EFFECT OF SEASON ON THE ENERGETICS, BODY COMPOSITION, AND CAGE ACTIVITY OF THE FIELD SPARROW

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ABSTRACT.—A linear correlation of existence metabolism (M_{kcal} = kcal·bird^{-1}·day^{-1}) with temperature (T = °C) was obtained for winter acclimatized Field Sparrows (*Spizella pusilla*) on a 10-h photoperiod (males: M_{kcal} = 15.59 − 0.285T; females: M_{kcal} = 14.69 − 0.261T). A curvilinear relationship was obtained for summer acclimatized birds on a 15-h photoperiod (males: M_{kcal} = 16.40 + 0.0001T^3 − 0.0002T^2 − 0.3662T; females: M_{kcal} = 15.87 + 0.0036T^2 − 0.3911T). Significant differences between summer- and winter-acclimatized birds occurred only at temperatures below 0°C. The lower limit of temperature tolerance was −13° to −14°C under a constant 10-h photoperiod and under fluctuating outdoor conditions and was somewhat lower under a constant 15-h photoperiod. The upper limit of temperature tolerance was about 41°C in the summer. With caged birds under fluctuating outdoor conditions, there was an increase in metabolized energy, existence metabolism, body protein, weight, and lipid content in the autumn and a decrease in the spring. During cold waves in winter, there was commonly an immediate drop in weight before increased metabolized energy brought recovery. In half of the birds, recovery was incomplete and mortality resulted. Coefficients of food utilization varied from 0.71 under a 10-h photoperiod to 0.79 under a 15-h photoperiod and from 0.72 to 0.86 under outdoor conditions. With death from cold or heat stress there was a loss of water, lipids, and proteins. The loss of water was greater under heat stress. Nocturnal activity (*Zugunruhe*) developed in a different pattern in spring than in autumn and was not accompanied by premigratory fattening in the spring. In several respects, the metabolic and behavioral responses of the Field Sparrow are intermediate between those of long distance migrants and permanent residents, indicating that they may be evolving from a migratory to a nonmigratory status. *Received 26 January 1980, accepted 17 March 1980.*

THE Field Sparrow (*Spizella pusilla*) is a partial migrant in eastern North America, with most of the population in the northern part of the breeding range migrating southward in the autumn, although scattered individuals may remain at least through the early part of the winter (Fig. 1). The present study is concerned with the metabolic capacity of the species to adjust to seasonal changes in climate in east central Illinois and how this correlates with migratory behavior. There have been several recent studies of seasonal variations in basal metabolism and causes of seasonal acclimatization (Dawson and Carey 1976, Carey et al. 1978, Weathers and Caccimise 1978, Southwick 1980). This research is concerned, however, with seasonal variations in existence metabolism, a preliminary survey of which, involving several species, was made by Kendeigh et al. (1977).

Analysis will first be made of how existence metabolism of seasonally acclimatized birds responds to changes in temperature under constant 15-h and 10-h photoperiods, and then how adjustments are made under fluctuating outdoor conditions. Variations in metabolism are correlated with cage activity, weight, and body components. The experimental work was done from 1959 through 1962.

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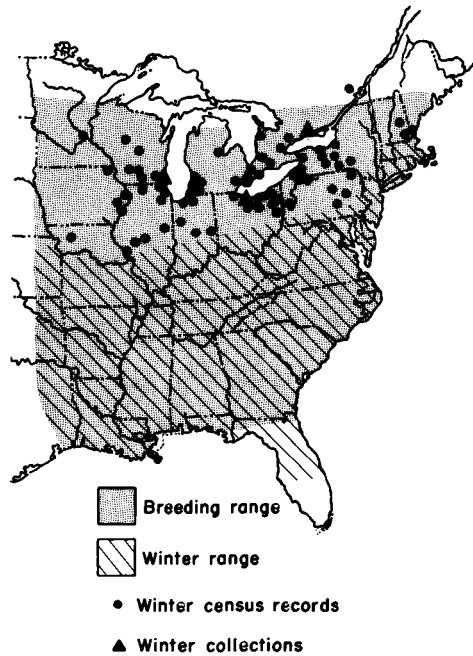
Fig. 1. Breeding and wintering distribution of the Field Sparrow in eastern North America.

METHODS

Capture and maintenance.—Wild birds were captured during the spring and summer and confined in an outdoor aviary until used. They were first fed a commercial seed mixture, which was then gradually changed to a homogeneous chick mash that was used in all experiments (University of Illinois chick starter No. 521, Kendeigh 1968). This chick mash had an energy value of 4.309 ± 0.020 kcal/g dry weight ($\bar{x}$ ± SE) (18.03 ± 0.084 kj/g).

Statistical differences were determined by the analysis of variance test. Differences were considered significant at the 5% confidence level. Regression lines were fitted by the least squares procedure, and standard errors of estimate are provided. Rates of metabolism are given in both heat units (M_{kcal} = kcal·bird^{-1}·day^{-1}) and in International Standard power units (M_{mW} = milliwatts). Conversion factors are: 1 kcal = 4.184 kilojoules (kj); 1 kcal·bird^{-1}·day^{-1} = 48.5 milliwatts (mW).

Indoor measurements.—For measuring existence metabolism under constant photoperiods indoors, the birds were placed singly in small (31 × 16 × 31 cm) metabolism cages as described by Martin (1967) and allowed a preliminary period of 6–9 days for acclimation. Measurements of food consumption were made over consecutive 3-day periods until the birds maintained constant weight (±0.3 g). The energy value of the excreta collected at the end of each period varied from 3.425 ± 0.005 kcal/g (14.33 ± 0.21 kj/g) in the outdoor experiments (see below) (n = 47) to 3.500 ± 0.005 kcal/g (14.64 ± 0.021 kj/g) in the 15-h photoperiod summer experiments (n = 48) to 3.534 ± 0.006 kcal/g (14.79 ± 0.025 kj/g) in the 10-h photoperiod winter experiments (n = 34). Total *excretory energy* subtracted from *gross energy* intake gave *metabolized energy,* which became *existence metabolism* when the bird maintained constant weight.

The summer acclimatized birds were first placed on a 15-h photoperiod (15L:9D) at 21°C. They were then divided into two groups, one group being subjected to progressively higher constant (±2°C) temperatures, the other to progressively lower temperatures. Lighting was provided by two 100-watt incandescent bulbs and controlled automatically (on at 0500, off at 2000). Relative humidity in the high temperature walk-in cabinet (31°C–42°C) varied between 40 and 60%, in the medium temperature cabinet (0°C–25°C) between 60 and 85%, and in the low temperature cabinet (−20°C–0°C) between 70 and 80%. Use was also made of a reach-in cabinet, lighted by 40-watt fluorescent bulbs, having a temperature range from 0° to −84°C. Snow or frost, instead of liquid water, was provided at temperatures below freezing.
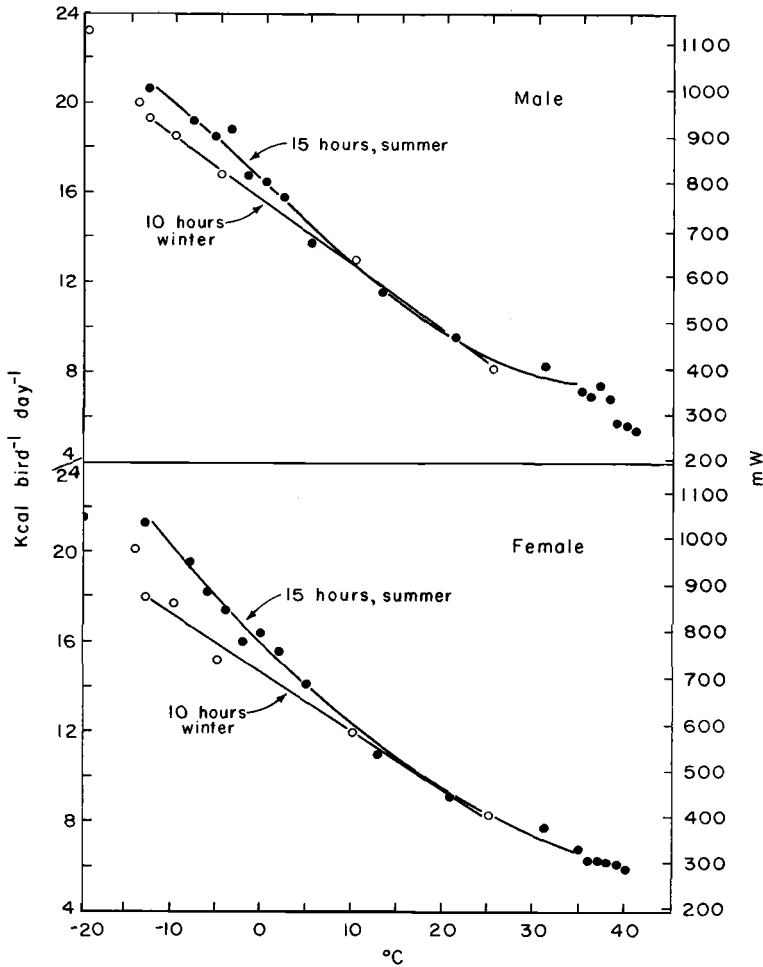
Fig. 2. Existence metabolism at constant temperatures and photoperiods.

For winter experiments, birds were transferred from the outdoor aviary in January and acclimated to a constant 10-h photoperiod (10L:14D; lights on at 0700, off at 1700) and 0°C for 4 days and then −5°C for another 6 days before the measurements were started at both low and high temperatures.

Usually 10 birds were started at each temperature in the summer experiments, but fewer birds (5–7) were available for the winter experiments. At extreme temperatures not all birds survived to complete the measurements. During the summer the birds were commonly run for 6–9 days at each temperature (extremes of 3 and 18 days), but in winter they were run for longer periods, usually 10–18 days (only 6 days at −14°C). Summer measurements began on 24 May and continued through the next 3 months; winter measurements were made between 15 January and 18 March.

The sexes were distinguished by dissection at the termination of the experiments. The average weight of the males in the experiment from −13° to 35°C was significantly heavier than the females in both summer (males, 12.8 ± 0.03 g, n = 84; females, 12.3 ± 0.04 g, n = 35) and winter (males, 15.2 ± 0.16 g, n = 15; females, 13.8 ± 0.17 g, n = 17). The winter weight of each sex was significantly higher than its summer weight. Weights did not vary with temperature except that above 35°C they declined, reaching 10.2 g in males and 10.4 g in females at 40°C in summer.

Outdoor measurements.—Metabolism cages, each containing a single bird, were placed out-of-doors under overhead shelter but exposed to natural changes in air temperature, as recorded nearby, and photoperiod. Convective losses from air currents were reduced by nearly full protection from north and

TABLE 1. Regression equations ($\pm$ SE) of metabolism on temperature ($T = {}^\circ$C) for the indoor experiments (-13°–35°C). For sample sizes, see text.

Photo-period (h of light)	Sex	M_{kcal}	M_{mW}
		Gross energy	
10 (winter)	M	$22.18 - 0.359T \pm 0.95$	$1,076 - 17.41T \pm 46$
	F	$20.44 - 0.322T \pm 0.45$	$989 - 15.62T \pm 22$
15 (summer)	M	$21.62 + 0.0048T^2 - 0.5248T \pm 0.42$	$1,049 + 0.233T^2 - 25.45T \pm 20$
	F	$20.63 + 0.0057T^2 - 0.5401T \pm 0.45$	$1,001 + 0.276T^2 - 26.19T \pm 22$
		Excretory energy	
10	M	$6.52 - 0.68T \pm 1.05$[a]	$315 - 3.30T \pm 51$
	F	$6.36 - 0.0032T^2 - 0.0125T \pm 0.70$[a]	$308 - 0.155T^2 - 0.61T \pm 34$
15	M	$5.42 + 0.0018T^2 - 0.1644T \pm 0.16$	$263 + 0.087T^2 - 7.97T \pm 8$
	F	$4.58 - 0.0001T^3 - 0.0046T^2$ $- 0.1457T \pm 0.29$	$222 - 0.0048T^3 + 0.223T^2$ $- 7.07T \pm 14$
		Existence metabolism	
10	M	$15.59 - 0.285T \pm 0.23$	$756 - 13.82T \pm 11$
	F	$14.69 - 0.261T \pm 0.40$	$712 - 12.66T \pm 19$
15	M	$16.40 + 0.0001T^3 - 0.0002T^2$ $- 0.3662T \pm 0.42$	$795 + 0.0048T^3 - 0.010T^2$ $- 17.76T \pm 20$
	F	$15.87 + 0.0036T^2 - 0.3911T \pm 0.37$	$770 + 0.175T^2 - 18.97T \pm 18$

[a] Difference between sexes not significant.

west winds and partial protection from east and south winds. The birds were then provided with standard chick mash, and measurements were made over consecutive 3-day periods of food consumption, excreta, weight, and molt. Molt was quantified by counting the number and kinds of feathers dropped in the cage, following a procedure similar to that used by West (1960).

Four groups were run: 2 females from mid-August 1959 to February 1960, 3 males and 1 female from mid-August 1961 to mid-August 1962, 4 males and 2 females from mid-August 1961 until they died from cold stress during December and January, and 2 males and 2 females, which survived the 10-h photoperiod experiments indoors, from February to mid August 1962.

Cage activity.—In each different experiment at least part of the cages, usually all, had moveable perches and floors suspended from a spring and connected to a micro-switch and electric current so that movements of the birds were registered on Esterline-Angus 20-point recorders. The records were tabulated in terms of the number of different 4-min periods per hour in which the birds were active. A single recorded movement as well as continuous activity during a 4-min period constituted one unit of activity. The daily activity was separated into its diurnal and nocturnal components. In the experiments conducted indoors, this was based on the time that the lights were turned on and off, except that movements of the birds during the first few minutes after the lights were turned off were counted as a continuation of the diurnal activity. Out-of-doors with more gradual transitions between light and dark periods, nocturnal activity was counted as beginning when the birds first settled down for the night and as ending when birds that had shown no nocturnal activity began their diurnal activity. The times of sunrise and sunset or of civil or nautical twilight could not be used, because the differences in light intensities on clear and cloudy days affected the time of beginning or ending the nocturnal activity. Although not a precise method for quantifying total activity, variations in number of activity units per period of time have relative significance.

Carcass analysis.—Procedures followed practices described by Odum (1960). Briefly stated, carcasses, including feathers, were oven-dried at 105°C to constant weight to determine water content. Lipid determinations, mostly neutral fats, were based on ether extracts obtained in a Soxhlet apparatus. Kjeldahl equipment was used for measurement of nitrogen, and grams nitrogen times 6.25 gave grams of protein. The wet weight of the bird minus water, ether-soluble lipids, and proteins was assumed to be carbohydrate and ash.
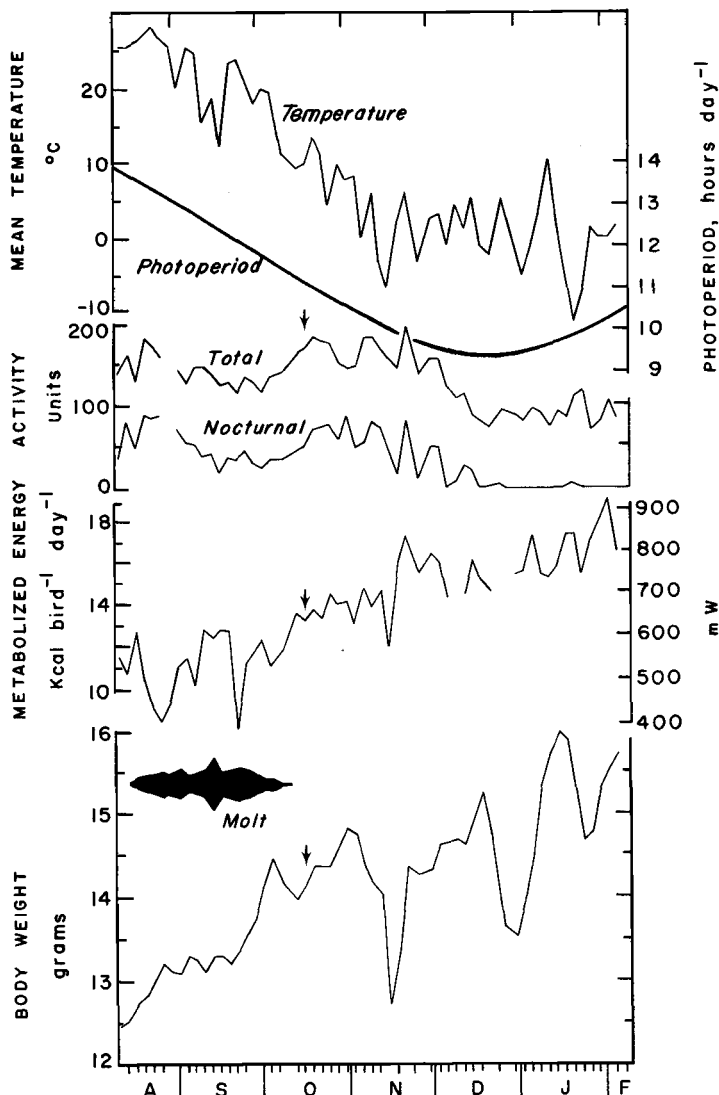
Fig. 3.   Average variations in three caged females out-of-doors during the autumn and winter, 1959–60. The arrow indicates accidental death of one bird.

RESULTS

INDOOR MEASUREMENTS

Regressions of metabolism on temperature.—The regressions of gross energy intake, excretory energy, and existence metabolism on temperature varied curvilinearly in summer but linearly in winter (Table 1, Fig. 2). Rates were slightly but significantly higher in males than females, except for excretory energy under the 10-h photoperiod. This is correlated with their greater weights.

Existence metabolism was significantly higher in the 15-h summer birds than in
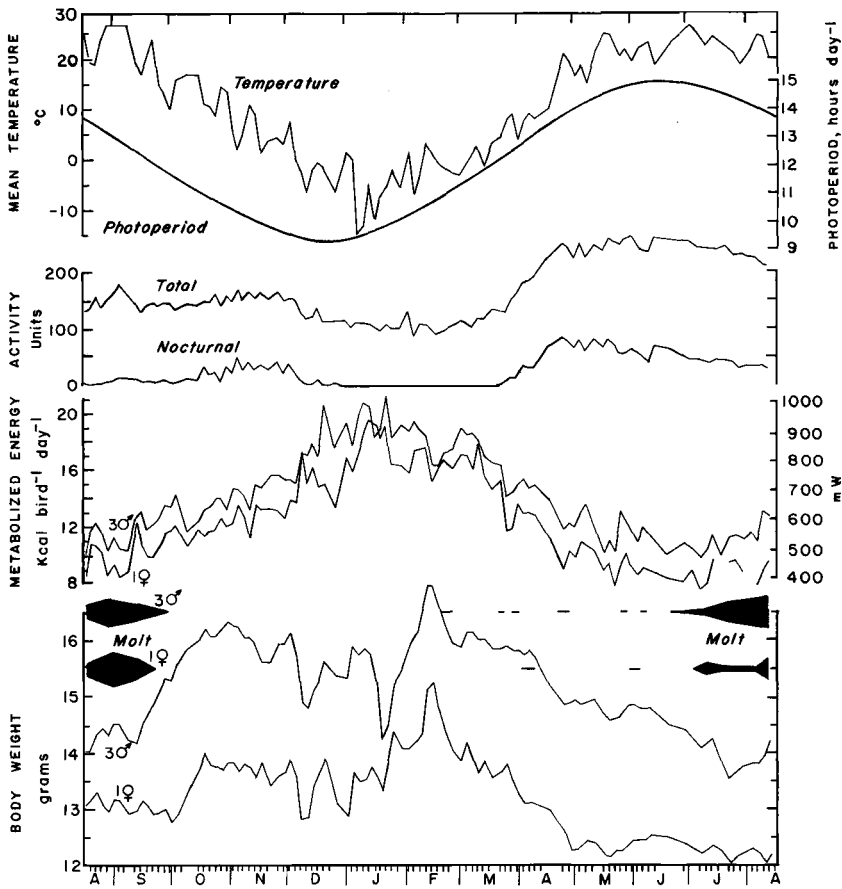
Fig. 4.   Average variations in caged birds that survived a full year (1961–62) out-of-doors. "Activity" also includes birds involved in Fig. 5.

the 10-h winter birds at temperatures below 0°C (Fig. 2). The birds had 5 more hours available for activity and feeding on the longer photoperiod, but this relation to photoperiod is modified somewhat by differences in temperature acclimatization (see below).

Tolerance of extreme temperatures.—All birds survived 4 days at −13°C during the summer and only half (3 males, 2 females) survived 6 days at −20°C. Unfortunately, no runs were made at intermediate temperatures. During the winter, all birds survived 18 days at −13°C, but only 2 (1 male, 1 female) out of 6 survived for 6 days at −14°C. The 4 birds that died were females. The greater tolerance to low temperature of the summer birds may be related to the longer photoperiods to which they were exposed.

No attempt has been made to determine tolerance of birds to high temperature in the winter. During the summer, existence metabolism decreased in males at temperatures above 35°C, well below rates predicted from the regression equations (Fig. 2). As noted above, weight also decreased. Four of 8 males died during a 3-day
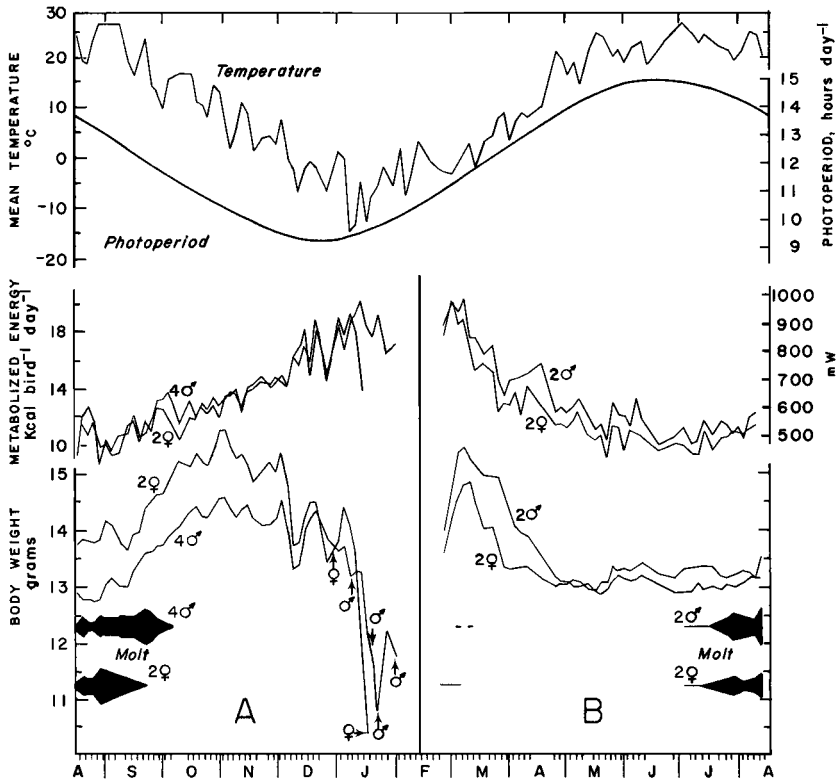
Fig. 5. Average variations in caged birds (A) that failed to survive out-of-doors (1961–62) and (B) that were placed out-of-doors after completion of experiments at constant temperatures and a 10-h photoperiod indoors.

period at 40°C and 2 died at 41°C. Both females survived 41°C; likewise their existence metabolism above 35°C decreased at approximately predictable rates. The number of records is small, but there is a suggestion that females tolerate heat better than males.

Cage activity.—Total 24-h activity of the birds under a 15-h photoperiod during the summer varied from 116 to 137 units over the temperature range of −2°–35°C. At higher temperatures, total activity decreased to 74 units at 41°C. For birds under 10-h photoperiods in the winter, total activity ranged from 67 to 98 units, with no significant differences between temperatures. Activity occurred throughout the light period, with seldom more than 1% of the total activity at either photoperiod occurring at night. Activity units per hour light were not significantly different between 10- and 15-h photoperiods, the greater total daily activity of the latter photoperiod being a reflection primarily of the more hours involved.

At the termination of the metabolic measurements of birds under the 10-h photoperiod in 1961, the photoperiod was increased to 15-h (18 March), while the temperature was maintained at 25°C. Within 3 days, nocturnal activity increased to 3% of the total and within 21 days it was 32%. Decreasing the photoperiod back to 10 h (6 April) for 40 days did not reduce the nocturnal activity.
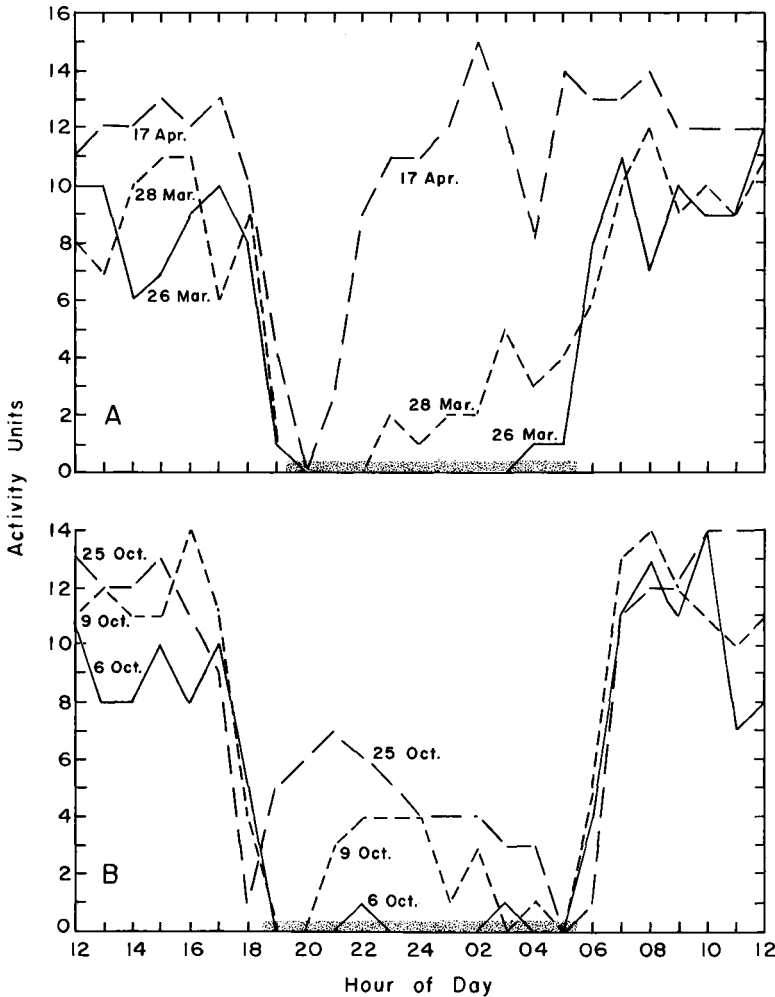
Fig. 6. Developing patterns of nocturnal activity (*Zugunruhe*) in (A) spring ($n = 11$) and (B) autumn ($n = 13$).

OUTDOOR MEASUREMENTS

General responses.—With decreasing temperature and photoperiod in the autumn and increasing temperature and photoperiod in the spring, the general metabolic response was an increase in metabolized energy in the autumn and a decrease in the spring, with rates in the summer fluctuating around a constant level (Figs. 3–5).

Weights began to increase near the end of the autumn molt and peaked during winter. Weights declined during the spring with no evidence of fattening during the migratory period. The increase in weight during the autumn is more likely in response to falling temperatures than as preparation for migration.

There was considerable nocturnal activity of three females during August 1959 (Fig. 3), but during the autumn of 1961 nocturnal activity did not become significant until molting was completed (Figs. 4, 5). Nocturnal activity mostly ceased during

December in both years but began again in late March and continued through the summer.

Nocturnal activity in spring was more intense than in autumn and extended over a longer period. The two nights of most intense activity in October averaged 49 units; in April they averaged 87 units. In the autumns of 1959 and 1961, nocturnal activity was recorded on 63 and 49% of the nights. In the spring, the birds were active on 95% of the nights.

In spring, nocturnal activity first developed in the hours before dawn, and, as intensity increased, it began earlier and earlier (Fig. 6A). When unrest was at its maximum, nocturnal activity did not start until about 2 h after dark but continued into daytime activity without a predawn break. In the autumn, nocturnal activity began and continued more intensely near the middle of the night (Fig. 6B). There was little or no activity immediately after dark or for 1 or 2 h before onset of light.

Nocturnal activity in spring was not correlated with increase in weight as the result of deposition of fat, as commonly occurs in migrant species (Figs. 4, 5). Whether premigratory deposition of fat occurs in free wild birds was not determined. In the autumn (Figs. 3, 4, 5) the marked increase in weight in September and October coincides more clearly with the cessation of molt than it does with the onset of nocturnal activity, as has been shown also for other species (Farner 1960, King and Farner 1963, Helms 1963).

Specific responses to "cold-waves."—During the winter of 1959–60, the two females were exposed to a drop in temperature to −6°C in November and to −10°C in January (Fig. 3). In each instance there was a sharp decrease in weight and some minor fluctuations in metabolized energy, with recovery of both to higher levels in subsequent warm periods.

There were two waves of moderate cold temperatures (−6°C) in December 1961 (Fig. 4, 5). Metabolized energy rose slightly during the first wave but not enough to prevent a drop in weight. During the second, both metabolized energy and weight dropped. In each instance there was recovery during subsequent warm weather except for 1 female, which died in early January.

Temperature dropped to −15°C during the 9 January 1961 period and stayed below 0°C for the rest of the month. There was an immediate rise in metabolized energy sufficient to maintain weight in 3 males and 1 female, but this high rate was not maintained in 4 males and 2 females, so that their weights declined and death ensued.

Of 10 birds exposed to cold periods in December and January 1961–62, 1 male died during exposure to −15°C, 1 male during exposure to −13°C, and 2 males during warmer periods following these low temperatures. One female died during a warmer period after exposure to −6°C, and one female died during a warmer period following exposure to temperatures of −15°C and −14°C. It thus appears that mortality often comes from failure to recover fully from cold stress and not from the cold stress itself. These low temperatures approximate the lower limit of temperature tolerance for the birds indoors under a 10-h photoperiod. Likewise, the maximum levels of metabolized energy attained by the birds out-of-doors of 21.3 kcal·bird^{-1}·day^{-1} (1,033 mW) in males and 19.7 kcal (955 mW) in females are comparable to the maximum rates of existence metabolism umder constant temperatures of 20.1 kcal·bird^{-1}·day^{-1} (975 mW).

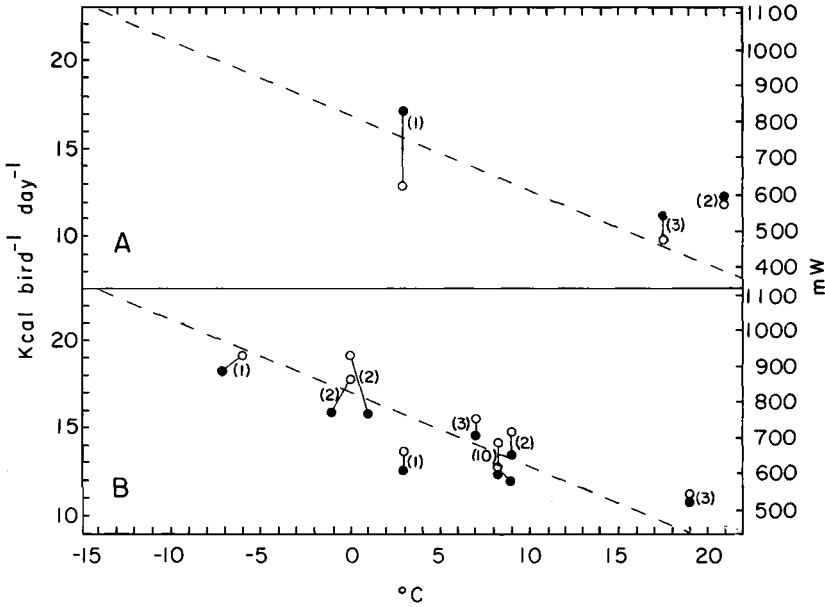Because there is often a drop in weight initially when the bird is subjected to cold

Fig. 7.   Comparison of existence metabolism at equivalent temperatures (± 1.0°C) between an early date (dot) and a later date (circle) when there was (A) an intervening cold period and (B) an intervening period with the same or higher temperature. Data for (A) were obtained between late October and May, data for (B) between March and late May. Numbers in parentheses indicate number of birds in comparison. All data and regression lines include both sexes.

stress, resulting from inadequate increase in metabolized energy, it appears that body fats are the first resource that is mobilized to overcome cold. The males that survived the winter of 1961–62 were heavier than the males that did not survive. The females that survived the winter of 1959–60 were also heavy. The one female that survived the winter of 1960–61 was lighter, however, than the two females that died. Heavier weight (more fat) is therefore advantageous for surviving over winter, but the ability to mobilize and continue high rates of metabolized energy is probably more important.

One interesting difference between the birds that survived over winter and those that did not is that those that survived began nocturnal activity 13–15 days earlier in the autumn than those that did not. The mean starting date for survivors was 10 October (range, 6–12 October) and for the nonsurvivors 23 October (range 13–30 October). The significance of this is not clear but indicates that the two groups differed in other ways than in resistance to cold. Because the birds were captured from the wild during the spring and summer, it is possible that migrants on their way to more northern latitudes were included in the experimental groups as well as local residents. Even if all the birds were potential residents, the observed differences between individuals may indicate genetic differentiation in an evolving population.

Acclimatization.—Existence metabolism was higher over winter following periods of cold temperature than it was at equivalent temperatures preceding these periods. Likewise, existence metabolism was lower in the spring following periods of the same or higher temperatures than it was preceding these periods (Fig. 7). These

periods during which existence metabolism was measured were close enough together so that the slight differences in photoperiod were not a factor. There is thus some acclimatization to a higher rate of metabolism in response to winter cold, but it is not sufficient to offset the influence of a 5-h shorter photoperiod compared with the summer.

The regression of existence metabolism on temperature for outdoor birds, using all the data for both sexes in the above comparisons (October through May) and weighting each temperature by the number of records at that temperature, follows the equation ($n = 46$):

$$M_{\text{kcal}} = 16.92 - 0.422T \pm 1.2, \text{ or } M_{\text{mW}} = 821 - 2.05T \pm 58.$$

This regression has a steeper slope than for indoor birds at constant temperatures and a 10-h photoperiod (Table 1). In winter, birds under fluctuating temperatures are more responsive to a drop in temperature than under constant temperatures (10-h photoperiod), although this is not true during the summer.

COEFFICIENTS OF FOOD UTILIZATION

Coefficients of food utilization or metabolizable energy coefficients (metabolized energy/gross energy intake) varied between individuals, but there were no consistent variations correlated with sex or temperature. The average coefficient of all birds under a 10-h photoperiod was 0.71 and under a 15-h photoperiod significantly higher, 0.79. The coefficient for birds out-of-doors varied between 0.72 and 0.86.

CARCASS ANALYSIS

Differences between wild and caged birds.—Seasonal changes in body components were followed only in caged birds because of the difficulty of securing wild birds in the winter. The relationship between caged and wild birds was determined only during the summer.

Although there were small differences in body components between wild birds killed in early June and late July, they are statistically insignificant (Table 2A, B, C). Birds that had been confined in the small experimental cages for a few weeks had essentially similar live weights and protein content as wild birds during July, but water content was lower and lipids, carbohydrates, and ash were higher. Birds that had been held in the larger flight cages tended to be intermediate in component values, and only the higher lipid content was significantly different from wild birds.

Seasonal changes.—Caged birds killed in November compared with those killed in July were significantly higher in live weight and all body components except water (Table 2C, D, E, F). A marked increase in live weight from July to November has also been noted in free-living Field Sparrows (Baldwin and Kendeigh 1938: 436–437). The increase in lipids is the largest component in the increase in live weight, 53% in birds in experimental cages and 57% in birds in the flight cages. The increase in protein content may be largely accounted for by the heavier plumage after the autumn molt (Kendeigh 1934: 335). Water as percent of live weight was lower in the November birds.

Odum and Parkinson (1951) with the White-throated Sparrow (*Zonotrichia albicollis*), Blem (1973) and Barnett (1970) with the House Sparrow (*Passer domesticus*), Helms and Smythe (1969) with the Tree Sparrow (*Spizella arborea*) and Carey

TABLE 2. Carcass analyses. The values given are averages (in grams ± SE) with the figures in parentheses being percentages of total live weight.

Live weight	Fat-free dry weight	Water	Lipids	Proteins	Carbohydrate and ash
A. Birds killed in the field 12–13 June 1962 (5 males, 1 female)					
13.45 ± 0.29	3.82 (28.4)	8.96 ± 0.20 (66.6)	0.671 ± 0.075 (5.0)	3.10 ± 0.02 (23.1)	0.713 ± 0.024 (5.3)
B. Birds killed in the field 19, 23 July 1962 (7 males, 5 females)					
12.97 ± 0.21	3.59 (27.7)	8.77 ± 0.16 (67.6)	0.609 ± 0.037 (4.7)	2.95 ± 0.05 (22.7)	0.646 ± 0.014 (5.0)
C. Birds from outdoor experimental cages killed 24 July 1962 (2 males, 2 females)					
12.77 ± 0.48	3.64 (28.5)	7.67 ± 0.37 (60.0)	1.46 ± 0.23 (11.4)	2.88 ± 0.05 (22.6)	0.765 ± 0.034 (6.0)
D. Birds from outdoor flight cages killed 24 July 1962 (3 males, 1 female)					
13.22 ± 0.43	3.66 (27.6)	8.50 ± 0.22 (64.3)	1.06 ± 0.15 (8.0)	2.94 ± 0.06 (22.2)	0.709 ± 0.089 (5.4)
E. Birds from outdoor experimental cages killed 8 November 1962 (5 males, 3 females)					
15.74 ± 0.27	4.25 (27.0)	8.45 ± 0.15 (53.7)	3.04 ± 0.17 (19.3)	3.33 ± 0.06 (21.1)	0.923 ± 0.032 (5.9)
F. Birds from outdoor flight cages killed 8 November 1962 (7 males, 4 females)					
15.20 ± 0.21	4.15 (27.3)	8.86 ± 0.08 (58.3)	2.19 ± 0.13 (14.4)	3.24 ± 0.05 (21.3)	0.913 ± 0.030 (6.0)
G. Birds that died from outdoor cold stress (4 males, 3 females)					
10.60 ± 0.41	3.79 (35.8)	6.64 ± 0.26 (62.6)	0.172 ± 0.008 (1.6)	2.73 ± 0.13 (25.7)	1.09 ± 0.08 (10.3)
H. Birds that died from indoor cold stress at constant temperature and 10-h photoperiod (4 females)					
9.45 ± 0.23	3.19 (33.8)	6.07 ± 0.13 (64.2)	0.184 ± 0.022 (1.9)	2.37 ± 0.09 (25.1)	0.847 ± 0.053 (9.0)
I. Birds that died from indoor cold stress at constant temperature and 15-h photoperiod (3 males, 2 females)					
11.17 ± 0.31	3.66 (32.8)	7.25 ± 0.23 (64.9)	0.256 ± 0.032 (2.3)	2.69 ± 0.07 (24.1)	0.976 ± 0.044 (8.7)
J. Birds that died from indoor heat stress at constant temperature and 15-h photoperiod (5 males)					
8.14 ± 0.35	2.94 (36.1)	4.72 ± 0.18 (58.1)	0.475 ± 0.161 (5.8)	2.37 ± 0.10 (29.2)	0.566 ± 0.041 (7.0)
K. Birds that died from starvation out-of-doors during the summer (1 male, 1 female)					
8.88 ± 0.32	3.08 (34.7)	5.55 ± 0.16 (62.1)	0.246 ± 0.119 (4.0)	2.44 ± 0.03 (26.9)	0.634 ± 0.019 (7.1)

et al. (1978) with the American Goldfinch (*Carduelis tristis*) found small increases in fat-free dry weight in the winter; Helms et al. (1967) found no such increase in the Dark-eyed Junco (*Junco hyemalis*) in the winter, while Zimmerman (1965b) states that in the Dickcissel (*Spiza americana*) males have significantly higher amounts of protein during the breeding season. The Dickcissel has an incomplete prenuptial molt of body feathers. Absolute water content did not vary significantly in any of these species except the American Goldfinch.

Death from cold stress.—There was a significant decrease in weight before the birds died from cold stress. Compared with birds killed in November (Table 2E, G), the loss of 5.14 g in birds dying from cold stress is accounted for by 54.3% lipids, 34.3% water, and 11.7% protein. Of the amount present in the November birds, the loss of lipids is 94.3%, of water is 21.5%, and of protein is 18.0%. The apparent slight gain in carbohydrate and ash is statistically insignificant.

Birds that died in experimental cages indoors under a constant 10-h photoperiod and temperature did so at a significantly lower weight than birds outdoors under fluctuating conditions (Table 2G, H). This was caused by lower amounts of water, lipids, and protein, the differences between which were not statistically significant, and carbohydrate and ash, the differences between which were. These differences are similar to those obtained by Zimmerman (1965b) with the Dickcissel.

Birds under a constant cold stress and a 15-h photoperiod died at a significantly higher weight, water, and protein content than birds under a 10-h photoperiod and with greater lipid reserve than birds outdoors (Table 2G, H, I). These differences cannot be attributed solely to the difference in photoperiod, as the birds under the 15-h photoperiod were summer acclimatized and the others were winter acclimatized. In the Dickcissel, birds dying during the summer under a 15-h photoperiod had body components of nearly the same values as those under a 10-h photoperiod (Zimmerman 1965b).

It appears that death from cold comes as lipids approach exhaustion. Nonfat dry weight may not be utilized until the lipid reserve drops below a certain level (Odum et al. 1964), and there may be little loss of water until protein and glycogen begin to be catabolized (Wishnofsky 1958). Actually, the percentage of water in the birds at time of death was higher than in nonstressed birds.

Death from heat stress.—Birds that died under heat stress and a 15-h photoperiod, compared with those that died as a result of cold stress (Table 2I, J), had a considerably lower weight, as a result of a great loss of water, as well as significant losses of protein, carbohydrate, and ash. The same differences were noted for the Dickcissel (Zimmerman 1965b) and White-throated Sparrow (Kontogiannis 1967). Higher levels of lipids remained at death from heat than from cold in the Field Sparrow and Dickcissel but not in the White-throated Sparrow. The loss of water is of special significance, because at high ambient temperature a rise in body temperature is resisted primarily by evaporative cooling.

Death from starvation.—Two birds starved to death during the summer (Table 2K). Weight and body components were similar to those in the heat stressed birds, except that the loss of water was not so great. Body components of the starved birds were also somewhat comparable with the birds that died under cold stress.

Overall.—Some birds that died from heat stress had a total weight as low as 7 g, while several birds that had not been stressed averaged 15 g. When all the carcasses are considered, regardless of how obtained, the increase in body components per

TABLE 3. Comparison of adjustments for overwintering and migration (values for sexes are averaged).

	Dickcissel[a]	Field Sparrow	House Sparrow[b]
A. *Migratory status*	Long distance migrant	Partial migrant	Permanent resident
B. *Lower limit of temperature tolerance:*			
10-h photoperiod (winter)	−1°C	−13°C	−31°C
15-h photoperiod (summer)	−2°	−13° to −20°	0°
Out-of-doors (winter)	−3°	−13° to −14°	−25°
C. *Maximum existence metabolism winter compared with summer*	−14%	−12%	+29%
D. *Existence metabolism lower under 10- compared with 15-h photoperiod*	At all temperatures	Below 0° only	Absent
E. *Increase in maximum metabolism per hour at 10- compared with 15-h photoperiod*	29%	32%	84%
F. *Increase in metabolized energy under fluctuating compared with constant conditions*	—	Below 12° only	At all temperatures
G. *Change in winter compared with summer:*			
Total weight	Decreases	+19%	+9%
Lipids	—	+108%	+67%
H. *Survival over winter*	None	One-half	Nearly all
I. *Premigratory fat deposition*	Present	None	None
J. *Zugunruhe*	Present	Present	Absent

[a] Zimmerman (1965a).
[b] Davis (1955), Blem (1973), Kendeigh et al. 1977.

gram increase in total weight averaged approximately 0.65 g water, 0.11 g protein, and 0.22 g lipids.

DISCUSSION

The Field Sparrow is intermediate in its metabolic responses to seasonal changes in temperature and photoperiod between those shown for the Dickcissel (Zimmerman 1965a), a long-distance migrant from the tropics, and the House Sparrow (Davis 1955, Blem 1973, Kendeigh et al. 1977), a permanent resident in east central Illinois. The responses of these latter two species are representative of migrant and resident species generally (Dolnik and Blyumental 1964, Berthold 1975) and of the differences between related migrant and resident species in the same family (Columbidae, Riddle et al. 1932, 1934), in the same genus (*Emberiza* Wallgren 1954), and between races in the same species (*Passer domesticus,* Dolnik and Gavrilov 1975).

In order to survive winter at northern latitudes, a bird must be able to tolerate temperatures considerably lower than those that occur during the breeding season. The Field Sparrow can tolerate lower temperatures than can the Dickcissel but not as low as the House Sparrow (Table 3B). There is very little seasonal variation in tolerance to low temperature in the Dickcissel or Field Sparrow but considerable variation in the House Sparrow. The House Sparrow is able to do this partly because it increases its metabolic capacity in the winter (Table 3C). The Field Sparrow shows some metabolic acclimatization to cold, but this is insufficient at low tem-

peratures to offset the shorter photoperiods. By decreasing its level of metabolic activity in the summer, the House Sparrow conserves energy and is better able to tolerate high temperature but thereby loses some of its tolerance to low temperature.

Changes in photoperiod have little effect on total energy intake in the House Sparrow, because its rate of feeding increases to compensate fully for shorter periods of daylight (Table 3D). The Field Sparrow is able to do this only at temperatures above 0°C, while the Dickcissel does not do so at any temperature. At its lower limits of temperature tolerance, the Field Sparrow increases its rate of feeding under a 10-h compared with a 15-h photoperiod, about the same as the Dickcissel, but these increases are only slightly more than one-third as much as in the House Sparrow (Table 3E).

Fluctuating outdoor temperatures stimulate higher metabolic rates than do constant temperatures (Table 3F). In the Field Sparrow this is evident only below 12°C; in the House Sparrow it occurs throughout the range of temperatures, as is true also for the Evening Grosbeak (*Hesperiphona vespertina*), another northern overwintering species (West and Hart 1966).

Dickcissels held outdoors decreased steadily in weight in late autumn as temperatures became lower and photoperiods shorter (Table 3G). The Field Sparrow, however, increased in weight and lipid storage as much, if not more, than the House Sparrow.

None of the caged Dickcissels survived the east-central Illinois winter of 1961–62. One-half of the Field Sparrows survived the winters of 1959–60 and 1961–62 (Table 3H). Caged House Sparrows normally survive over winter out-of-doors. On its wintering grounds (Fig. 1), the Field Sparrow is not normally exposed to mean monthly temperatures below 0°C, although temperatures along the northern border may occasionally drop below freezing. In east-central Illinois, the normal mean monthly temperature during December is −1.0°C, during January is −3.2°C, and during February is −1.6°C. During the above three winters, mean daily temperatures during December dropped below 0°C to more stressful levels on an average of 18 days and below −13°C on 1.3 days, during January below 0°C on 20 days and below −13°C on 3.0 days, and during February below 0°C on 18 days and below −13°C on 0.3 days.

The Field Sparrow differs from the Dickcissel but not from the House Sparrow in having no premigratory fat deposition but is similar to the Dickcissel in showing *Zugunruhe*.

The Field Sparrow thus shows some metabolic and behavioral responses to seasonal changes similar to resident species, but usually not to as pronounced a degree, and some responses similar to those of migrant species. We would expect that a species evolving permanent residency from a migratory status would pass through a stage such as that exhibited by the Field Sparrow. A resident species changing into a migratory one might also pass through such a stage. As there is evidence that several species have spread northward during the last century or so and there is no species known to have changed from residency to migratory behavior, however, the first alternative is more likely to be occurring. No significant differences were detected between individual Field Sparrows correlated with migratory status. We cannot exclude, however, the possibility that the responses are stabilized and that the species will continue as a partial migrant, but this seems improbable to us.

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