

SEASONAL CORRELATIONS OF RESERVE ENERGY OF THE RED-WINGED BLACKBIRD

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INTRODUCTION

Animals have a reserve energy supply which they use when an external source is scarce or unavailable. This reserve energy supply may also be utilized when an increase in energy is needed due to a physiological change within the animal itself. Various factors within the biological and physical environment influence the rate of deposition and utilization of the reserve energy supply as well as the reproductive cycle of the particular species. The present study investigated relationship between the energy reserve of the Red-winged Blackbird (*Agelaius phoeniceus*) and attempted to correlate it with the ambient temperature and reproductive cycle of the species.

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METHODS

Arrival and departure dates of Red-winged Blackbirds were determined from dates when first migratory flocks in the spring and last migratory flocks in the fall were observed.

Birds were collected weekly within a 15-mile radius of State College, from the middle of March through July in 1962 and from the first of May through August in 1961. In 1964 a few birds were collected to determine if the pattern of changes in the reproductive cycle was similar to 1961 and 1962. The following data were recorded: body weight with an accuracy of ± 0.05 g., weight of gonads with an accuracy of ± 0.05 mg., weight of abdominal, cervical and subscapular fat deposits (only abdominal fat deposits were weighed in 1961) with an accuracy of ± 0.05 mg. The abdominal fat deposit refers to the large fat body found in the abdominal region; the cervical fat body refers to the large fat body found in the interfurcular region; and the subscapular fat body is ovoid in shape, lies in the subscapular region, and is the same as the lateral thoracic fat body described by McGreal and Farner (1956). Birds were collected in the same areas throughout the breeding season both years and collections were made between 8:00 A.M. and 11:00 A.M. During March and early April only mature male birds that appeared to be attempting to establish a territory were collected. It is possible that some transients were collected; however, if the behavior of the birds is observed, the number of transients is probably kept at a minimum. Birds were not found in sufficiently large numbers to be sampled adequately after the first week of August. Although birds are sometimes observed in the State College area as late as October, it is

not known whether they are migrants or summer residents.

The following method described by Brenner and Malin (1965) was used to estimate the reserve energy supply and total body fat of the birds. The reserve energy available to birds is equal to $0.7 W$, where W = weight in grams and 0.7 is derived from the proportion of the initial weight of the bird after it was deprived of food until death. The reserve energy may also be derived from the following equation: $\frac{\text{g fat}}{9 \text{ K Cal}} = \frac{0.08W}{X}$ $X = .7W$. In this equation W = weight in grams and 0.08 is equal to the proportion of the live weight of the bird which is fat. The fat content of 14 birds determined by either extraction of total body fat, varied from 9.3 per cent to 7.8 per cent with a mean of 7.9 ± 0.94 per cent of the live weight. The total body fat of 14 birds was determined by the following procedure. The birds were minced and then dried at 70 C to a moisture-free basis for 24 hours. The moisture-free birds were then extracted in petroleum ether for 24 hours. The total body fat was calculated as the difference in weight between the moisture-free birds before and after ether extraction. The total body fat was then expressed as a percentage of the live weight.

The testes and ovaries were sectioned at 6μ and stained with hematoxylin and eosin for histological study. The presence or absence of spermatozoa and ovarian follicles was recorded.

Stomach contents were collected, dried at 70 C for 24 hours and percentages of insect and vegetable matter were determined by weight. The caloric contents of various insects, grains, grass, and sedge seeds (dried at 70 C) were determined by a plain oxygen-bomb calorimeter. The various nutrients of plant and animal material were determined by standard biochemical methods given by Maynard and Loosli (1962).

The temperature data were obtained from the weather station at the College of Mineral Industries of Pennsylvania State University and from the United States Weather Bureau.

RESULTS

The following results are based on 73 males and 28 females collected in 1962 and 77 males and 43 females collected in 1961. Males were heavier when they arrived in March than they were at the end of the breeding season. The mean weight of males in March was 67.9 g; their weight decreased to a mean of 62.0 g in July (Table 1). The mean weight of female was 42.1 g in May and decreased to 38.9 in July (Table 2). The regression equation for weight decrease of males in 1962 was $Y = 70.1 - 1.98X$ (Y = body weight in grams and X = time in months) and was not statistically different from the regression for the weight decrease of males in 1961 ($Y = 68.1 - 1.00X$, $P > .30$). The weight regression for females was $Y = 45.8 - 1.50X$ and $Y = 49.5 - 1.98X$ in 1961 and 1962, respectively. The regressions for female weight decrease were not statistically different ($P > .70$). The regressions for males and females were not statistically different ($P > .40$, 1961) ($P > .50$, 1962) (Fig. 1).

TABLE 1. BODY WEIGHT AND KCAL OF RESERVE ENERGY AVAILABLE TO MALE RED-WINGED BLACKBIRDS

Month	1961				1962				
	birds	Body weight* g	S. E.	KCal of available energy	S. E.	N birds	Body weight* g	S. E.	KCal of available energy
March	0	—	—	—	—	12	67.9	0.659	47.5
April	0	—	—	—	—	23	67.8	0.144	47.5
May	43	65.0	0.130	45.7	0.097	15	62.7	1.570	44.1
June	16	64.4	0.145	44.7	0.079	11	61.8	0.786	43.3
July	17	63.0	0.660	44.1	0.137	12	61.0	1.080	42.7
August	1	62.0	—	43.4	—	—	—	—	0.755

*weight of bird collected in the field

TABLE 2. BODY WEIGHT AND KCAL OF RESERVE ENERGY AVAILABLE TO FEMALE RED-WINGED BLACKBIRDS

Month	1961				1962				
	N birds	Body weight* g	S. E.	KCal of available energy	S. E.	N birds	Body weight* g	S. E.	KCal of available energy
April	—	—	—	—	—	1	42.0	—	29.4
May	22	43.3	0.320	30.4	0.047	8	42.1	0.795	29.5
June	9	41.4	0.606	29.3	0.165	7	40.3	1.680	28.2
July	10	40.2	0.255	28.2	0.057	12	37.6	1.070	26.3
August	2	37.2	0.465	26.1	0.325	—	—	—	0.550

*Weight of birds collected in the field

TABLE 3. WEIGHT AND PERCENT OF FAT IN THREE DEPOTS* IN MALE AND FEMALE RED-WINGED BLACKBIRDS

Month	N birds	Males weight (mg)	S. E.	% of total Fat in depots	N birds	Females weight (mg)	S. E.	% of total Fat in depots
March	12	1443.5	51.08	25.3				
April	23	449.3	35.65	7.9	1	193.2		5.3
May	15	167.5	28.86	3.2	8	245.1	20.00	7.2
June	11	64.2	14.00	1.3	7	163.6	16.93	5.1
July	12	188.4	45.30	3.8	12	135.0	33.50	4.5

*Abdominal, cervical and subscapular.

TABLE 4. PERCENTAGE OF TOTAL DEPOT FAT IN THE THREE DEPOTS IN RED-WINGED BLACKBIRDS IN 1962

Month	N birds	Males			Females		
		abdominal weight	Cervical	Subscapular S. E.	abdominal weight	Cervical	Subscapular S. E.
March	12	41.0	2.38	33.0	4.36	27.3	3.28
April	23	29.2	1.94	47.3	1.12	24.1	1.12
May	15	22.2	1.58	41.6	5.05	25.4	1.18
June	11	21.9	3.22	52.5	4.09	25.6	1.66
July	12	21.7	4.60	46.1	3.10	32.4	4.60

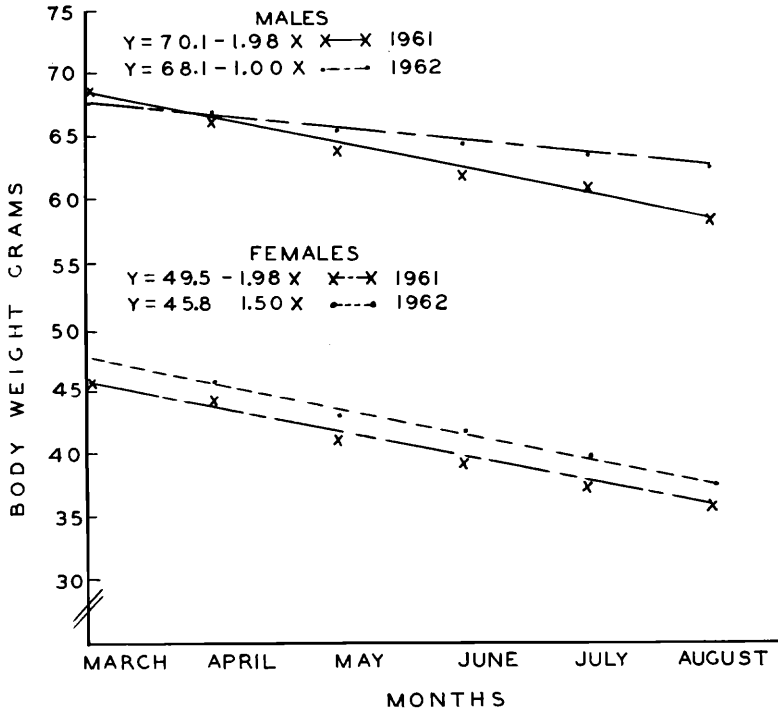


Figure 1. The decrease of body weight in male (1961, $P < .01$; 1962 $P < .03$) and female (1961, $P < .02$; 1962, $P < .01$) redwinged blackbirds throughout the breeding season.

In males the weight of the fat in three depots (abdominal, cervical, and subscapular) decreased from a mean of 144.5 mg in March to a mean of 64.2 mg in June and then increased to a mean of 188.4 mg by the end of July. The females followed a similar pattern; the mean weight in May was 245.1 mg and then decreased to 135.0 mg in July (Table 3).

The percentage of total depot fat in the abdominal depot was 41.0 in March and this decreased to 29.2 by April. The percentage of total depot fat in the cervical depot was 33.0 in March and increased to 47.3 in April. The percentage of the total depot fat in all three depots remained the same from May through July (Table 4). The percentage of the total depot fat in the subscapular depot did not change markedly from March through July; the mean percentage of total depot fat in the subscapular depot was 29.1. Females were not collected in March and only one bird was collected in April; hence, percentages of total depot fat in these three depots cannot be compared during these months. The percentage of total fat in any one of the three depots did not change significantly from May through July (Table 5). In 1961 only abdominal fat was weighed; however, it followed a pattern similar to that of total depot fat

TABLE 5. WEIGHT OF ABDOMINAL FAT IN 1961

Month	Males			Females		
	No. of Birds	Weight mg.	S.E.	No. of Birds	Weight	S.E.
May	45	40.7	7.70	20	105.0	3.54
June	25	30.0	13.80	8	68.3	8.16
July	15	35.0	7.45	10	20.4	1.00
August				7	33.3	8.43

(Table 5). In March 25.3 per cent of the total reserve energy was in the three major depots and this decreased to 1.3 per cent by the end of June. The reserve energy in depots increased to 3.8 per cent in July. In females the percentage of reserve energy in the three depots decreased from 7.2 per cent in May to 4.5 per cent in July (Table 3).

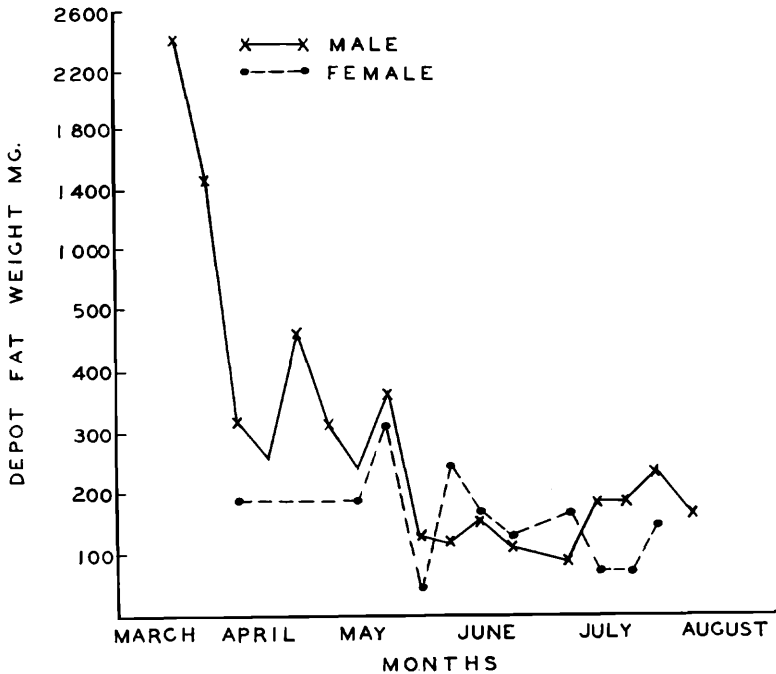


Figure 2. The decrease of fat in depots of redwinged blackbirds throughout the breeding season.

The rapid decrease in fat in the three depots is correlated with the rapid increase in testicular weight (Fig. 2 and 3). Spermatozoa were not present in the testes until the second week of April and between the second and third week of April the weight of fat in the depots also increased. The mean environmental temperature was between 10 and 12 C during the period when spermatozoa were first observed in the testes. Changes in reproductive condition demand energy and also appear to cause a change in the pattern of fat deposition. The total body fat did not decrease at the same rapid rate as the depot fat during the second week of April.

Birds begin to utilize their reserve energy as soon as they arrive on the breeding grounds. At low temperatures the existence energy requirements of birds increase. Therefore, the temperature on the breeding grounds when the birds arrive in the spring may have an effect on the utilization of their reserve energy supply.

Male Red-winged Blackbirds arrive in central Pennsylvania in mid-March and females arrive approximately two or three weeks later. The arrival of the species is well correlated with temperature. (Fig. 4). The males arrived in the State College area by the middle of March in the following years: 1958, 1961, 1962 and 1964. The males arrived at the end of March in 1959 and 1960. Arrival was not observed in 1963. In the years when the birds arrived two weeks late the temperature was low, then rose rapidly (Fig. 4). Departure dates in the fall do not correlate as well with temperature as do the arrival dates in the spring.

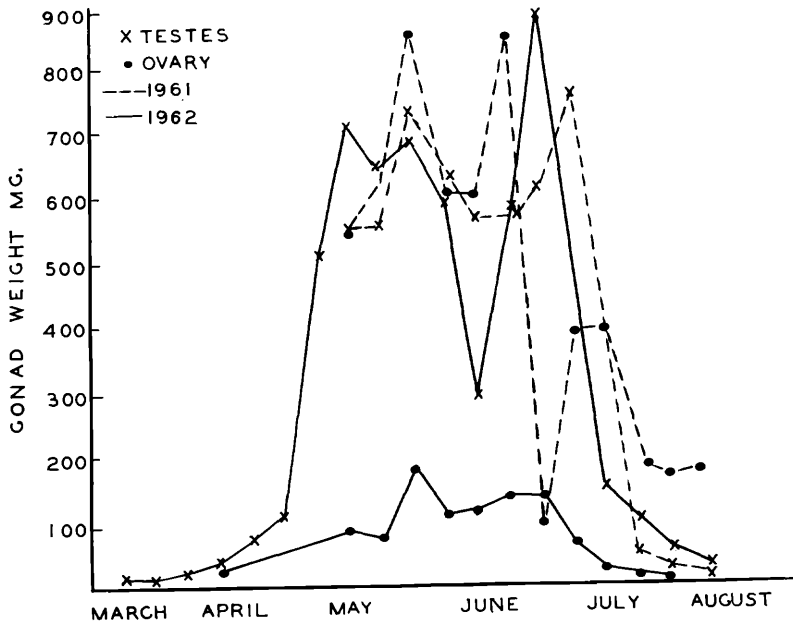


Figure 3. The weight of the gonads of redwinged blackbirds throughout the breeding season.

The reserve energy supply would also be affected by the energy requirements of incubation. The energy cost of incubation is also correlated with temperature. The energy cost of incubation was calculated from the following formula (Kendeigh 1963a):

$$\frac{\text{KCal} = n. w. h. b. (t_c - t_{na}). i. (1 - c. a.)}{1000}$$

- n = number of eggs in clutch (3.3)
 w = mean weight of eggs (4 g)
 *h = specific heat per gram of egg (.80 cal)
 i = interval of time (24 hr)
 *b = rate of cooling (5.2 cal/hr) per 1 C difference in nest temp.
 *t_c = egg temp. (35 C)
 *t_{na} = nest air temp. (air temp.)
 *c = per cent egg surface covered by incubating bird (app. 25 per cent)
 *a = per cent time bird is incubating (75 per cent app.)

*Figures from Kendeigh (1963 a). These figures may not apply directly to the Red-winged Blackbird because they were calculated for the House Wren (*Troglodytes aedon*) a hole-nesting species; however, they will serve as a basis for comparison of the energy requirements of incubation of Red-winged Blackbird populations in different geographic areas.

Considering present findings along with those of Lefebvre (1961), Crebbs (1960), Orians, (1961 a, b), and Strosnider and Gleason (1960), it was found that a significant variation did not occur in the energy cost of incubation ($P > .75$) and it varied from approxi-

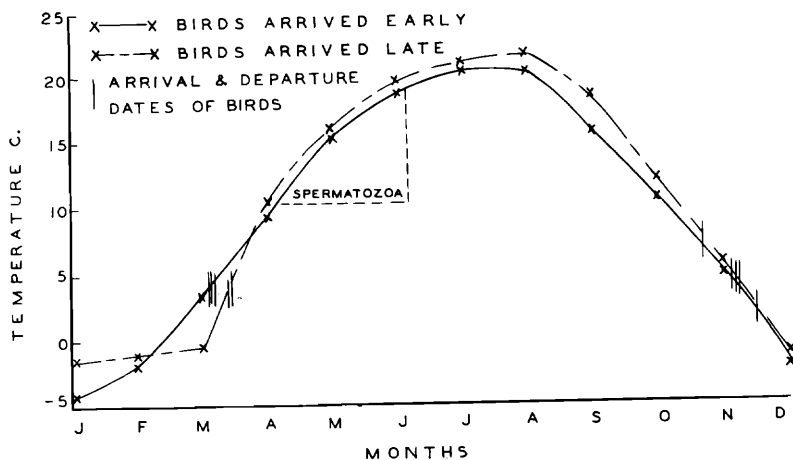


Figure 4. The arrival and departure of redwinged blackbirds in relation to environmental temperature.

TABLE 6. BREEDING SEASONS OF THE RED-WINGED BLACKBIRD IN CERTAIN GEOGRAPHICAL AREAS

Location	Months	Temperature C		Mean Temp.	KCal required for incubation/day	% of the reserve energy utilized/day	References
		Mean Max	Mean Min.				
Central Calif.	Apr., May	20	10	15	21.2	73.6	Orians, 1961 a & b
Southeastern Virginia	May, June	23	8.5	15.8	20.3	70.5	Crebs 1960
Lake Itasca State Park Minnesota	June, July	25.5	10.5	17.8	18.1	62.8	Lefebvre 1961 Stronsmider & Gleason 1960
Centre County Pennsylvania	May, June	23.6	11.4	17.5	18.5	64.2	This study

TABLE 7. PERCENTAGE OF VARIOUS FOOD COMPONENTS AVAILABLE TO BIRDS IN DIFFERENT TYPES OF FOOD

Food	Nutrient				
	Ether extract (Fat)	Crude fiber	Ash	Crude protein	Nitrogen-free extract (Carbohydrate)
Corn	2.84	4.00	1.10	7.06	85.00
Oats	3.56	1.78	1.49	5.49	87.68
Grass and sedge seeds	4.04	2.43	1.15	5.30	87.10
Grasshoppers	4.15	3.16	0.34	25.80	66.56
Honey bee	2.06	1.79	0.52	31.41	64.22
Bumble bee	4.14	4.33	1.11	27.34	63.08
Scarab beetle	4.92	1.31	0.32	33.75	59.70

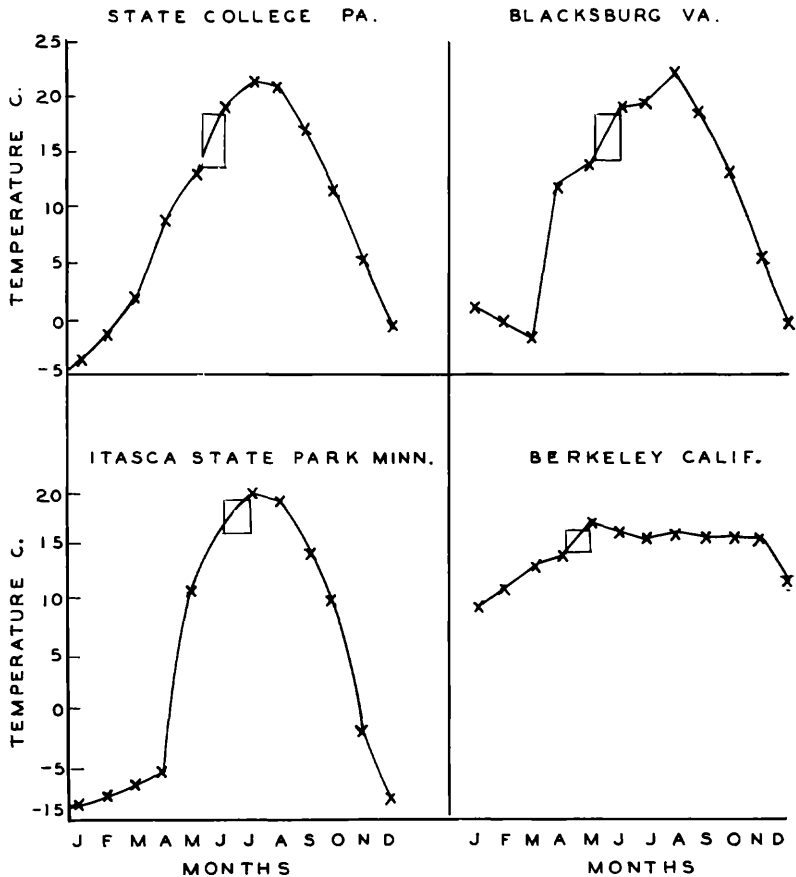


Figure 5. The nesting of redwinged blackbirds in different geographic areas in relation to environmental temperature.

mately 18.3 KCal/day in Minnesota and Pennsylvania to approximately 20.8 KCal/day in California and Virginia. Air temperature during the breeding season also did not vary significantly from one geographic area to another ($P > .75$). The air temperature ranged from 17.7 C in Pennsylvania and Minnesota to 15.4 C in California and Virginia. The energy cost of incubation varied from 62.8 per cent to 73.6 per cent of the available reserve energy of the female per day (mean energy reserve of 28.8 KCal) (Table 6). These estimates of the energy requirements of incubation are based on the average air temperature, not the nest temperature. The nest temperature probably is always a few degrees above the average air temperature and this increase in average nest temperature would reduce the energy requirements of incubation. The months in which nesting occurs range from April and May in California to June and July in Minnesota. The increase in the temperature in the spring

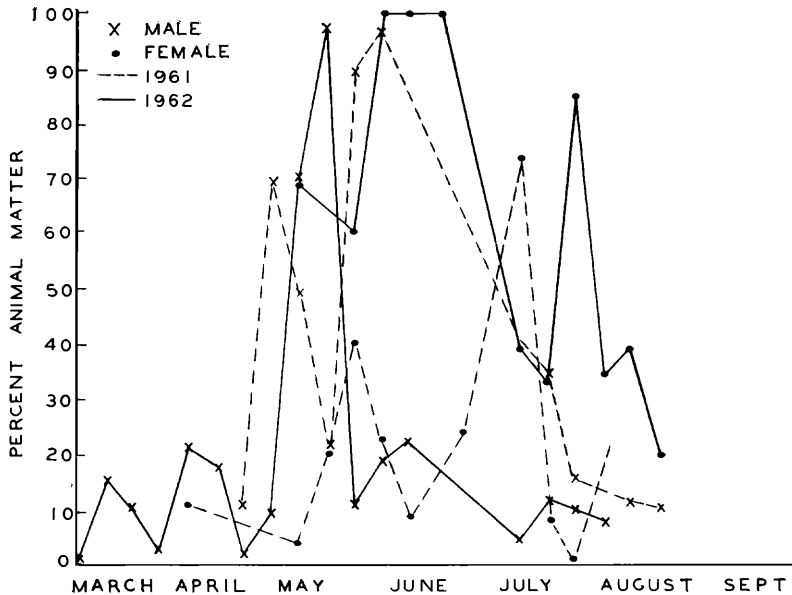


Figure 6. The percentage of animal material in the diet of redwinged blackbirds during the breeding season.

varies from one geographical area to another and appears to control the start of nesting. (Fig. 5).

The birds fed on grain and weed seeds until nesting begins in May, and then a substantial part of the diet consisted of insects. In males, insects consisted of 56.0 per cent and 32.9 per cent of the diet in 1961 and 1962 respectively, during May and June. The insects in the diet of the females decreased from 82.2 per cent in 1961 to 24.4 per cent in 1962 during May and June. These differences in the per cent of insects in the diet between 1961 and 1962 may be due to sampling rather than a different feeding behavior by the birds. The second peak of insects in the diet of the females (Fig. 6) may have been due to birds that were renesting.

The protein content of the diet obviously increased when insects became a substantial part of the diet; thus, the crude protein-nitrogen free extract (carbohydrate) ratio would change appreciably as the birds changed from seed to an insect diet (Table 7). The energy intake per gram of food, however, did not change greatly with the feeding habits of the birds, for it was found that the mean amount of energy in the seed diet was 4.2 KCal/g and in insects 4.9 KCal/g (Table 8).

DISCUSSION

Various factors in the biological and physical environment have been demonstrated to influence the energy requirements of birds as well as their reproductive cycle. It was demonstrated by Brenner (1966) that the increasing photoperiod and temperature during

TABLE 8. KCal OF ENERGY PER GRAM OF VARIOUS FOODS OF THE RED-WINGED BLACKBIRD

Food	KCal of energy	Food	KCal of energy
Corn	4.0	Meal worm	4.7
Oats	4.1	Grasshopper	4.8
Grass and sedge seeds	4.4	Bumble bee	5.0
Mean	4.2	Honey bee	4.6
		June bug	5.0
		Scarab beetle	5.2
		Cricket	5.3
		Mean	4.9

the breeding season resulted in a decrease in the existence energy requirements of the Red-winged Blackbird. Both photoperiod and temperature have also been demonstrated to influence the reproductive cycle of birds. Since the experiments of Rowan (1925) a great deal of work has been done on the role of photoperiod in migration and the reproductive cycle of birds (Farner, 1959, 1964; Wolfson 1959, 1960 a and Blumenthal and Dolnik, 1962). However, various other investigators have shown that the environment temperature may regulate the start of egg laying in various species of birds (Haartman, 1963; Kluijver, 1951 and Kendeigh, 1963 b). Brenner (in press) indicated that temperature may regulate nesting activity of different populations of Red-winged Blackbirds within the same geographic area.

The breeding season of most avian species corresponds to a period when an abundant food supply is available for the young. The results of this study illustrate that insects form a substantial part of the diet of the Red-winged Blackbirds during the breeding season. It was shown by Brenner (1964, in press) that the number of female and young Red-winged Blackbirds present in a population corresponded to the energy available to the populations as insects. The influence of energy intake may be important in stimulating breeding activity, but little experimental evidence is available. A reduced food intake depresses gonadal activity in domestic fowl (Breneman, 1955). In further support of the theory that energy availability may be a factor in regulating breeding activity of birds is a study by Marshall (1952) which indicated that the stimulus for the Starling (*Sturnus vulgaris*) breeding out of season may be the food provided by man. Orians (1960) reported that the Tricolored Blackbird (*Agelaius tricolor*) may breed in the fall in California. This phenomenon is thought to be induced by irrigation and its effect on the vegetation and insect food.

The change from a diet of seeds to insects in the spring has also been reported for the Redpoll (*Carduelis flammea*) (Peiponen, 1962) and for the Myrtle Warbler (*Dendroica coronata*) by Yarbrough and Johnston (1965). During the breeding season some birds may re-

quire a higher protein diet than during the remainder of the year. A study by Nelson and Evans (1953) on the rat demonstrated that in an absence of dietary protein a reproductive failure occurs due to a lack of ovarian hormones. Leathem (1959) stated that in the male rat a lack of protein results in limited testicular growth and sperm formation and even a lack of testosterone secretion, as a result of a reduction in the level of circulating pituitary gonadotropic hormones. However, the change from a plant to insect diet may also be due to the increased availability of insects during the breeding season. During the breeding season seeds were less available to the population whereas insects were in abundance. The change in the feeding habits of birds needs more experimental work before the dietary changes and effect on the reproductive processes can be firmly established.

If a relationship exists between energy availability or the type of food available to a population and the reproductive cycle of a particular species it may be possible to theorize that similar factors in the environment may influence both phenomena. The results of this study demonstrated that nesting occurs within an average temperature of between 15 C and 18 C in four geographic areas. However, the months in which nesting occurs ranged from April and May in California to June and July in Minnesota. The environmental temperature may regulate the nesting season of birds through the energy cost of incubation. Kendeigh (1963 b) concluded that the onset of egg laying in the House Wren is regulated to the general time of the year by the development of the gonads under the stimulus of photoperiod, to the time of month by their return to the breeding grounds, and to the precise day by temperature. It has also been demonstrated that temperature affects the external energy supply of breeding birds, which is insects (Headlee, 1929; Johnson, 1940, 1942 and Richards, 1964) as well as the reproductive cycle of some species of birds. These data suggest that temperature or its influence on the available energy supply (insects) may regulate the start of nesting activity of birds that inhabit temperate regions.

The same factors in the biological and physical environment that influence the external energy supply and the reproductive cycle of birds probably also have a significant role in the deposition and utilization of the reserve energy supply (fat) within the population. It was been shown by King and Farner (1959) and Wolfson (1960b) that birds increase in weight and fat deposition prior to spring migration. However, Lofts *et al.* (1963) demonstrated that the accumulation of fat *per se* may not be a stimulus for migration to occur; however, it may be important in regard to the reproductive activity of birds on the breeding grounds. The interaction between temperature and nesting activity of birds may be in the energy cost of the various reproductive processes and their effect on the reserve energy supply available to the population. The diminishing body weight in breeding birds (Oakeson, 1954; Irving, 1960; Hanson, 1962; Blumenthal and Dolnik, 1962; Thompson and Coutlee, 1964 and King *et al.*, 1965) may be due to breeding activities or secondary endocrine influences caused by increased gonadal activity. The rapid decrease in fat in the three areas of fat deposition occurred approxi-

mately two to three weeks after the birds arrived on the breeding grounds. During this same period the testes show an increase in sudanophilic activity in the Leydig cells, which indicates an increase in steroid production (Vandenbergh, 1961) and also the males are beginning to establish territories which suggests an increase in aggressive behavior within the population. It was demonstrated by Brenner (1965) that testosterone influences the amount and pattern of fat deposition in Red-winged Blackbirds and Starlings. A similar phenomenon may occur in some reptiles. Hahn and Tinke (1965) stated that the annual fat cycles in the lizard *Uta stansburiana* is associated with reproduction. In females fat bodies decline in late winter and early spring when deutoplasm is deposited in the follicles. Ovariectomy eliminated rapid mobilization from the fat bodies which occurred in the sham operated controls. Males have a similar fat cycle, but the fat bodies are much smaller.

It has been observed that some permanent resident species also increase their body weight in the spring. It was demonstrated by Kirkpatrick (1944) that female Ring-necked Pheasants (*Phasianus colchicus*) increased their body weight in the spring; however there was not a corresponding increase in males. These data are similar to those reported by Wilson (1911) for the Red Grouse (*Lagopus lagopus scoticus*) and to the observations of Hegen (1942) for the Willow Grouse (*Lagopus l. lagopus*). It is plausible that the increase in the reserve energy available to the population in the spring may be used for reproduction rather than for migration *per se* since some permanent resident species also increase their body weight in the spring. The greater amount of fat deposition in the spring over the fall as shown by King (1963) and King *et al.* (1963) may further substantiate the hypothesis that the greater amount of fat deposition in the spring may be more for reproduction rather than for migration *per se*.

When Red-winged Blackbirds arrive in March, food is not plentiful, and a reserve energy supply may be necessary to enable the males to establish and maintain territories and carry out other reproductive processes. An energy reserve is also necessary to enable the female to incubate the eggs and raise the young. The environmental temperature would have an effect on the rate of utilization of the reserve energy supply of the population due to the increase in the existence energy requirements at decreasing temperatures. The relationship between temperature and reproduction, and their effect on the reserve energy supply available to the population, will probably vary from species to species, depending on body size and the temperature throughout the geographic range of the species.

SUMMARY

A study of the reserve energy available to the Red-winged Blackbird (*Agelaius phoeniceus*) was undertaken in Centre County, Pennsylvania, during 1961 and 1962. The body weight of males decreased from a mean of 67.9 g in March to a mean of 62.0 g in July. The mean weight of females was 42.1 g in May and decreased to 38.9 g in July. Regressions for weight decrease of both males and

females in 1962 were not statistically different from those in 1961. Regressions for males and females also were not statistically different. The weight of fat in the three areas of deposition decreased at a faster rate than did the total body fat. The rapid decrease of fat in deposits appears to be correlated with the rapid increase in testicular size in April.

The relationship between temperature and reproduction and their effect on reserve energy of a population is discussed. The survival value of increased fat deposition in the spring may pertain, in part, to the fact that the reserve energy supply is utilized largely for reproduction or during inclement weather rather than for migration *per se*.

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THE IDENTIFICATION OF AUTUMNAL INDIGO BUNTINGS

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Despite Dwight's careful study (1900) of plumages and molts in passerine birds, it is necessary, on occasion, to modify and refine his descriptive findings. Such is the case with the Indigo Bunting (*Passerina cyanea*), a species whose autumnal sex and age groups can be perplexing to the bird-bander. In the course of a long-range study of this species' migratory characteristics, I have retained in captivity, for periods of time up to five years, 35 individuals representing both sexes as well as first-year and adult birds. Several hundred birds have been handled in banding operations in northern Florida, and about 200 migrants have been examined from TV tower casualties. It has been possible, therefore, to allocate plumage types to definite sex and age groups, corroborated by dissection, and also to note sequences of molts and plumages in captive birds.

Several methods have been suggested to distinguish live first-year (immature) from adult passerine birds in autumn in the absence of distinctive plumage or other apparent differences. Norris (1961), for example, reported a simple, effective technique for examining the skull roof for the degree of ossification. Viewing the skull through bare, wet skin with a hand lens in strong light, he could