and 43.7°C. In fasted Tree Sparrows, extreme T_b's were 35.6°C

TABLE 2. Body temperature comparisons of fasted (experimental) and fed (control) Dark-eyed Juncos and Tree Sparrows.[a,b]

	Within species		Between species	
Time	Experimental vs. control juncos Medians/n_e, n_c (U,P)	Experimental vs. control Tree Sparrows Medians/n_e, n_c (U,P)	Control juncos vs. control Tree Sparrows Medians/n_j, n_s (U,P)	Experimental juncos vs. experimental Tree Sparrows Medians/n_j, n_s (U,P)
2330	39.4, 39.6/6, 8 (15, n.s.)	41.0, 40.6/6, 4 (9, n.s.)	39.6, 40.6/8, 4 (3, $P < 0.014$)	39.4, 41.0/6, 6 (0, $P < 0.001$)
0730	41.4, 41.4/8, 9 (36, n.s.)	42.2, 42.2/7, 4 (13.5, n.s.)	41.4, 42.2/9, 4 (14, n.s.)	41.1, 42.2/8, 7 (18.5, n.s.)
1130	41.1, 42.2/8, 4 (4.5, $P < 0.030$)	41.7, 42.7/7, 4 (1, $P < 0.006$)	42.2, 42.7/4, 4 (5, n.s.)	41.1, 41.7/8, 7 (15, n.s.)
1530	42.4, 42.4/7, 3 (10, n.s.)	42.0, 43.0/6, 3 (0.5, $P < 0.018$)	42.4, 43.0/3, 3 (2, n.s.)	42.4, 42.0/7, 6 (7, $P < 0.026$)
1930	39.3, 40.8/8, 4 (4.5, $P < 0.030$)	38.5, 41.4/7, 4 (0, $P < 0.003$)	40.8, 41.4/4, 4 (6.5, n.s.)	39.3, 38.5/8, 7 (17, n.s.)
2330	38.8, 41.4/11, 5 (4.5, $P < 0.010$)	39.4, 40.2/6, 4 (6, n.s.)	41.4, 40.2/5, 4 (2, $P < 0.032$)	38.8, 39.4/11, 6 (29, n.s.)
0330	38.6, 40.5/7, 3 (2, $P < 0.033$)	—	—	38.6, 40.0/7, 2 (2, n.s.)
0730	42.0, 42.2/11, 4 (16, n.s.)	—	42.2, 41.8/4, 4 (8, n.s.)	—
1130	41.0, 42.3/6, 6 (5.5, $P < 0.026$)	—	42.3, 42.1/6, 3 (8.5, n.s.)	—
1530	40.9, 42.6/3, 6 (4.5, n.s.)	—	42.6, 42.8/6, 2 (5, n.s.)	—
1930	—	—	42.2, 41.7/4, 2 (4, n.s.)	—

[a] n_e = sample size of experimental birds of indicated species; n_c = sample size of controls; n_j = sample size of juncos of indicated category (i.e. experimentals or controls); n_s = sample size of Tree Sparrows.

[b] U values are the Mann-Whitney statistic, P values are one-tailed probabilities from Siegal (1956).

and 42.8°C, and in control Tree Sparrows, 38.1°C and 43.8°C.

Activity.—We had expected nocturnal activity in fasted individuals, because previous workers had reported it [Ketterson and King 1977, C. W. Helms pers. obs. of White-throated Sparrows (*Zonotrichia albicollis*)], but virtually none was observed. During the day the fasted birds of both species were more active than controls (Fig. 4 and 5, Mann-Whitney *U*-tests). When the activity of experimentals and controls is compared for each 1.5-h block, fasting Tree Sparrows became significantly more active than their controls beginning at 1300 on the first full day of fasting. By comparison, fasted juncos first became significantly more active than their controls at 1300 on the second full day of fasting. For both species, once the difference between experimentals and controls appeared, it remained until the final measurements were made and even tended to increase progressively.

Sexual differences.—In Table 3 there is a comparison for each species of experimental birds according to sex. Males of both species had longer wings than females, male juncos had significantly heavier initial weights and final weights, and male and female Tree Sparrows did not differ significantly in weight either at the outset or the termination of experiments. In neither species did the sexes differ significantly in absolute weight loss, percentage weight loss, or rate of weight loss. Furthermore, and contrary to expectation (Ketterson

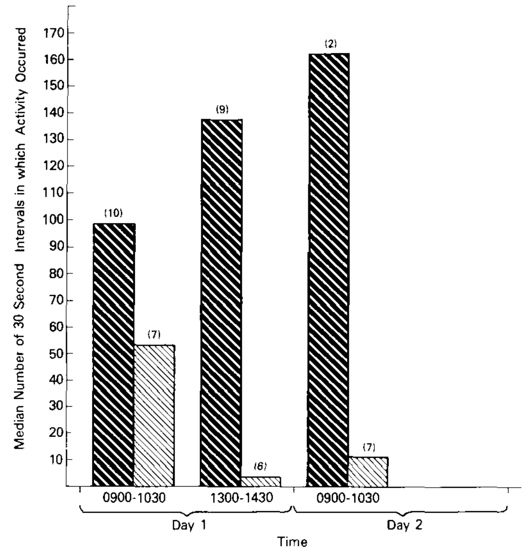

Fig. 4. Daytime activity of fasted and fed Tree Sparrows in a 10°C cold room. Dark bars = fasted Tree Sparrows, light bars = fed Tree Sparrows. Sample size is indicated in parentheses.

and Nolan 1976, 1978; Ketterson and King 1977), no significant sexual difference in fasting endurance was detected.

Discussion

The finding that the average experimental junco could fast for about 43 h at an ambient temperature a few degrees above freezing and that the average Tree Sparrow could last about 30 h is consistent with the determination by Ketterson and King (1977) that the mean fasting endurance of another sparrow, the White-crowned Sparrow, is about 38.6 h. White-crowned Sparrows typically carry fat reserves (as a percentage of body weight) larger than those of Tree Sparrows but smaller than those of juncos (King and Farner 1966, Helms et al. 1967, Helms and Smythe 1969).

Because our experiments began late in the day when fat stores are near their peak in the daily fat cycle, our results suggest that free-living juncos whose food first became unavailable in the late afternoon might be expected to last that night and the following day and night. Tree Sparrows under the same conditions might last that night and the following day. Juncos under conditions comparable to those of the experiment would probably survive if food became available again during or immediately after the second night of fasting, whereas Tree Sparrows, even if they had access to food late in the day of the first day of fasting, would be forced to endure another long night and presumably would die.

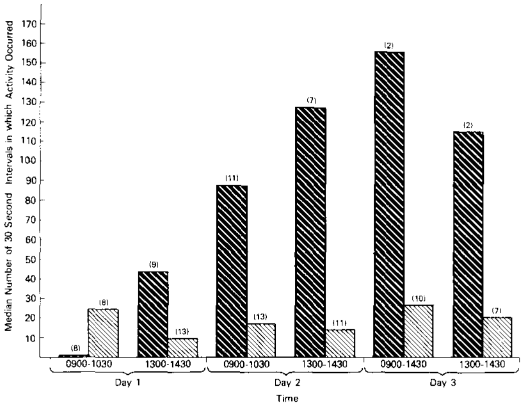

Fig. 5. Daytime activity of fasted and fed Dark-eyed Juncos in a 10°C cold room. Dark bars = fasted juncos, light bars = fed juncos. Sample size is indicated in parentheses.

We found no evidence that Tree Sparrows reduce metabolic expenditure during fasting to a greater degree than juncos. Unlike Black-capped Chickadees (*Parus atricapillus*), which regulate nocturnal T_b about 10–12°C below diurnal T_b (Chaplin 1974), our Tree Sparrows dropped their T_b by only about 1–2°C, i.e. no more than juncos. Neither was there an activity response that would seem to result in energy saving: Tree Sparrows, like juncos, became hyperactive. Interestingly, the timing of the hyperactivity—later in juncos—implies that it is not triggered by the time since feeding occurred, but rather at some level of remaining energy stores. Although, as indicated above, the activity response shown by a fasted bird does not necessarily imply a concurrent increase in energy expenditure, the Tree Sparrow's early increase of activity cannot be construed as an unusual energy-saving adaptation to permit it to carry lower fat stores than juncos.

The reasons for the difference in fat levels of Tree Sparrows and juncos remain obscure, but four possibilities may deserve attention. The first two relate to the relative need for stored energy reserves in the two species.

First, under natural conditions, the species may differ in the actual cost of thermoregulation due to differences in microhabitats selected for roosting or a tendency toward nocturnal huddling, i.e. differences that would not be apparent when housed singly under laboratory conditions. We find no evidence in the literature that juncos or Tree Sparrows huddle at night, however, as do some species (Kendeigh 1945, Frazer and Nolan 1959, King and Farner 1966, King 1972, Haftorn 1972, Chaplin 1974), and both Kendeigh (1945) and Bent (1968) describe roosting behavior that seems much the same for juncos and Tree Sparrows. Kendeigh reports that "the slate-colored junco and tree sparrow normally spend the night in dense ground vegetation or in thickets." We observed both juncos and Tree Sparrows in winter roosts in a large outdoor aviary; the behavior and locations chosen by the two seemed about the same, and no huddling was observed in either species. As a second consideration regarding the relative need for stored energy in the two species, the feeding behavior of Tree Sparrows may be sufficiently flexible to permit them to forage and find food in situations in which juncos must fast. For example, Tree Sparrows may turn more readily than juncos from ground-feeding to foraging from plants emerging from snow cover. Reports of the feeding habits of the two species (Knappen 1934, Baumgartner 1937, Bent 1968, Coulter pers. comm.) do not reveal whether Tree Sparrows have such an advantage, but the subject warrants investigation.

The third and fourth possibilities that may account for the difference in stored fat are related to the idea that fat storage may impose costs and that the magnitude of the cost may vary as a function of the habitats selected by a species or as a function of its body size. That is, it may be disadvantageous to be too fat (Helms and Smythe 1969). Thus, if the foraging locations of Tree Sparrows make them more vulnerable than juncos to avian predators and if an increase in fat stores lowers the probability of escape, perhaps through lowered agility, Tree Sparrows might sacrifice a measure of fasting endurance for the sake of increased agility. According to Helms and Drury (1960), Tree Sparrows do feed in more open areas than juncos, and we too have found that juncos stay nearer to cover than do Tree Sparrows. Studies on the relative agility of the two species at various levels of fat deposition are currently un-

TABLE 3. Characteristics of male and female fasted Dark-eyed Juncos and Tree Sparrows in a 10°C cold room.

	Juncos[a]				Tree Sparrows[a]			
Measurement	♂♂ (n = 13)	♀♀ (n = 5)	t	P	♂♂ (n = 3)	♀♀ (n = 7)	t	P
Wing length (mm)[b]	81.1 ± 0.62	76.0 ± 0.55	4.72	<0.001	79.3 ± 0.88	74.3 ± 0.36	6.51	<0.001
Initial weight (g)[c]	21.40 ± 0.39	19.20 ± 0.47	3.10	<0.01	19.00 ± 0.67	18.00 ± 0.33	1.50	n.s.
Final weight (g)[d]	16.02 ± 0.22	14.64 ± 0.21	3.62	<0.01	15.30 ± 0.31	14.50 ± 0.29	1.62	n.s.
Weight loss (g)[e]	5.37 ± 0.44	4.60 ± 0.43	1.00	n.s.	3.37 ± 0.54	3.47 ± 0.19	0.24	n.s.
Percentage weight loss[f]	24.8 ± 1.62	23.8 ± 1.76	0.35	n.s.	17.6 ± 2.20	19.3 ± 0.94	0.84	n.s.
Rate of loss (g/h)[g]	0.120 ± 0.003	0.120 ± 0.012	0.06	n.s.	0.120 ± 0.015	0.119 ± 0.011	0.06	n.s.
Fasting endurance (h)[h]	44.93 ± 3.70	38.66 ± 2.23	1.01	n.s.	28.72 ± 5.60	29.85 ± 2.05	0.24	n.s.

[a] Mean ± 1 SE.

[b] Flattened wing.

[c] Four h after capture (i.e. gut contents voided).

[d] At time bird believed to be within 4 h of death.

[e] (Initial weight − final weight).

[f] (Weight loss/initial weight) × 100.

[g] (Weight loss/h endured).

[h] Number of hours elapsed between time initial weight taken (i.e. 4 h after capture) and termination of experiment (see text).

derway. Fourth, the cost of locomotion may increase with level of fat deposition, and the extent of the increase could be greater to the smaller-bodied Tree Sparrow. Paladino and King (1979) have estimated the cost of transport in terrestrial locomotion (cm^3 O_2 $(g - km)^{-1}$) as equal to 3.2 (grams body mass)$^{-0.26}$. Thus, if an individual's body weight were to increase from 15 to 20 g, per-gram cost of transport would decrease from 1.56 to 1.45, but per-bird cost would increase from 23.7 to 29.4 cm^3 O_2 km^{-1}, i.e. 19.2%. A comparable increase in weight from 21 to 26 g would alter the per-bird cost from 30.5 to 35.7 cm^3 O_2 km^{-1} or 14.6%. Use of a similar equation for the cost of transport described by Fedak and Seeherman (1979) gives comparable results (18.7%, 14.3%). These differences are obviously small and may have little biological significance. The relative cost, however, of hopping on a treadmill to lean and fat individuals of both species is currently under investigation.

The absence of the expected sexual difference in fasting endurance remains unexplained. Two points regarding our methods, however, make us uncertain about the generality of our data on this point. First, samples were small, and we note that the larger sexual difference among juncos was in the expected direction. Second, the initial weight of subjects differed between trials, presumably because the weather in the days preceding capture efforts was, as is usual for Indiana, quite variable. When prior weather was cold and snowy (trials 1 and 4), subjects tended to be fatter than when prior temperatures were mild (trials 2, 3, 5, and 6). This fact did not affect our species comparisons, because equal proportions of juncos and Tree Sparrows began each trial. Had more females than males been the subjects of trials 1 and 4, while more males than females had been the subjects of the other trials, the failure to observe a sexual difference could have been attributed to chance. Within species, however, both sexes were represented in each trial, so there was no obvious bias. Still, the effect of the differences in initial weight among trials was to increase the variance in fasting endurance, making statistical significance less likely. For this reason we feel the question of a sexual difference in fasting endurance deserves further attention, but note that a causal relationship between fasting endurance and geographic variation in winter sex ratio must be viewed with increased skepticism (Myers 1981). In any case, it seems worth emphasizing that, because fat stores for a species differ from time to time and place to place, it is not possible to characterize just one value for a species' fasting endurance.

Although the reasons for the different levels of winter fat in Tree Sparrows and Dark-eyed Juncos have not been clarified, what is clear is that the two species respond to fasting in the same manner and that Tree Sparrows, when deprived of food, become stressed sooner than juncos unless they resort to some energy-saving behavior that we have not yet been able to detect.

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LITERATURE CITED

BALDWIN, S. D., & S. C. KENDEIGH. 1932. Physiology of the temperature of birds. Sci. Publ. Cleveland Mus. Nat. Hist. 3: 1–196.

BAUMGARTNER, A. M. 1937. Food and feeding habits of the Tree Sparrow. Wilson Bull. 49: 65–80.

———. 1938. Seasonal variations in the Tree Sparrow. Auk 55: 603–613.

BENT, A. C. 1968. Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows, and allies. U.S. Nat. Mus. Bull. No. 237, part 2.

BIEBACH, V. H. 1977. Reduktion des Energiestoffwechsels und der Körpertemperatur hungernder Amseln (*Turdus merula*). J. Ornithol. 118: 294–300.

CALDER, W. A. 1974. Consequences of body size for avian energetics. Pp. 86–151 *in* Avian energetics (R. A. Payntner, Ed.). Publ. Nuttall Ornithol. Club, No. 15.

CHAPLIN, S. B. 1974. Daily energetics of the Black-capped Chickadee, *Parus atricapillus,* in winter. J. Comp. Physiol. 89: 321–330.

EYSTER, M. B. 1954. Quantitative measurement of the influence of photoperiod, temperature, and season on the activity of captive song birds. Ecol. Monogr. 24: 1–28.

FEDAK, M. A., & H. J. SEEHERMAN. 1979. Reappraisal of energetics of locomotion shows identical cost in bipeds and quadrepeds including ostrich and horse. Nature 282: 713–716.

FRAZER, A., & V. NOLAN, JR. 1959. Communal roosting by the Eastern Bluebird in winter. Bird-Banding 30: 219–226.

HAFTORN, S. 1972. Hypothermia of tits in arctic winter. Ornis Scandinavica 3: 153–166.

HART, J. S. 1962. Seasonal acclimitization in four species of small wild birds. Physiol. Zool. 35: 224–236.

HELMS, C. W., & W. H. DRURY, JR. 1960. Winter and migratory weight and fat: field studies in some North American buntings. Bird-Banding 31: 1–40.

———, & R. B. SMYTHE. 1969. Variation in major body components of the Tree Sparrow (*Spizella arborea*) sampled within the winter range. Wilson Bull. 81: 281–291.

———, W. H. AUSSIKER, E. B. BOWER, & S. D. FRETWELL. 1967. A biometric study of major body components of the Slate-colored Junco, *Junco hyemalis*. Condor 69: 560–578.

IVACIC, D. L., & R. F. LABISKY. 1973. Metabolic responses of Mourning Doves to short-term food and temperature stresses in winter. Wilson Bull. 85: 182–196.

KENDEIGH, S. C. 1945. Resistance to hunger in birds. J. Wildl. Mgmt. 9: 217–226.

———. 1949. Effect of temperature and season on energy resources of the English Sparrow. Auk 66: 113–127.

KETTERSON, E. D., & V. NOLAN, JR. 1976. Geographic variation and its climatic correlates in the sex ratio of eastern-wintering Dark-eyed Juncos (*Junco hyemalis hyemalis*). Ecology 57: 679–693.

———, & ———. 1978. Overnight weight loss in Dark-eyed Juncos (*Junco hyemalis*). Auk 95: 755–758.

———, & ———. 1979. Seasonal, annual, and geographic variation in sex ratio in wintering populations of Dark-eyed Juncos (*Junco hyemalis*). Auk 96: 532–536.

———, & J. R. KING. 1977. Metabolic and behavioral responses to fasting in the White-crowned Sparrow (*Zonotrichia leucophrys gambelii*). Physiol. Zool. 50: 115–129.

KING, J. R. 1972. Adaptive periodic fat storage in birds. Pp. 200–217 *in* Proc. 15th Ornithol. Congr. (K. H. Voous, Ed.). Leiden, Brill.

———, & D. S. FARNER. 1966. The adaptive role of winter fattening in the White-crowned Sparrow with comments on its regulation. Amer. Natur. 100: 403–418.

———, S. BARKER, & 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.

KNAPPEN, P. 1934. Insects in the winter food of the Tree Sparrow. Auk 51: 93.

KONTOGIANNIS, J. E. 1967. Day and night changes in body weight of the White-throated Sparrow, *Zonotrichia albicollis*. Auk 84: 390–395.

LINSDALE, J. M., & E. L. SUMNER. 1934. Winter weights of Golden-crowned and Fox sparrows. Condor 36: 107–112.

MERKEL, F. W. 1966. The sequence of events leading to migratory restlessness. Ostrich (suppl. 6): 239–248.

MYERS, J. P. 1981. A test of three hypotheses for latitudinal segregation of the sexes in wintering birds. Can. J. Zool. 59: 1527–1534.

ODUM, E. P. 1949. Weight variations in wintering White-throated Sparrows in relation to temperature and migration. Wilson Bull. 61: 3–14.

PALADINO, F. V. 1979. Energetics of terrestrial locomotion in White-crowned Sparrows (*Zonotrichia leucophorys gambelii*). Unpublished Ph.D. dissertation. Pullman, Washington, Washington State Univ.

———, & J. R. KING. 1979. Energetic cost of terrestrial locomotion: biped and quadruped runners compared. Rev. Can. Biol. 38: 321–323.

PULLIAM, H. R., & F. ENDERS. 1971. The feeding ecology of five sympatric finch species. Ecology 52: 557–566.

SIEGAL, S. 1956. Nonparametric statistics for the behavioral sciences. New York, McGraw-Hill.

WAGNER, H. O. 1937. Der Einfluss von Aussenfaktoren auf den Tagesrhythmus während der Zugphase. Vogelzug 8: 47–54.

WILLSON, M. F. 1971. Seed selection in some North American finches. Condor 73: 415–429.

WEST, G. C. 1967. Nutrition of Tree Sparrows during winter in central Illinois. Ecology 48: 58–67.

WOLFSON, A. 1945. The role of the pituitary, fat deposition, and body weight in bird migration. Condor 47: 95–147.