BIOENERGETICS OF THE DICKCISSEL, SPIZA AMERICANA[1]

JOHN L. ZIMMERMAN

Department of Zoölogy, Kansas State University, Manhattan

INTRODUCTION

THE success of a species is measured by its survival, and to survive is to work, to expend energy. Since economical utilization of energy is intimately associated with adaptation to a particular environment, the bioenergetics of a species is a basic determinant of its niche requirements. Endotherms have been emancipated from the normal thermal vagaries of their environment but, at the same time, have been shackled to an obligatory level of energy expenditure in order to maintain the homeothermic condition. This has been shown to be of grave importance to birds (Kendeigh, 1945). It has also been demonstrated that the maintenance of a satisfactory energy balance is reflected in the distribution of species (Cox, 1961), in the adjustment to the annual march of temperature and photoperiod (Davis, 1955), and in the dispartite range of migratory species (Seibert, 1949; Wallgren, 1954). Furthermore, availability of sufficient energy for the young has been suggested as the ultimate factor in the evolution of specific breeding seasons (Baker, 1938; Thomson, 1950; Marshall, 1951).

The dickcissel, *Spiza americana*, spends the greater part of the year in tropical America, but from May to September it breeds in the north temperate zone. This migrational pattern suggests that the short days and cold temperatures of winter are not compatible with its existence; yet within about the last twenty years (Packard, 1952) it has become a regular, although uncommon, winter visitant to New England and the middle Atlantic coast of the United States (Gross, 1956). This study is concerned with the energy requirements and temperature tolerances of the dickcissel in relation to its distribution and to the events in its annual cycle.

METHODS

Experimental work was conducted at Champaign, Illinois, from June to December, 1960, and from May, 1961, to October, 1962. From January to mid-May, 1961, additional investigations were made in Central America at the Canal Zone Biological Area, Barro Colorado Island, Canal Zone.

Illinois birds were obtained with Japanese mist nets in Piatt County, while in the tropics dickcissels were captured from wintering flocks near Tocumen and Pacora, Republic of Panama, and from

migrating flocks on Barro Colorado Island. Some birds used in Illinois during 1961 and 1962 were caught during the spring migration of 1961 in the Canal Zone and set to Champaign by air express.

Determinations of energy requirements were made with birds in small individual cages that measured 32 × 31.5 × 16.5 cm and that were equipped with a mechanical means of registering movement so that a continuous record of activity by individual birds was recorded on channels of a 20-point Esterline-Angus operations recorder running at a chart speed of 3.8 cm (1.5 inches) per hour (see Martin, 1964). Due to this slow chart speed, however, the amount of activity per hour was tabulated as the number of 4-min periods in which any activity was recorded. The total activity recorded during a 24-hr period was separated into that occurring during the dark and light periods. The cages were set in low, closely fitting pans in order that all spilled food, guano, and feathers could be collected.

Newly captured birds were given a mixture of seeds and then changed over to the experimental food by gradually decreasing the proportion of seeds. The experimental food was University of Illinois Chick Starter Feed No. 521, which was ground fine enough to pass through $\frac{1}{16}$-inch mesh screening so that it would be more homogeneous and thereby minimize selection by the birds. There was no significant difference in the caloric value of samples of food taken intermittently during the course of experiments in Illinois in 1960 (4.317 ± 0.02 kcal per g), or throughout 1961–1962 in Illinois (4.309 ± 0.02 kcal per g), or during the period of work in the Canal Zone in 1961 (4.242 ± 0.02 kcal per g). The change from seeds to mash was accomplished either while the birds were in large flight

cages or after they had become adjusted to the individual cages. A high level of mortality, occasionally as great as 50 per cent, occurred during this shift. Sufficient food was provided to allow ad libitum feeding, and water was always available. Because initial results suggested that the availability of water for drinking affects the maintenance of the Canada goose, Branta canadensis, at subfreezing temperatures (Williams, 1964), dickcissels were provided in some experiments with either snow (the most available form of moisture) or water when ambient temperatures were below freezing.

Both in Illinois and in the Canal Zone, experimental birds held outdoors were subjected to natural temperature, photoperiod, humidity, and air movements but were protected from precipitation and from direct insolation for most of the day. Work done at constant temperatures and photoperiods was accomplished in thermostatically controlled walk-in cabinets that provided temperatures from 45 C to 0 C, and in a smaller cabinet that ranged from 0 C to −80 C. Humidity was not closely controlled in these cabinets. Periodic psychrometric measurements revealed no relative humidity values differing from those reported by West (1960) for the cabinets in Illinois or by Cox (1961) for those at the Canal Zone Biological Area. At warmer ambient temperatures, humidity was not high enough to modify temperature-dependent metabolic responses (Salt, 1952; Wallgren, 1954). Incandescent lamps provided light of more than sufficient intensity at floor level for known photostimulated effects (West, 1960). West also measured air movement in the one cabinet utilizing forced air, and it was found to be of a magnitude that would not significantly affect the sensible tem-

perature and thereby bias metabolic measurement.

Three constant photoperiods were used in these experiments. Postnuptial birds were exposed to cold temperatures at a 10-hr photoperiod, that of the coldest period of the temperate winter. Other postnuptial individuals were subjected to high temperatures at a 12-hr period, that of their tropical wintering grounds. Since the wild population, exclusive of those wintering at temperate latitudes,

period. At the beginning and end of each run the birds were weighed at the same time of day on a balance accurate to 0.1 g. Fat was recorded on a modified McCabe Index (McCabe, 1943). Molt was quantified on the basis of the number of feathers dropped during a measurement period according to the following scheme: 1.0 equals one flight feather equals five body feathers equals fifteen head and neck feathers. The molt intensity value is the sum of all the shed

TABLE 1

AMBIENT TEMPERATURES AT DEATH

(Deg. C)

Condition	No. at Start	First Death (Deg C)	50% Mortality (Deg C)	No. surviving beyond Temperature of 50% mortality	Last Death (Deg C)
Cold stress, outdoors:[a]					
With snow..........	6	− 3	− 3	3	−16
With water........	10	− 4	− 8	5	−20
Cold stress, 15 hr:					
With snow..........	5	− 1	− 2	1	Not determined
With water........	5	−14	−14	1	Not determined
Cold stress, 10 hr:					
With snow..........	10	0	− 1	4	− 9
Heat stress, 12 hr......	8	42	44	3	Not determined
Heat stress, 15 hr......	10	43	44	2	Not determined

[a] Temperature given for outdoor birds is the mean temperature for 24 hr preceding death.

is exposed to the widest range of environmental temperatures on the breeding grounds (from near 0 C on occasional May nights to 40 C or higher on summer afternoons), spring birds were studied over the whole range of tolerable temperatures at a 15-hr photoperiod, that of the longest day at the latitude of central Illinois.

The measurement of metabolism was based on food consumption adapted from Kleiber and Dougherty (1934) and introduced for use with wild birds by Kendeigh (1949). The definitions of terminology used in this paper are given by Cox (1961). Metabolism was measured over a 2–5-day, but usually a 3-day

feathers in terms of their numerical equivalents. The uneaten food and the guano from each cage were dried to a constant weight at 68 C, then rapidly separated by using a $\frac{1}{16}$-inch mesh screen and weighed. The dry weight of a food sample from every period was determined so that the dry weight of the food supplied could be calculated from its wet weight.

Samples of food and guano were frozen for subsequent calorimetric analysis. Caloric values were determined with a Parr adiabatic oxygen bomb calorimeter by duplicate runs on each sample.

The lethal temperature at any photoperiod is defined as that temperature by

which 50% of the individuals exposed to the conditions had died.

Procedures for statistical analysis of data were taken from Dixon and Massey (1957) and Jacob and Seif (n.d.). A probability level of 0.05 was required for significance. The indicated variation associated with means is the standard error.

TEMPERATURE TOLERANCE

Table 1 gives the temperature at first death, 50% mortality (lethal temperature), and, for cases in which it was determined, the temperature at the last death. No summer females were used to determine the limits of tolerance at a 15-hr photoperiod, but for postnuptial birds at 10- and 12-hr photoperiods and those

TABLE 2

AVERAGE CALORIC VALUE OF GUANO[a]

(Kcal per g dry wt)

N	Date	Mean	N	Temperature (Deg C)	Mean
	Outdoors, Illinois, 1960			10 Hr, Cold	
6.......	June 29–July 11	3.604±0.03	8.......	2	3.502±0.02
6.......	Aug. 29–Sept. 28	3.516± .02	8.......	4	3.493± .03
6.......	Oct. 28–Nov. 10	3.665± .01	8.......	5	3.460± .03
6.......	Nov. 27–Dec. 21	3.681±0.03	8.......	10	3.458± .03
			8.......	13	3.613± .02
	Outdoors, Illinois, 1961–1962		8.......	21	3.607±0.03
10.......	May 25–July 18	3.496±0.02		12 Hr, Hot	
10.......	Sept. 5–9	3.421± .01			
10.......	Oct. 26–30	3.399± .02	8.......	30	3.418±0.02
10.......	Dec. 4–Jan. 11	3.510±0.01	8.......	39	3.586± .02
			8.......	43	3.569±0.03
	Outdoors, Canal Zone, 1961			15 Hr, Cold, 1961	
12.......	Jan. 31–Feb. 21	3.567±0.01			
12.......	Mar. 20–29	3.564± .01	10.......	13	3.513±0.06
12.......	Apr. 19–29	3.478±0.03	10.......	29	3.494±0.02
	12 Hr, 29 C, Canal Zone			15 Hr, Cold, 1962	
8.......	Jan. 31–Feb. 28	3.588±0.05			
8.......	Mar. 20–30	3.562± .01	10.......	− 6	3.579±0.02
8.......	Apr. 13–29	3.447±0.02	10.......	3	3.557± .01
			10.......	21	3.532±0.02
				15 Hr, Hot	
			10.......	21	3.505±0.01
			10.......	37	3.541± .01
			10.......	43	3.525±0.02

[a] For each set of conditions values within the same brace or outside of braces are similar; values not in the same brace are significantly different from each other; values outside of braces are significantly different from values within braces.

exposed to the outdoor conditions of the Illinois winter there was no difference in tolerance limits between the sexes.

CALORIC VALUE OF THE GUANO

In each of the environmental situations in which metabolism was measured, no significant difference in the caloric value of the guano was detected between individuals or between the sexes. There were, however, significant differences between the mean values according to date or environmental temperature under all conditions except at a 15-hr constant photoperiod (Table 2).

EXISTENCE ENERGY

Body-weight data are presented according to temperature and photoperiod in Table 3. The weights of the males were significantly different from those of the females, except at 15 hr. At this photoperiod the weights of the few females used were similar to the males due to their longer retention of vernal-fat stores. The weight trend with temperature was toward significantly minimum levels at both the low and high lethal temperatures in all birds except females at 10- and 15-hr photoperiods. Molt was negligible in all these birds. Activity data for

TABLE 3

BODY WEIGHT AT EXISTENCE ENERGY CONDITIONS

(Grams)

Temp.	Males	Females	Temp.	Males	Females
	10-Hr Photoperiod			15-Hr Photoperiod	
− 6....	31.4±0.32 (2)[a]	24.7±0.47 (5)	−12....	28.3±0.68 (4)	....
− 3....	30.7 (1)	25.4± .17 (5)	− 8....	28.1±0.53 (4)	....
− 1....	29.6± .35 (5)	25.9± .14 (2)	− 6....	28.0±0.44 (6)	....
2....	30.6± .15 (2)	24.7± .30 (4)	− 4....	28.2±0.30 (9)	....
3....	31.4± .58 (6)	26.5± .77 (7)	− 2....	28.1±0.33 (10)	....
4....	30.6± .61 (15)	26.6± .54 (10)	− 1....	28.8±0.03 (20)	....
5....	32.8± .64 (9)	26.4± .68 (8)	1....	29.8±0.35 (15)	....
7....	32.3± .78 (10)	26.8± .66 (13)	2....	30.0±0.29 (21)	....
9....	31.5± .40 (5)	25.5± .13 (4)	5....	32.0±0.67 (26)	29.8±1.66 (6)
10....	35.5± .81 (11)	27.1± .83 (7)	13....	34.1±0.80 (27)	34.4±1.02 (4)
11....	31.4± .30 (9)	25.6± .10 (9)	21....	34.0±0.57 (48)	34.6±0.54 (4)
13....	29.7± .70 (7)	26.1± .15 (7)	29....	40.3±1.42 (5)	34.2±0.89 (9)
15....	29.4± .63 (4)	25.5± .35 (3)	31....	33.4±1.52 (8)	....
16....	30.5± .46 (6)	25.1± .25 (6)	35....	32.9±1.05 (13)	....
18....	30.2± .38 (8)	24.5± .35 (8)	36....	30.6±0.49 (4)	....
20....	29.5±0.25 (4)	25.7±0.81 (4)	37....	30.0±0.45 (2)	....
			38....	29.6±0.68 (4)	....
	12-Hr Photoperiod		39....	27.2±0.50 (17)	....
			40....	27.1±0.43 (14)	....
30....	32.5±1.08 (6)	27.0±1.04 (6)	42....	26.0±0.39 (14)	....
33....	31.8±1.39 (4)	27.9±1.37 (7)	43....	25.2±0.49 (8)	....
34....	30.8±2.80 (2)	30.0±3.10 (2)	44....	23.1±0.60 (7)	....
35....	37.2±1.29 (5)	27.9±1.42 (5)			
38....	30.5±1.57 (5)	24.8±0.47 (4)			
39....	29.5±1.52 (8)	24.8±0.46 (8)			
40....	31.4±3.13 (4)	24.3±0.65 (6)			
42....	27.5±1.48 (8)	22.7±0.46 (4)			
44....	23.4±0.36 (7)	19.3±0.72 (4)			

[a] Number in parentheses is number of measurements taken at each temperature, each measurement being the average of the weights at the beginning and end of each measurement period, providing that these weights differed by no more than 0.5 g.

the birds under constant conditions are presented in Table 4.

Relationships with temperature.—The regressions between ambient temperature and gross energy (kcal of food eaten), excretory energy (kcal of guano eliminated), and metabolized energy (gross energy minus excretory energy) at existence energy levels are presented in Table 5. There are no significant regressions from 37 C to 44 C in 15-hr birds or from 38 C to 44 C in 12-hr birds. Furthermore at a photoperiod of 12 hr there is no significant regression from 30 C to 35 C in gross energy or excretory energy per bird per day in males or metabolized energy per bird per day in either sex. In all other cases these functions express a generally inverse relationship with tem-

perature. The formulas were calculated by the orthogonal polynomial method of Carmer and Seif (1963).

Gross energy (G.E.) per bird per day.— At both 10 and 12 hr, gross energy in males was greater than, and significantly different from, the level of the females, although only at 5 C and 10-hr photoperiod was there a significand difference in the rate per hour of photoperiod (Table 6). These differences reflect the larger size of the males. This is made evident by the fact that at 15 hr, where females were similar in weight to the males, there is no significant difference in gross energy intake nor in the rate per hour. Gross energy per bird per hour of photoperiod at 15 and 12 hr is similar, and even though their daily intake is less, the

TABLE 4

AVERAGE ACTIVITY AT CONSTANT PHOTOPERIODS

Temp. (Deg C)	N^a	Total[b]	% Nocturnal	Temp. (Deg C)	N^a	Total[b]	% Nocturnal
	10 Hr				12 Hr		
− 1.........	24	141	6	40.........	24	145	10
1.........	18	129	5	41.........	8	158	13
3.........	30	136	10	42.........	48	153	22
4.........	106	145	10	44.........	74	194	34
5.........	30	146	14				
7.........	167	142	14		15 Hr		
9.........	36	144	12				
10.........	99	143	10				
11.........	78	145	8	− 1.........	14	175	2
13.........	36	146	13	1.........	12	169	2
15.........	37	150	15	2.........	18	180	2
16.........	36	151	17	5.........	36	182	1
18.........	57	137	16	13.........	18	188	5
20.........	79	133	10	21.........	16	191	8
				31.........	14	107	3
	12 Hr			35.........	11	142	4
				36.........	30	169	3
				37.........	6	166	5
30.........	15	148	5	38.........	12	168	9
33.........	15	147	10	39.........	12	153	4
34.........	26	139	11	40.........	18	150	6
38.........	36	129	10	42.........	12	160	10
39.........	36	141	9	44.........	2	104	19

[a] N = (No. of birds) × (no. of days).

[b] Total is no. of 4-min periods during 24 hr. bird was active at least once.

hourly rate of intake is greater in 10-hr birds and significantly different from that of 15-hr birds.

Excretory energy (E.E.) per bird per day.—These regressions are also presented in Figure 1. Males have a significantly greater average output of guano than females, except at a 15-hr photoperiod. The cubic regressions in 10-hr birds indicate a reduction in the change of the rate of excretory energy with temperature from 7 C to 12 C in males and from 7 C to 13 C in females. In males at 15 hr there is a slight decrease from 9 C to 21 C. The fact that data for excretory energy in 15-hr females are illustrated by a linear rather than a cubic regression probably results from these data being collected from only 5 C to 29 C, a range encompassing the span of reduced output and mostly excluding the ranges of greater increase in output at higher and lower temperatures in males. At 15 hr this reduction is due to a decrease in the amount of guano eliminated, since the same caloric value per gram was used for calculations at all applicable temperatures. At 10 hr the rate of change decreases as temperature drops 20 C to 13 C. Since there was no significant differences in the caloric value of the guano in this temperature range

TABLE 5

REGRESSIONS BETWEEN TEMPERATURE AND METABOLISM[a]

Photoperiod and Valid Range for x (Deg C)	Gross Energy per Bird per Day	Excretory Energy per Bird per Day
10 hours:		
— 1– 20....	♂♂$y=36.152-0.700388x$	♂♂$y=10.793-0.653309x+0.070824x^2-$ $0.002521x^3$
— 1– 20....	♀♀$y=33.273-0.626234x$	♀♀$y=10.249-0.841093x+0.088752x^2-$ $0.002875x^3$
12 hours:		
30– 35....	♂♂ none, $y=14.916$	♂♂ none, $y=4.320$
38– 44....	♂♂ none, $y=12.462$	♂♂ none, $y=3.806$
30– 35....	♀♀ $y=32.915-0.590952x$	♀♀ $y=10.591-0.20748x$
38– 44....	♀♀ none, $y=10.180$	♀♀ none, $y=2.949$
15 hours:		
–12–– 2....	♂♂ $y=44.755-0.791718x$	♂♂ $y=15.221-0.216629x$
— 2– 36....	♂♂$y=41.856-1.10377x+0.028719x^2-$ $0.000558x^3$	♂♂ $y=13.193-0.41706x+0.014562x^2-$ $0.000283x^3$
37– 44....	♂♂ none, $y=13.332$	♂♂ none, $y=4.028$
5– 29....	♀♀ $y=40.713-0.783451x$	♀♀ $y=11.534-0.238011x$

	Metabolized Energy per Bird per Day	Metabolized Energy per Gram per Day
10 hours:		
— 1– 20....	♂♂ $y=25.369-0.054869x-$ $0.069765x^2+0.002484x^3$	♂♂ $y=0.84767-0.024044x+0.000391x^2$
— 1– 20....	♀♀ $y=24.374-0.51765x$	♀♀ $y=0.98067-0.034464x+0.000757x^2$
12 hours:		
30– 35....	♂♂ none, $y=10.597$	♂♂ $y=0.68685-0.011183x$
38– 44....	♂♂ none, $y=8.657$	♂♂ none, $y=0.31595$
30– 35....	♀♀ none, $y=9.724$	♀♀ $y=0.86774-0.015758x$
38– 44....	♀♀ none, $y=7.231$	♀♀ none, $y=0.30801$
15 hours:		
–12–– 2....	♂♂ $y=29.583-0.569651x$	♂♂ $y=1.05050-0.020072x$
— 2– 36....	♂♂ $y=28.535-0.517091x$	♂♂ $y=0.98644-0.042318x+$ $0.0012598x^2-0.0000171x^3$
37– 44....	♀♀ none, $y=9.350$	♂♂ none, $y=0.35711$
5– 29....	$y=29.179-0.545425x$	♀♀ $y=0.96672-0.020573x$

[a] y in kcal; x in deg C.

(see Table 2) and accordingly a single value was used in calculations, this decrease is again due to a reduction in the amount of guano produced. The reason for reduced guano output was not investigated in these experiments. Possible explanations may involve reduced gut motility resulting from increased adrenal gland (chromaffin cells) activity and sympathetic stimulation associated with the demands of thermoregulation (Turner, 1960, p. 223–233; Höhn, 1961) or an increase in the length of the gut with the advent of "winter" conditions (Davis,

TABLE 6

RATE OF FEEDING

(G.E. in kcal per bird per hr of photoperiod[a])

Photoperiod and Temperature (Deg C)	Male	Female
15 hours:		
− 1....	2.939±0.06 (22)[a]	....
5....	2.436± .03 (25)	2.431±0.05 (6)
13....	2.088± .05 (27)	2.058± .12 (4)
20–21....	1.655± .03 (48)	1.601±0.04 (4)
30–31....	1.240± .03 (8)	....
38....	0.859± .09 (4)	....
42....	0.941±0.04 (14)	....
12 hours:		
30–31....	1.548±0.19 (7)	1.183±0.08 (7)
38....	0.875± .12 (5)	0.918± .13 (4)
42....	0.944±0.08 (8)	0.888±0.06 (5)
10 hours:		
− 1....	3.630±0.11 (6)	3.541±0.20 (2)
5....	3.223± .09 (10)	2.930± .07 (10)
13....	2.713± .10 (8)	2.692± .06 (7)
20–21....	2.315±0.09 (2)	2.109±0.08 (4)

[a] The number in parentheses is the number of observations.

1961). The reduction of feces output, even while gross energy is increasing, must result from longer retention of food in the gut. This retardation of the movement of the gut contents is of apparently such slight magnitude in 15-hr males that no change in the caloric value of the guano resulted. At 10 hr, however, there was a significant decrease between 13 C and 10 C in the caloric value per gram of guano (see Table 2) which was probably

due to the more complete digestion and absorption allowed by the decreased rate of passage of the gut contents. This reduction in the caloric value per gram accentuates the decline due to the amount of guano so that the regression of excretory energy reaches an inflection and in females actually becomes positively correlated with temperature! An estimation
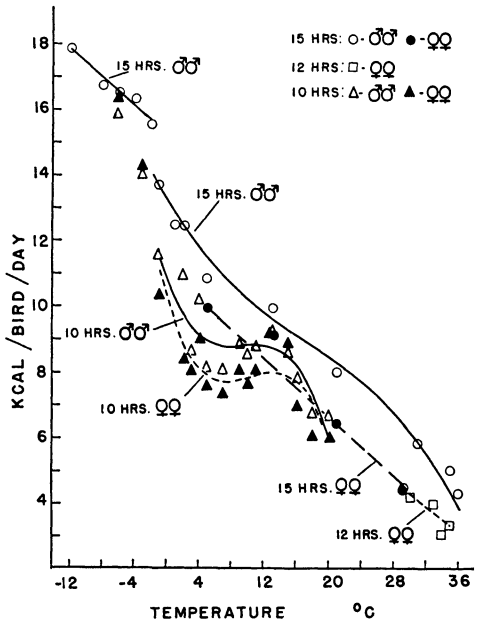

FIG. 1.—Relation of excretory energy to ambient temperature.

of the energy conservation resulting from this response can be made by linearly extending the rates of the curves at the highest temperatures in Figure 1. In each case the difference in height between the linear and the observed curve indicates the kilocalories per bird per day saved. There are no further significant changes in the calories per gram of the guano as temperature decreases, so the curves again reflect changes in the amount of excrement produced. With continued decrease in temperature and a concomitant greater and greater food intake, the limit in reduced amounts of feces is ap-

parently reached, the second inflection in the curves occurs, and excretory energy again increases. This change may be simply a proportional increase above maximum gut capacity due to the increasing gross energy.

Metabolized energy (M.E.) per gram per day.—The relationship between basal metabolic rate and body size in birds has been reviewed by King and Farner
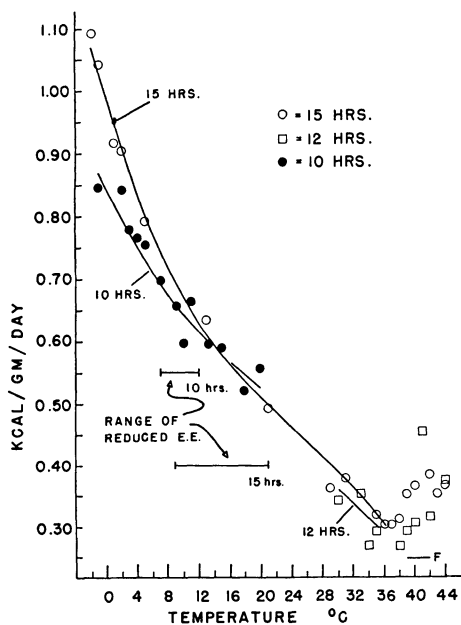

FIG. 2.—Relation of metabolized energy of males to the ambient temperature.

(1961), but there has been no analysis reported concerning the dependency of existence levels of metabolism on weight. Since the weight of the dickcissel under experimental conditions varied according to sex and ambient temperature, some adjustment for body size seemed desirable. In lieu of any demonstrated relationship between existence energy and weight, the metabolized energy was analyzed on a per gram wet-weight basis in an attempt to make some sort of parity possible. Only at a 10-hr photoperiod was there a significant difference be-

tween the sexes in the M.E. per g per day. At 12 hr, even though males were significantly heavier than females, the amounts of the M.E. per g per day were similar.

The levels of the curves of 15-hr birds of both sexes are generally higher than those of 10-hr birds, but this difference is only significant at −1 C in the males. The higher level of metabolism of 15-hr males is significantly different from that of 12-hr males. This increase in metabolized energy at long photoperiods does not grant the bird any great physiological advantage under cold stress. The lower lethal temperature at 15 hr was reduced one degree below that at 10 hr, but this seems insignificant in comparison to the magnitude of the metabolic difference. A longer photoperiod would afford an advantage if G.E. per bird per hour at 15 hr were at least equal to the intake rate at 10 hr so that the longer day would allow greater energy storage for the dark period, which is critical for cold-survival (Kendeigh, 1945). But the opposite is the case (see Table 6). The rate of M.E. per bird per hour likewise is inversely related to photoperiod. Similar results have been reported in other species (Davis, 1955; West, 1960; Cox, 1961). I feel that this difference is simply an obligatory demand on birds at a longer photoperiod due to the maintenance of body temperature several degrees above the nocturnal level for a longer time and the greater total activity (see Table 4) during the longer light period. The percentage of nocturnal activity, on the other hand, was similar and generally low at all photoperiods so that the metabolic difference was not due to nightly unrest, as suggested by West (1960) for the tree sparrow, *Spizella arborea.*

In Figure 2 these data are illustrated for males at each photoperiod. The re-

gressions for females have been omitted for clarity. They differ at all photoperiods from those of the males in having a higher average level and a greater rate of linear increase, although these differences cannot be significantly demonstrated in every case. Even though there is no significant regression at 15 hr from 37 C to 44 C or at 12 hr between 38 C and 44 C, there is an upward trend in the M.E. per g per day within these temperature ranges at each photoperiod. It therefore appears that there is no zone of thermal neutrality, but just a point of lowest metabolism at the critical temperature. With 15-hr males this occurs at 36 C at a level of 0.298 kcal per g per day, while with 12-hr males it is at 38 C at a level of 0.267 kcal per g per day. The lack of a zone of thermal neutrality in small birds as well as the non-linear relationship between metabolism and temperature has been reviewed by West (1962).

The basal metabolic rate was not measured, but it was estimated on the basis of weight by averaging the values obtained utilizing the equations of Brody and Proctor (1932) and King and Farner (1961)(line F, Fig. 2). As is to be expected at existence energy feeding levels and with the birds awake and active, the metabolism at thermal neutrality is increased above the basal rate.

The regressions of M.E. per g per day in males at 10- and 15-hr photoperiods intersect at 15 C, that at 15 hr increasing more rapidly than the 10-hr rate at temperatures below this point. Although data were not collected above 20 C in 10-hr birds, it seems reasonable to assume that this quadratic regression would actually be cubic and follow that of the 15-hr males with increasing temperature in order that metabolized energy would approach a moderate level at thermal neutrality. From the critical tempera-

ture to 15 C the curve at 15 hr is almost linear, and it is suggested that the 10-hr curve would not differ significantly. The rapidly increasing effect of physical regulation necessitates only moderate metabolic increases in this temperature range. Since the curves diverge below 15 C, indicative of a photoperiod differential in the metabolic response, and since the mechanisms of physical regulation should show no photoperiod difference, it is hypothesized that the role of chemical regulation becomes of greater importance below 15 C in the male dickcissel. If there were no change in the relative roles of chemical and physical regulation, the curves would continue at the same linear rate below 15 C. Both curves, however, increase at an increasing rate as temperatures decrease to the lower lethal limit. Calculations of insulation indices (see West, 1962) for these birds show that, after rapidly increasing with decreasing temperature, insulation is 93% of the maximum in 10-hr birds and 97% of the maximum in 15-hr birds at 15 C. The maximum insulation index is reached at 5 C and 10 C in 10-hr and 15-hr males, respectively. In females the metabolized energy regressions at 10 and 15 hr intersect at a similar temperature (16 C).

The temperature ranges of reduced excretory energy at 10 and 15 hr are indicated in Figure 2. The relationship of these reductions to the intersection of the metabolized energy curves as well as the effect of reduced excretory energy on the efficiency of food utilization (see below) lead to the conclusion that this energy saving effect is a real metabolic adjustment for thermoregulation.

Efficiency of food utilization.—This measure is defined as the metabolized energy divided by the gross energy times 100 (Fig. 3). Although only the data for 15-hr males span the entire range of temperatures tolerated, the other photoperi-

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ods support the observation that there are two peaks of efficiency. Kendeigh (1949), Seibert (1949), and West (1960) found that the efficiency of utilization increased from low temperatures to high temperatures, and Davis (1955) described a single peak at 18 C. In the dickcissel, one peak is at the higher temperatures, just below the critical temperature for 12-hr birds (35 C) and a few degrees below the critical temperature in

ciency of utilization rises sharply and exceeds that of the 15-hr males, whose reduced excretory energy results only from a decline in the amount of guano eliminated.

Existence energy at 12 hr with constant temperature.—In order to measure the existence energy of wintering dickcissels, birds were kept on Barro Colorado Island at a 12-hr photoperiod and at a constant temperature that approximated the aver-
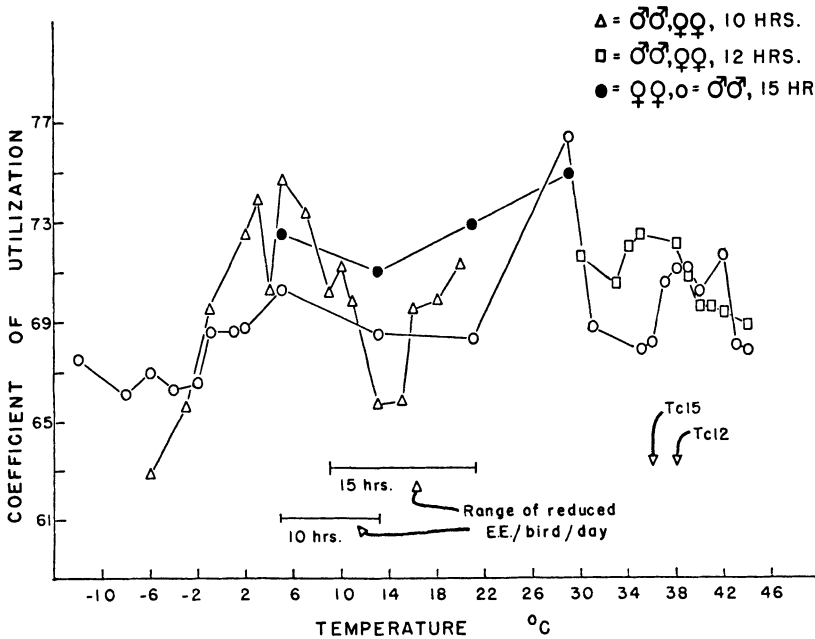

Fig. 3.—Efficiency of food utilization at various temperatures at 10-, 12-, and 15-hr photoperiod

15-hr birds (29 C). The second peak, shown in 15- and 10-hr birds, is associated with the period of reduced excretory energy output. An increase in the efficiency of food utilization begins just at the point of inflection in the excretory energy curves for 15-hr males (21 C) and 10-hr birds of both sexes (13 C). In 10-hr birds, whose reduced excretory energy results from both a decrease in the amount of guano and a significant drop in its caloric value per gram, the effi-

age for their winter range in Panama (Table 7). The weights of males are significantly different from the females. As with birds under a changing temperature regime at 12 hr, G.E. per bird per day, E.E. per bird per day, and M.E. per bird per day are greater in males than in the females, while there is no significant difference between the sexes in M.E. per gram per day. Molt and fat classes in these birds were similar to birds held outdoors in the Canal Zone.

MEASUREMENTS UNDER
OUTDOOR CONDITIONS

The greater weight of males is significantly different from that of females. Table 8 compares average weights at several periods throughout the year that are indicative of the course of the annual weight cycle (see Figs. 5–7). High weight is associated with premigratory fat deposition, and there is no difference between the magnitudes of the spring and autumn responses.

Birds held outdoors beyond the time of fall migration and exposed to the Illinois winter decreased steadily in weight from the premigratory peak and eventually died under cold stress. This positive relation with fall and winter tem-

TABLE 7

EXISTENCE ENERGY AT 29 C AND 12-HR PHOTOPERIOD

(Kcal)

	Males	Females
G.E. per bird per day.......	18.250 ±0.94	14.991 ±0.53
E.E. per bird per day.......	5.826 ±0.33	4.771 ±0.24
M.E. per bird per day......	12.425 ±0.62	10.220 ±0.29
M.E. per g per day........	0.3575±0.02	0.3677±0.01
Wet weight................	35.1 ±1.46	28.1 ±1.65
N........................	5	5

TABLE 8

WEIGHTS OF OUTDOOR BIRDS

(Grams)

Date[a]	Condition	N	Mean[b]
Males:			
Feb. 8, 1961.........	Tropical winter	7	28.5±1.17
Aug. 12, 1961.........	Postnuptial molt	6	28.5±0.58
Dec. 1, 1960.........	Temperate winter	5	29.8±1.28
Dec. 14, 1961.........	Temperate winter	5	29.9±0.60
Dec. 26, 1961.........	Temperate winter	4	30.0±0.70
Apr. 6, 1961.........	Prenuptial molt	7	30.2±0.78
Mar. 25, 1961.........	Tropical winter	7	31.6±0.68
Aug. 31, 1960.........	Temperate summer	5	35.0±1.60
Sept. 23, 1961.........	Stored autumnal fat	6	36.8±1.96
May 3, 1961.........	Stored vernal fat	7	37.5±1.03
Oct. 15, 1960.........	Stored autumnal fat	5	38.6±2.20
June 19, 1961.........	Stored vernal fat	4	40.1±2.14
Females:			
Dec. 1, 1960.........	Temperate winter	1	22.9
Dec. 26, 1961.........	Temperate winter	2	23.4±0.24
Aug. 31, 1960.........	Temperate summer	1	24.0
Dec. 11, 1961.........	Temperate winter	4	25.0±0.39
Feb. 18, 1961.........	Tropical winter	4	25.1±1.44
Aug. 16, 1961.........	Postnuptial molt	4	25.4±0.23
Apr. 4, 1961.........	Prenuptial molt	5	25.8±1.28
Sept. 25, 1961.........	Stored autumnal fat	4	29.0±0.58
June 16, 1961.........	Stored vernal fat	3	31.1±1.11
May 1, 1961.........	Stored vernal fat	7	32.6±1.35
Oct. 15, 1960.........	Stored autumnal fat	1	34.2

[a] Mid-date of measurement period.

[b] Means within the same brace are similar; means not inclosed by the same brace are significantly different.

peratures was paralleled by birds in constant-temperature cabinets under a decreasing cold temperature regime. This response is directly opposed to that of temperature-wintering species in which there is an inverse weight response to temperature (Baldwin and Kendeigh, 1938; Odum and Perkinson, 1951; Davis, 1955; Helms and Drury, 1960). The dickcissel cannot "overcompensate" un-

period. This molt, which is certainly non-adaptive in that it occurs at temperatures when maximum insulation is needed, probably results from some disruption arising from cold stress.

Average total daily activity and the average percentage of nocturnal activity per day are illustrated for 1961 in Figure 4. Probably only the abrupt increases in nocturnal activity beginning at the end
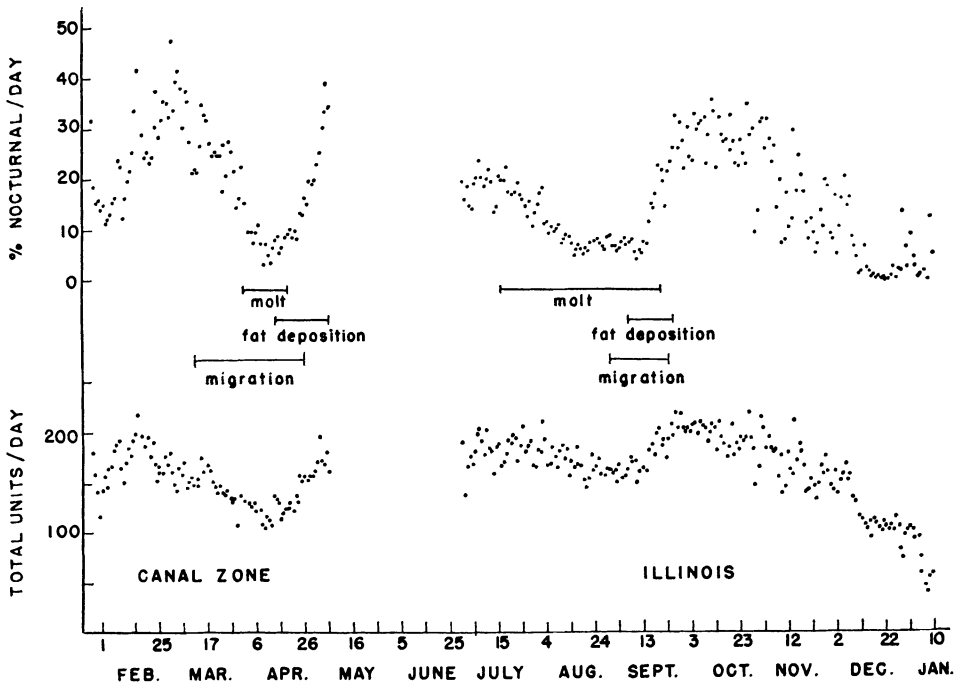

FIG. 4.—Activity of birds caged outdoors in the Canal Zone and in Illinois during 1961

der the influence of decreasing temperatures as do temperate winter residents as a means of adaptation to winter cold (Kendeigh, West, and Cox, 1961).

The two annual molts of captives corresponded to these molts in the wild population except that the molting period was somewhat protracted. An abnormal molt, occasionally very abrupt and heavy and involving only the body feathers, occurred in birds exposed to the Illinois winter, and also in birds at colder temperatures at a 10-hr constant photo-

of April and during mid-September, being coincident with premigratory fat deposition and overlapping the period of the species' normal migration, can be properly considered as expressions of *Zugunruhe*.

DISCUSSION

Productive energy.—The productive energy (metabolized energy minus existence energy) calculated for outdoor birds along with the time course of their weight and molt, and the environmental tem-

perature are presented in Figures 5–7. In general, periods of negative productive energy, when the bird is in a negative energy balance, are characterized by loss of weight and usually a reduction in total activity. Positive productive energy allows work beyond existence and is correlated with weight increase and premigratory fat deposition, molt, and higher activity levels, particularly greater nocturnal activity.

Maximum potential energy.—The maximum potential energy, that is, the highest metabolized energy measured, is significantly different between photope-

riods, that at 15 hr being greater than that at 10 hr. Long days, therefore, are advantageous in terms of the maximum level of available metabolized energy. At a 15-hr photoperiod the maximum potential energy was not ascertained in females since they were not measured at the lowest temperature that could be tolerated, but this value was calculated on the basis of the percentage difference between the sexes at 10 hr.

Distribution, migration, and energy balance.—The area of greatest breeding density of the dickcissel (Aldrich, 1948) is generally congruent with the tall-grass
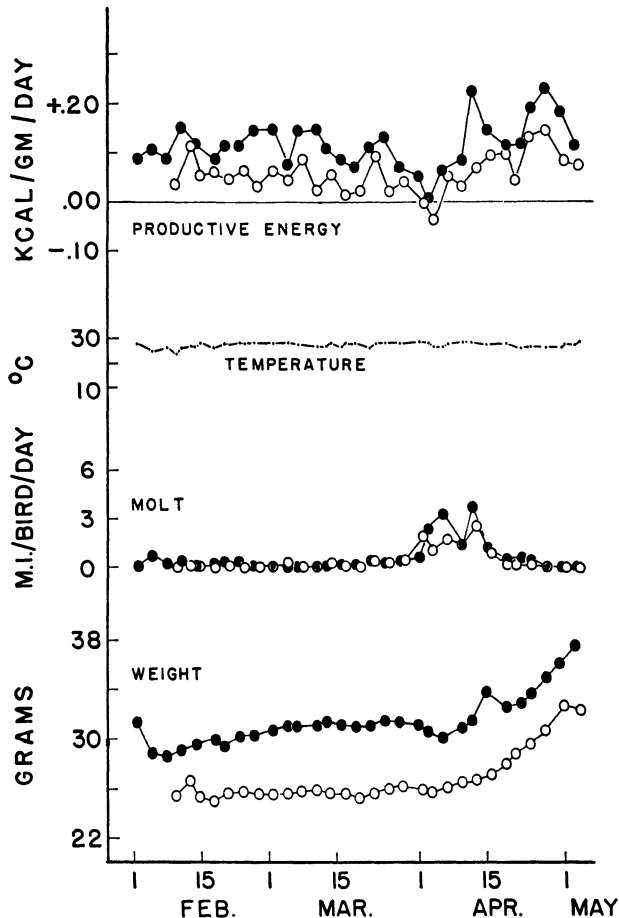

FIG. 5.—Productive energy, body weight, molt, and ambient temperature in the Canal Zone, February–May, 1961, for females (*open circles*) and males (*solid circles*).

prairie. To the east of this main nesting range the species is an erratic summer resident (Wetmore and Lincoln, 1928; Gross, 1956; Mayfield, 1962). The spring migration begins in March and April (Friedmann and Smith, 1955; ffrench, 1960; Zimmerman, 1963). The first migrants enter the southern United States by mid-April (Stevenson, 1957), pass through the mid-west in late April and

tranuptial area by the end of August (Griscom, 1932; Loetscher, 1955).

On the basis of the mean monthly air temperatures and average photoperiods, the maximum productive energy (maximum potential energy corrected for existence requirements) was calculated for the entire year at the northern (Winnipeg, Manitoba), central (Champaign, Illinois), and southern (Galveston, Texas)
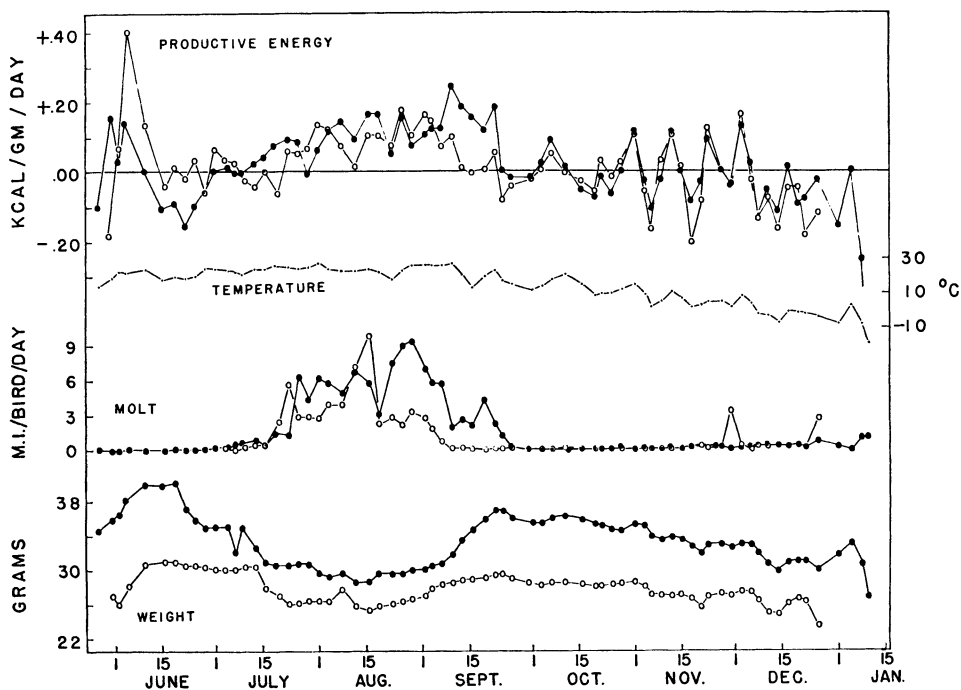

FIG. 6.—Productive energy, body weight, molt, and ambient temperature in Illinois, June, 1961–January, 1962, for females (*open circles*) and males (*solid circles*).

early May (Cooke, 1888; Taber, 1947), and reach the northern limit of their summer range in June (Cooke, 1888). In Illinois, nesting reaches a peak in June and early July (Gross, 1921). After the completion of the postnuptial molt in late August, autumn migration begins, and continues in the United States through October (Tordoff and Mengel, 1956; Johnston and Haines, 1957; Stoddard, 1962). Some individuals reach the con-

regions of the dickcissel's breeding range as well as for the Canal Zone and Merida, Yucatan (Fig. 8). Values for the maximum potential and existence energies at photoperiods other than those at which experiments were conducted were interpolated.

The average productive energy for the three months the dickcissel occurs at Winnipeg is 0.547 kcal per g per day for males and 0.675 kcal per g per day for

females. At this latitude, which is several degrees north of its main nesting range, breeding may occur only during the more favorable years. These values, based on average temperatures, may approach but probably underestimate the minimal energy necessary for successful reproduction. Farther north the duration as well as the level of positive productive energy are probably subminimal.

Although less than levels in Illinois and Texas, the productive energy obtainable in Yucatan, far to the south of the nesting area, seems sufficient for reproduction. Factors other than the attain-

ment of a favorable energy balance during breeding must limit its southward distribution in summer.

West (1960) concluded that the prenuptial migration of the tree sparrow did not give a more favorable energy balance on the breeding grounds than could be had in summer on the winter range. Cox (1961) demonstrated that if certain resident neotropical finches emulated the migration schedule of the dickcissel, it would be in vain in that the slight gain in maximum productive energy at the latitude of Illinois would be too little, too late for reproduction. Except for dickcis-
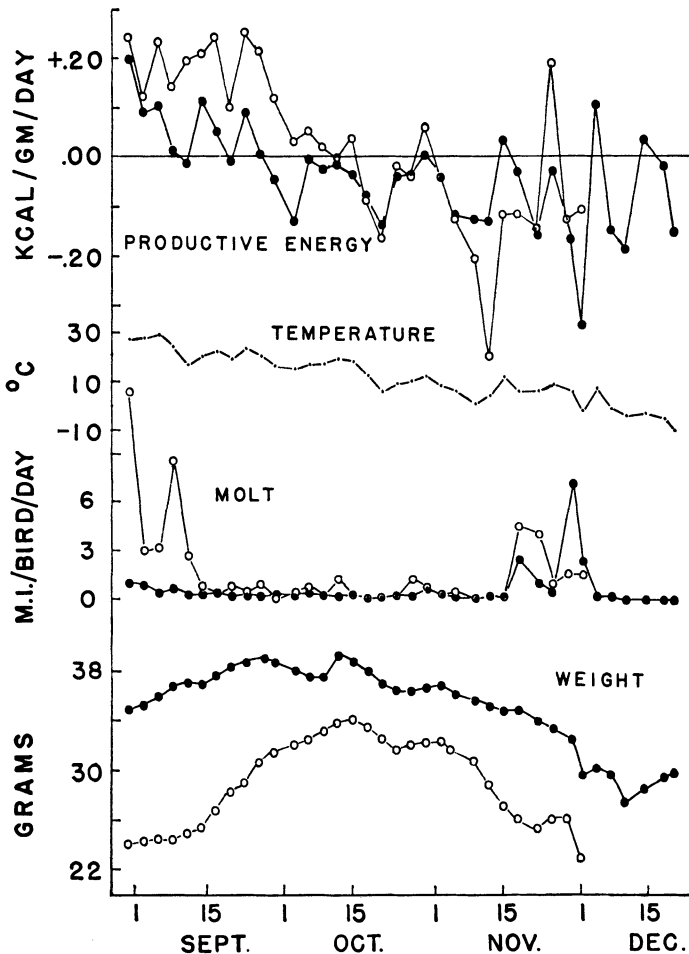

FIG. 7.—Productive energy, body weight, molt, and ambient temperature in Illinois, September–December, 1960, for females (open circles) and males (solid circles).

sels at the northern limit of their breeding range, migration in the spring does result in a substantial gain in productive energy. Furthermore, migration is so timed that nesting activity begins at about the time this increase can first be obtained. The tree sparrow experiences a mean decrease of 14 C in environmental temperature by migrating to Churchill, Manitoba, compared with what it would experience if it stayed in Illinois for the summer. Thus the energy-demanding effects of temperature override the ad-
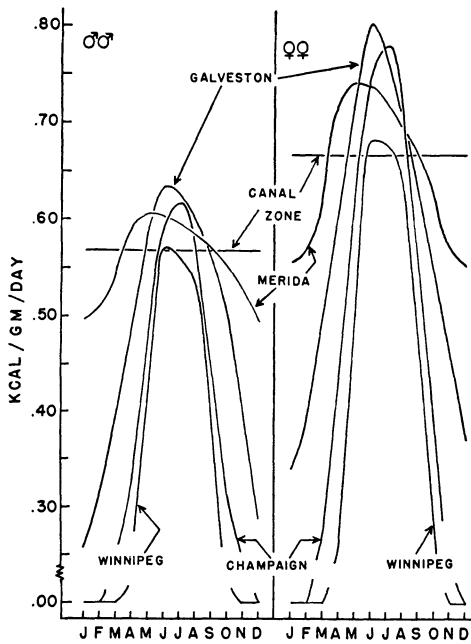

FIG. 8.—Maximum productive energy throughout the year at Winnipeg, Man., Champaign, Ill., Galveston, Tex., Merida, Yucatan, and the Canal Zone.

vantages of longer photoperiod and result in less productive energy (West, 1960). The dickcissel suffers only a 5 C decrease in Illinois during the breeding season compared with the average for the same months in the Canal Zone, and the advantage of the longer photoperiod in its case is made manifest.

Fall migration occurs during the month in which the maximum productive energy drops below the Canal Zone level. Although the timing of the autumn departure is probably most immediately correlated with the termination of the postnuptial molt, productive energy must be obtainable for the accumulation of premigratory fat stores, at least enough for the initial step southward. As can be seen in Figures 6 and 7, the maintenance of positive energy balance became more and more difficult after the period of the species' normal fall migration had passed. Because it departs in the early autumn, the dickcissel has been considered one of those species that anticipates adverse environmental conditions by a wide margin, yet in terms of energy balance it leaves "just in time."

The small, but regular population that overwinters on the New England coast may be defying its temperature tolerance limits, since January and February means do drop below the low lethal limit. If water is obtainable rather than snow, the lethal limit may be lowered sufficiently to allow the dickcissel to survive the maritime winter at this latitude. Open water is perhaps readily available along the densely populated east coast because of pollution. The dickcissel's regular association with the house sparrow, *Passer domesticus* (Packard, 1952; Eisenmann, *personal communication*), also increases its chances for survival, both from the use of feeding stations and roosting behavior.

Survival during the winter at the latitude of Galveston presents no tolerance problems, and many individuals occasionally overwinter on the Gulf Coast. Whether the loss in maximum productive energy experienced by remaining at this latitude rather than continuing to the tropics is limiting, is not known. Certainly the elimination of such an energy-draining as well as hazardous ac-

tivity as extended, often over-water migration would be advantageous. Perhaps the dickcissel is preadapted by its evolution and dispersion from its presumed tropical origin so that it can now tolerate winter conditions in the southern edge of its breeding range. If those individuals who are presently capitalizing on this potentiality do indeed gain some reproductive advantage in the subsequent nesting season, this positive selection, coupled with possible selection against a long migratory journey, might in time lead to the dickcissel's spending its entire annual cycle at temperate latitudes.

SUMMARY

The energy requirements of the dickcissel were measured on its tropical wintering and temperate breeding ranges, both under outdoor conditions and in controlled temperature cabinets at 10-, 12-, and 15-hr photoperiods.

There was a significant difference between the body weight of the sexes in captivity, except with summer birds on a 15-hr photoperiod where females were similar to males due to their longer retention of vernal-fat stores. Body weight decreased significantly from just below the critical temperature to the upper lethal limit. Weights also decreased significantly to the lower limit of temperature tolerance, a response paralleled by outdoor birds during the temperate winter. There is, therefore, no inverse relationship between weight and temperature when exposed to winter conditions. Greatest body weights in outdoor captives occurred at the peaks of vernal and autumnal premigratory fat deposition.

The upper lethal limit of temperature tolerance at 12- and 15-hr photoperiods was 44 C. At 10-hr photoperiod the lower limit was −1 C, and at 15 hr it was −2 C. Birds exposed outdoors to the Illinois winter died at a mean daily temperature of −3 C. Having water instead of snow available for drinking at subfreezing temperatures decreased the lower lethal temperature.

There was no difference in the calories per gram of dry guano between individuals, but there were significant differences between environmental conditions, except at 15-hr photoperiods.

At a 12-hr photoperiod the critical temperature was 38 C and at 15 hr it was 36 C. No zone of thermal neutrality but rather a single thermal neutral point existed. Below the critical temperature there are inverse relationships between the ambient temperature and the existence levels of gross energy, excretory energy, and metabolized energy.

The cubic regressions of excretory energy per bird per day illustrate the energy conservation resulting from decreased output of excreta, and in 10-hr birds from a significant decrease in the caloric value of the guano as well. This response was apparent from 9 C to 21 C in 15-hr males and from 7 C to 13 C in 10-hr birds.

It is suggested that below 15 C–16 C, the role of chemical regulation in homeothermy becomes greater in importance than that of physical regulation in the dickcissel.

There were two peaks in the efficiency of food utilization in relation to temperature. One was just below the critical temperature, and the other was within the temperature range concurrent with the period of reduced excretory energy.

The dickcissel gains in productive energy by spring migration from the tropics to the north-temperate breeding grounds and by returning to the tropics in autumn. Furthermore, the spring migration is so timed that nesting activity begins at about the time this increase can be first obtained. Fall migration removes the dickcissel from its nesting

latitude just prior to environmental conditions that result in an unfavorable energy balance.

Northward distribution in the summer is probably limited both by the magnitude and duration of productive energy available for reproduction. Although productive energy decreases to the south of its summer distribution, the present southern limit of the dickcissel's breeding range appears to be dependent on other factors.

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