THE BIOENERGETICS OF CAPTIVE BLUE-WINGED TEAL UNDER CONTROLLED AND OUTDOOR CONDITIONS

RAY B. OWEN, JR.[1]

Department of Zoology
University of Illinois
Urbana, Illinois 61801

An understanding of avian bioenergetics is necessary before one can comprehend how birds utilize their natural resources. It is also important, from an evolutionary standpoint, for the understanding of how available energy regulates various activities during the yearly cycle and how it limits distribution. Until recently little work has been done to relate the energy requirements of birds in the field to those in the laboratory.

This investigation concerns the bioenergetics of caged Blue-winged Teal (*Anas discors*) held under controlled and outdoor conditions and was part of an attempt to find a method for estimating the energy requirements of free-living birds (Owen 1969). Special emphasis is placed on the comparison of outdoor and indoor birds and on the use of multiple regression analyses to partition the effects of numerous variables affecting metabolism.

Blue-winged Teal were selected for this study since there has been little bioenergetics work on waterfowl, or on 300–400 g birds. The teal were obtained from the breeding area around Delta, Manitoba, and Jamestown, North Dakota, and from fall migrants passing through Illinois. Blue-winged Teal breed predominantly in the northwest central part of the United States, through the prairie provinces of Canada, and up into British Columbia. They winter from the southern edge of the United States through Central America and the West Indies to the northern part of South America. They are one of the first waterfowl species to migrate south in the autumn and last to come north in the spring.

EXPERIMENTS UNDER CONTROLLED CONDITIONS

METHODS

The relationships among photoperiod, temperature, and metabolism under laboratory conditions were determined by the method first developed by Kendeigh (1949). This method entails subtracting the caloric value of the excreta (excretory energy) from the caloric value of the food ingested (gross energy intake). The value obtained is equal to the amount of energy utilized (metabolized energy) and during periods of constant weight is called existence energy. Productive energy is that energy metabolized over and above that needed for existence. Efficiency of food utilization is equal to metabolized energy divided by gross energy intake.

The teal were held individually in metabolism cages 46 × 32½ × 45 cm. Some of the cages had a floating floor attached in each corner to a microswitch. Movement by the birds activated one of the switches and was recorded on an Esterline-Angus 20-point recorder. One unit of activity represented the activation of at least one microswitch during a 5-min period. Maximum activity was therefore 12 units per hr. A pan was placed under each cage to collect the feces, and a hole punched in one corner of the pan permitted drainage of excess water. Two male and three female teal (not always the same birds) were used in all experiments and were acclimated to each experimental condition for about two weeks. Birds were fed Duck Growena, a prepared food in pellet form from Ralston Purina Company. The food had a nitrogen content of 3.02 ± 0.12 (mean ± SE) per cent and a caloric value of 4.38 ± 0.01 kcal/g.

Under each experimental condition three consecutive three-day periods of constant weight were obtained for each bird. Constant weight is defined as a change of less than 1.5 per cent in mean weight. Once acclimation had occurred, the birds were weighed to the nearest 0.1 g at 13:00 and given a known amount of food. Between 200 and 400 ml of water were given to each bird daily. At the end of each three-day period the teal were weighed and the number of feathers molted was recorded in grams, based upon previous determination of the weights of each type of feather. The unused food and excrement were also collected at this time and dried at 65°C to constant weight. Blem (1968) noted that there was no appreciable loss in the energy content of teal excrement dried at this temperature. The moisture content of the food supplied was determined for each period, and periodic determinations were made on a Parr oxygen-bomb calorimeter to determine its caloric value. The caloric value of the food not eaten subtracted from that of the initial amount of food gave the gross energy intake. The liquid effluent from the base pans was dried, weighed, and a caloric value obtained, which, when added to that of the excrement, gave excretory energy. Nitrogen content of the feces was obtained using the Kjeldahl method.

Photoperiods of 12 and 15 hr were chosen to determine the effects of photoperiod on metabolism. The former approximates the photoperiod encountered on the wintering grounds and during migration, while 15 hr is close to the photoperiod at the start of nesting. One group of birds was tested under each photoperiod at each of four temperatures (0, 10, 20, and 30°C). The 12-hr birds were tested at four additional temperatures (−28, −18, −10, and +35°C) to complete the relationship between temperature and energy utilization. In subsequent experiments temperature

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[1] Present address: School of Forest Resources, University of Maine, Orono, Maine 04473.

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TABLE 1. Environmental characteristics within the temperature cabinets.

	Experimental temperatures		Relative humidity (%)	Light intensity (ft-c)
	Mean (°C)	max. deviation (°C)		
High temperature walk-in	30, 35	1.5	35–50	20–70
Medium temperature walk-in	10, 20	2.0	85–95	75–85
Cold temperature walk-in	–18, –10, 0	2.5	80–90	75–80
Extreme cold reach-in unit	–28	4.0	90–98	10

tolerances were studied by progressively acclimating two groups of teal to higher or lower temperatures.

The experiments were conducted in three walk-in temperature cabinets and a specially constructed refrigerator unit (table 1). Humidity values at high temperatures were sufficiently low not to affect metabolism (Salt 1952; Wallgren 1954). At freezing temperatures small aquarium heaters kept the drinking water at about 1°C.

A probability level of 0.05 was required for significance in all statistical testing. The nonlinear multiple regression analyses were performed as suggested by Zar (1969).

RESULTS AND DISCUSSION

Photoperiod. Teal on a 12-hr photoperiod showed significant weight gains at lower temperatures (table 2), and under both photoperiods mean weights of males and females were significantly different at all temperatures.

Between 0 and 30°C there was no significant difference between existence metabolism under 12- and 15-hr photoperiods. Williams (1965) obtained similar results with Canada Geese (*Branta canadensis*). The teal exhibited some nocturnal activity under all conditions, which may be characteristic of waterfowl (Williams 1965).

Temperature and metabolism. Regression lines calculated for gross energy intake and existence metabolism were significantly different between males and females when metabolism was placed on a per bird basis, although excretory energy values were the same for both sexes. The relationships between temperature and existence energy for each sex and between temperature and gross energy for males were linear (fig. 1), while gross energy intake vs. temperature for females was best represented by a quartic equation. Excretory energy exhibited a quadratic regression on temperature, being low at high temperatures and leveling off at low temperatures.

The metabolic differences between males and females are apparently due to differences in mean weight (males, 362.84 ± 10.41 g; females, 329.6 ± 2.98 g). When existence energy is expressed on a per kilogram of body weight basis, females have a slightly higher value than males. When calculated per unit of surface area, or per weight$^{0.67}$, there was no difference between sexes for gross energy intake, excretory energy, or existence metabolism vs. temperature.

Excretory energy leveled off below –10°C, although a linear relationship has been shown in other species (Kendeigh 1949; Davis 1955;

TABLE 2. Data for controlled experiments.

Temperature (°C)	Weight						Feather loss/3 days		
	Male			Female					
	$\bar{x}$ g	SE	n	$\bar{x}$ g	SE	n	$\bar{x}$ g	SE	n
12 hr photoperiod									
35	352.0	11.0	2	309.3	8.5	3	.0708	.0259	5
30	348.5	5.5	2	293.3	15.4	3	.1256	.0836	5
20	340.0	17.0	2	303.3	15.8	3	.0418	.0252	5
10	343.0	5.0	2	297.7	16.6	3	.1388	.0832	5
0	359.0		1	307.7	16.7	3	.4601	.2080	5
–10	360.0		1	316.3	2.6	3	.1437	.0904	5
–18	384.0	3.0	2	334.0	4.0	3	.0378	.0050	5
–28	360.0	11.0	2	321.5	2.5	3	.0428	.0101	4
15 hr photoperiod									
30	329.0		1	307.7	3.3	2	.4247	.1403	4
20	342.5	8.5	2	306.3	4.8	3	.2895	.1004	5
10	325.5	0.5	2	315.7	7.6	3	.1879	.0354	5
2	323.5	4.5	2	307.7	8.2	3	.1015	.0377	5
0	411.0		1	309.3	11.6	3	.2181	.0724	4

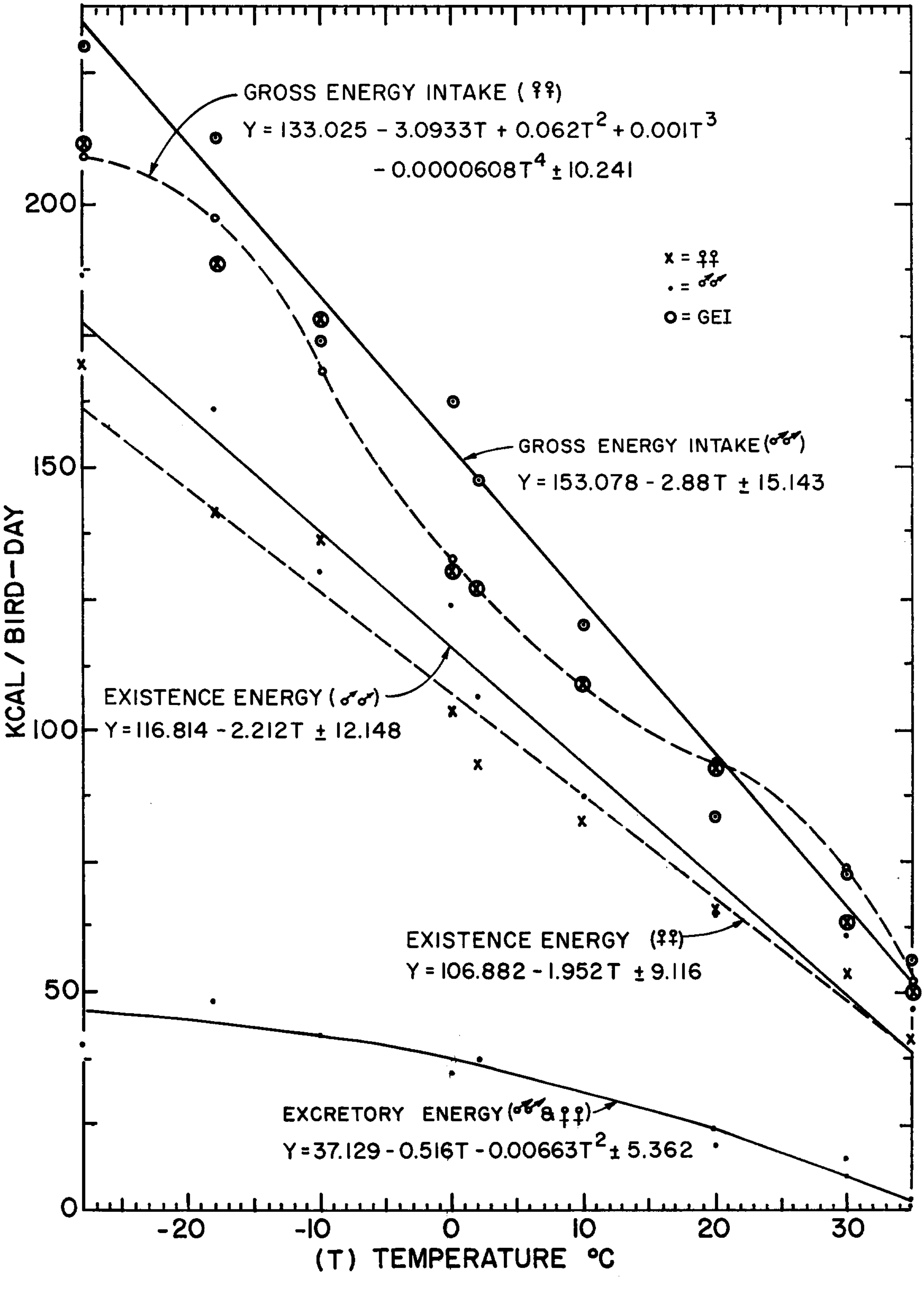

FIGURE 1. Relationship of gross energy intake (GEI), existence energy, and excretory energy to ambient temperature in Blue-winged Teal under controlled conditions. All regression equations are shown ± standard error of estimate.

West 1960; Williams 1965). The curvilinear relationship in teal is due primarily to a drop in the actual amount of fecal material voided and partly to a decreased caloric value of the feces (fig. 2). This decrease in the caloric value of the feces at lower temperatures brings an increase in the coefficient of utilization (fig. 2). Except for an indication in geese (*Branta canadensis;* Williams 1965) and redpolls (*Acanthis* spp.; Brooks 1968), other species (all passerines) have failed to exhibit such an increase (Kendeigh 1949; Davis 1955; West 1960; Zimmerman 1965). The coefficient of utilization also increased at high temperatures. Both below and above 30°C the nitrogen content of the feces increased (fig. 2).

At low temperatures the regression lines for gross energy intake and excretory energy diverge, indicating that there may be more protein assimilation at this extreme. Since the birds were at constant weight and presumably in nitrogen balance, the excess protein had to be broken down and the nitrogen excreted. This might account for the increased nitrogen in the excreta at this extreme and also the lowered caloric value, as uric acid contains less energy per gram than the food ingested.

Temperature tolerance. Blue-winged Teal can tolerate an unusually wide range of temperatures. The lower temperature limit was not obtained with the facilities available, but individual birds withstood mean temperatures ranging from –42 to –48°C with no apparent adverse effects. This is remarkable for a species that rarely encounters freezing temperatures in the field.

Perhaps even more remarkable is their ability to withstand high temperatures. Williams (1965) noted that the high lethal ambient temperature for Canada Geese was close to 41°C and Kendeigh (1969) stated that the ambient lethal temperature for some passerine species is 46–47°C. One Blue-winged Teal died at 46°C, but three others maintained weight at 48°C and tolerated 50°C for 24 hr, at which time the experiment was terminated. Teal are probably able to withstand high temperatures because of their ability to pant vigorously and also to consume large amounts of water. The birds which were least stressed by heat passed as much as one liter of water per day through the alimentary tract. The water in the dishes was 5–6°C below air temperature due to evaporative cooling.

The dense plumage of teal reduces the effects of both temperature extremes. At low ambient temperatures the outward movement of heat is retarded, while the reverse is true when ambient temperatures exceed body temperatures. There was no molt at either temperature extreme.

Weight change and metabolism. The relationship of weight gain and weight loss to metabolized energy (ME) was calculated at four different temperatures: 30, 10, 0, and –10°C. The slopes of the linear regression lines for ME vs. weight gain or weight loss were not different at any temperature, nor were they different between temperatures. This permits the use of a single mean value, 5.0 kcal/g change in weight per day, to express the relationship between metabolism and weight change. This value is lower than some previous estimates (Odum 1960, 9.0 kcal; King 1961, 7.0 kcal) and may be attributed partially to changes in water balance.

A modified method for determining existence energy. The finding that the change in metabolism associated with weight gain and loss is the same and that this does not vary with temperature enables one to determine existence energy by a new, quick method. First a linear regression equation for metabolism vs. change in weight for each experimental condition is calculated. This not only gives information about the relationship of energy and weight change, as shown above, but, by plotting the Y-intercept for each temperature against temperature, a line for existence energy is obtained. A regression line calculated in this manner did not differ significantly from the line for existence metabolism calculated in the conventional way and given earlier in this paper.

EXPERIMENTS OUT-OF-DOORS

METHODS

In early August 1966 two male and three female teal that had completed their postnuptial molt were placed in outdoor metabolism cages. The cages provided protection from rain, direct sunlight, and strong north winds. During the first week of December one female died and was replaced. Temperature, activity, molt, and metabolism were continuously recorded for 15 months; at the end of this period the birds had again completed the postnuptial molt.

The same methods were used to measure metabolism, activity, and molt as had been employed in the laboratory. The cages of one female and one male

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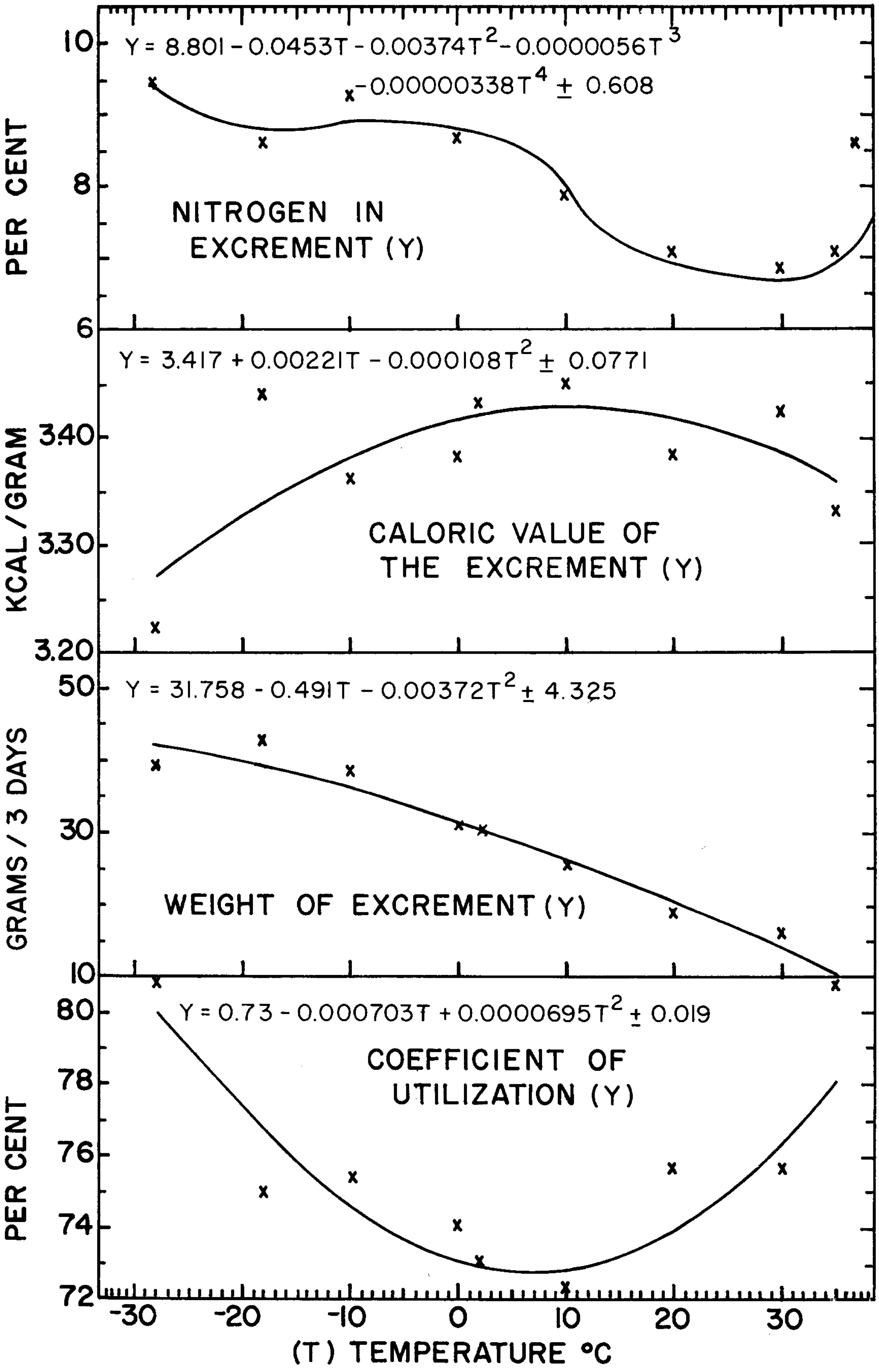
FIGURE 2. Relationship of the nitrogen content, caloric value, and weight of the excrement, and coefficient of utilization to ambient temperatures in Blue-winged Teal under controlled conditions.


Y = 8.801 - 0.0453T - 0.00374T2 - 0.0000056T3
-0.00000338T4 ± 0.608
NITROGEN IN EXCREMENT (Y)
PER CENT
10
8
6
Y = 3.417 + 0.00221T - 0.000108T2 ± 0.0771
CALORIC VALUE OF THE EXCREMENT (Y)
KCAL / GRAM
3.40
3.30
3.20
Y = 31.758 - 0.491T - 0.00372T2 ± 4.325
WEIGHT OF EXCREMENT (Y)
GRAMS / 3 DAYS
50
30
10
Y = 0.73 - 0.000703T + 0.0000695T2 ± 0.019
COEFFICIENT OF UTILIZATION (Y)
PER CENT
80
78
76
74
72
-30
-20
-10
0
10
20
30
(T) TEMPERATURE °C

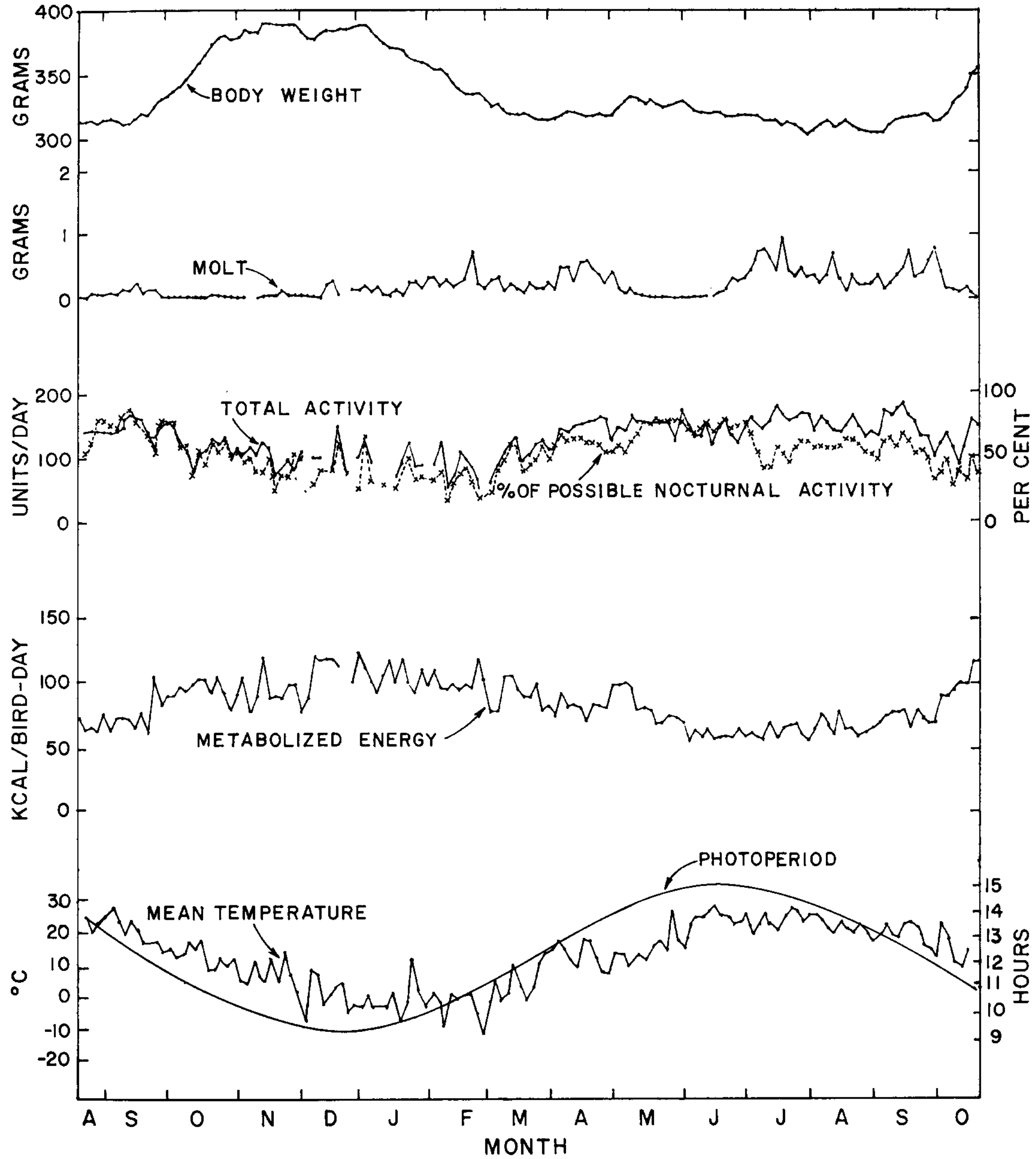


FIGURE 3. Seasonal changes in body weight, molt, activity, and metabolized energy of five caged Blue-winged Teal held out-of-doors. Ambient temperature and photoperiod are given for comparison.

were wired for recording activity, but during midwinter the floating floors often froze and these periods were eliminated from all analyses. Activity was calculated as total daily activity and per cent of total possible nocturnal activity between civil sunset and civil sunrise. A thermocouple was placed next to one metabolism cage and temperatures were recorded automatically every 20 min. From these readings a mean temperature was obtained for each three-day period.

Outdoor existence energy was determined by plotting metabolized energy against temperature for all periods when the weight of the ducks held constant (± 1.5 per cent). This was done on a seasonal and yearly basis. Annual changes in productive energy were obtained by comparing metabolized energy during a period with existence energy calculated for the temperature occurring during that period.

RESULTS AND DISCUSSION

All birds exhibited the same general trends throughout the year (fig. 3).

Metabolized energy (ME). The regression equation $Y = -0.962T + 5.81W^{0.512} + 5.316\Delta W - 0.224PT - 1.344P + 16.67M \pm 13.656$ (where Y = metabolized energy, T = temperature, W = body weight, ΔW = change in body weight, PT = preceding temperature, P =

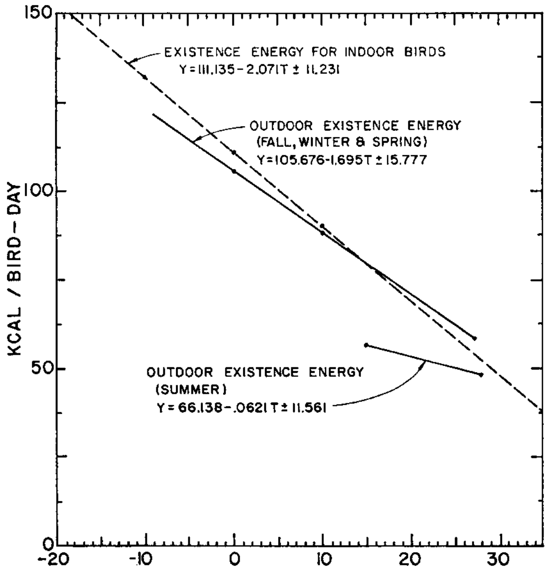


FIGURE 4. Comparison of existence energy of five Blue-winged Teal held out-of-doors with birds tested under controlled conditions.

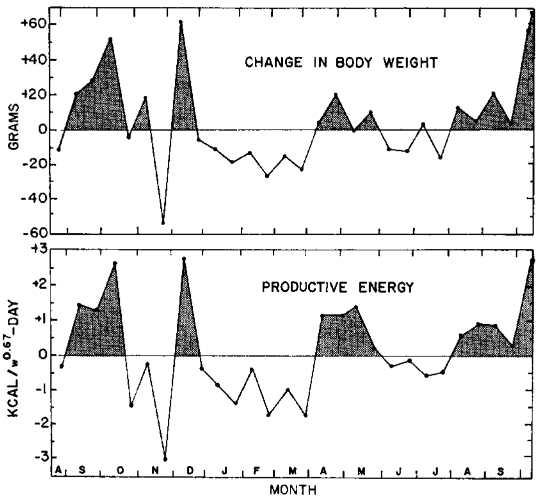


FIGURE 5. Seasonal changes in body weight and productive energy for one Blue-winged Teal (R-12). Zero productive energy represents existence energy at the particular temperature occurring during the period of measurement.

photoperiod, and M = molt) was calculated to determine the relationship between ME and the variables measured. Throughout the entire year major changes in ME were associated with changes in weight. The caloric value of 1 g change in weight varied between 2.9 and 7.0 during the year. Dolnik (1968), working with the Chaffinch (*Fringilla coelebs*), noted that the values varied between 2.0 and 9.0 kcal/g, depending on the season, obesity, energy balance, and degree of activity.

The relationship between ME and temperature appears to be quite complex. Davis (1955) and Olson (1965) stated that caged song birds out-of-doors do not adjust their rate of food intake as fast as the temperature changes, especially when the temperature change is rapid. In the present study the mean temperature of the three-day period preceding the period for which data are given had a significant effect on ME, indicating that more than three days are required for complete metabolic adjustment. With a sudden drop in temperature, food intake often dropped initially or remained the same, as the birds relied on their fat reserves. After a few days the teal would then accelerate their rate of feeding, often continuing after the temperature again rose. This indicated that the birds in the field may attempt to "wait out" cold snaps, seeking additional food only when body reserves reach some low level.

Body weight and photoperiod both had a significant effect on ME. Although no dependence could be found for metabolism on weight of feathers dropped during each three-day period, the importance of molt was apparent when it was prorated over the period of new feather growth. Variation in total daily activity and nocturnal activity as measured had no significant effect on metabolism.

Existence and productive energy. No significant differences were found between equations for outdoor existence energy vs. temperature, calculated separately for autumn, winter, and spring, but the regression line for summer had a significantly flatter slope (fig. 4). During the summer the mean temperature range is small (12.5°C) and metabolic adjustments are slight in relation to changes in temperature. Perhaps physical regulation of body temperature is more important at this time. Both existence energy regression lines for outdoor birds have significantly flatter slopes than for indoor birds. Davis (1955) and West (1960) found similar results and attributed them to a lag effect, due to sluggish adjustment to variable ambient temperatures. Further evidence for this has been given in the preceding section.

Productive energy was calculated in two ways, first using the existence energy values from the indoor birds, and then using the seasonal existence energy values from the outdoor birds, but no difference could be detected between the two methods. There was a significant correlation between weight change and productive energy throughout the year (fig. 5).

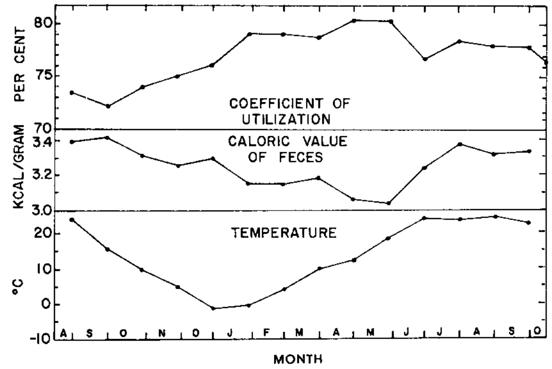


FIGURE 6. Seasonal changes in the caloric value of the feces and coefficient of utilization of five Blue-winged Teal held out-of-doors. Ambient temperature is given for comparison.

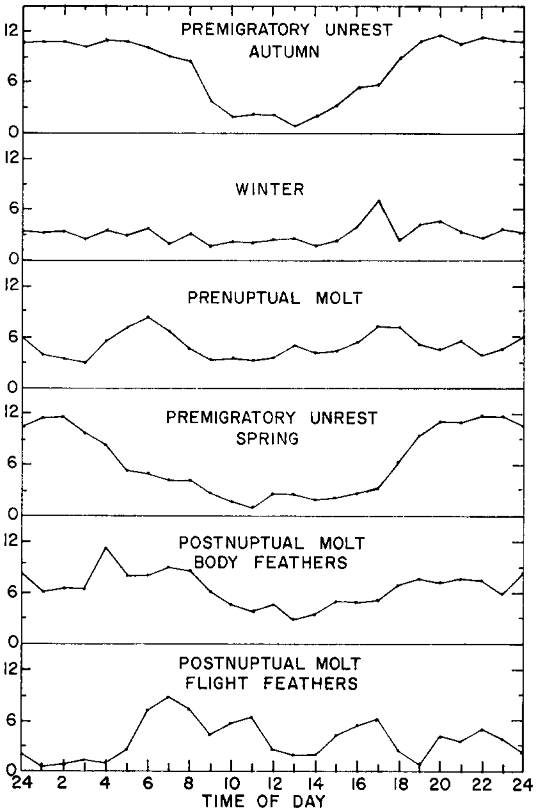


FIGURE 7. Changes in the daily pattern of activity of Blue-winged Teal during premigratory periods, winter, and molt. Data are averaged for two caged birds held out-of-doors. Left hand scale is in counts per hour.

Coefficient of utilization and caloric value of the feces. The coefficient of utilization and the caloric value of the feces show similar significant but opposite seasonal changes (fig. 6). During winter, teal became more efficient in the digestion and utilization of food, and the caloric value per unit weight of the feces decreased as temperature decreased. Brooks (1965) noted a similar relation in redpolls (*Acanthis* spp.). This apparent temperature response is very much like the one exhibited by the teal maintained under constant conditions. The outdoor birds did not respond immediately to the increasing temperatures of spring but maintained their high efficiency until about 1 June.

Seasonal changes in body weight, molt, and activity. Body weight of the teal increased about 25 per cent during the fall (fig. 3). This reaction to decreasing temperature is typical of many song birds wintering in the North Temperate Zone (Baldwin and Kendeigh 1938; Helms and Drury 1960; King and Farner 1966). Beginning in January, while ambient temperature continued low, however, the birds began gradually to lose weight. A small amount of vernal fat deposition began at the end of April and lasted nearly two weeks. This premigratory response was delayed by the prenuptial molt and occurred almost one month after Blue-winged Teal normally begin migrating through the Champaign, Illinois, area (Smith 1930). Body weights were lowest during the summer.

The prenuptial molt, involving only body contour feathers, occurred mainly during April and ended abruptly nine days after the beginning of "premigratory" fat deposition. The postnuptial molt included body feathers and flight feathers. The body eclipse molt occurred in July. Only three ducks dropped their flight feathers, one in August and two in September. This delayed or non-occurrence of flight feather molt is typical of ducks confined in small cages and may have interfered with the development of an autumn "premigratory" fat deposition.

Throughout the year there were considerable chages in the amount of daily activity and its temporal pattern (fig. 7). During migratory periods nocturnal activity increased. This type of response has been used to indicate a nocturnal migrant's physiological readiness to migrate. In the winter nocturnal activity was minimal. West (1962) noted that activity during cold weather reduces the insulative capacity of the feathers and increases heat loss. Molt has a depressing effect on nocturnal activity, especially during the flightless period. At this time teal in the wild are vulnerable to predation and become quite secretive.

Figure 8 shows the close relationship between the physiological, behavioral, and environmental changes during the spring migra-

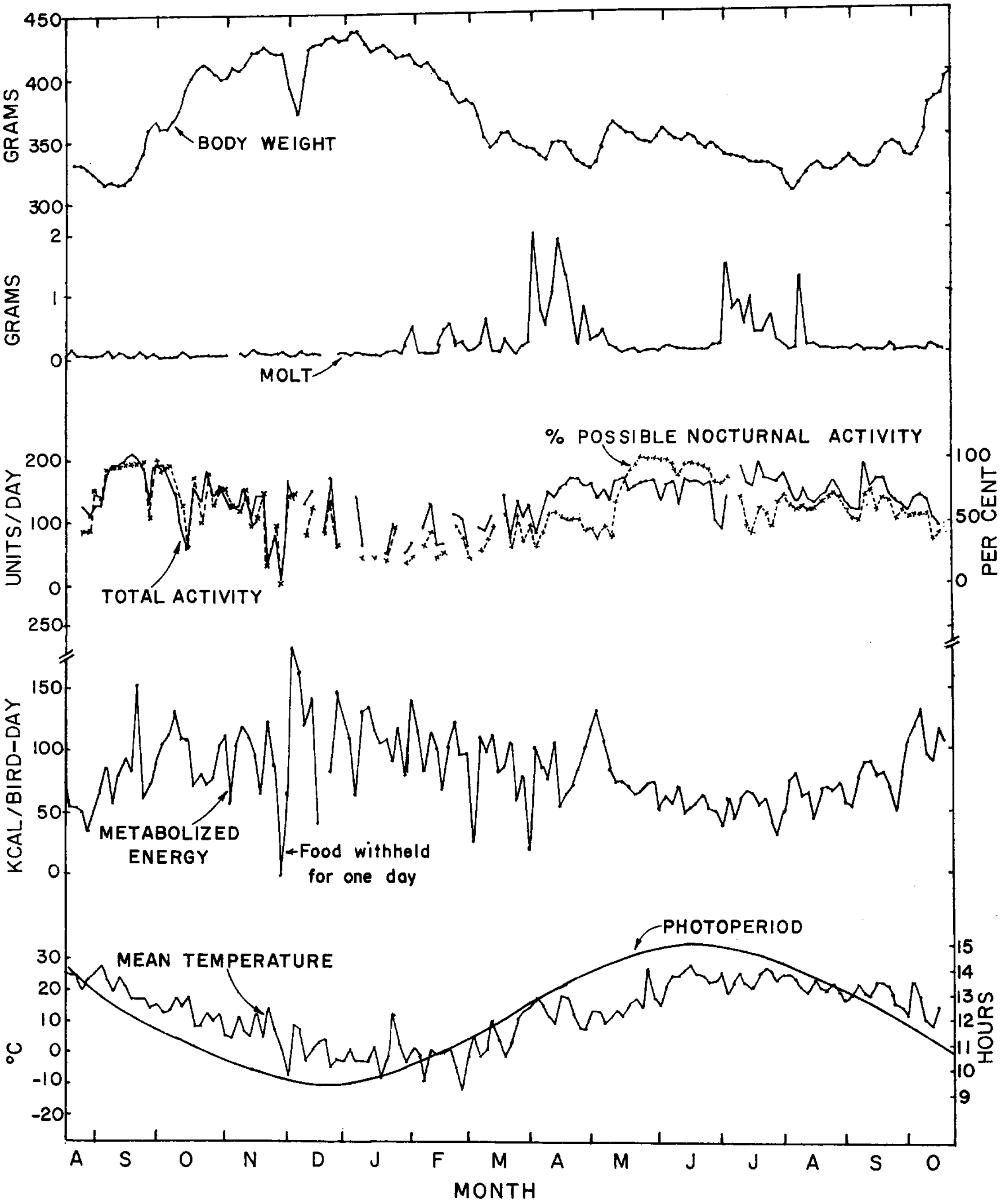


FIGURE 8. Seasonal changes in body weight, molt, activity, and metabolized energy of one female Blue-winged Teal held out-of-doors.

tory period. The prenuptial molt lasted three months but was heaviest during April. It was immediately followed by a period of hyperphagia and a 50-g increase in body weight. Nocturnal activity also increased at this time but only after the molt was completed and peak weight was reached. The sequence of events indicates that there may be some inhibitory effect of molt on prevernal fat deposition and nocturnal activity. Kendeigh et al. (1960) associated this with energy conservation.

CONCLUSION

The present study was an attempt to determine the effects of numerous variables on the energetics of a species. With the development of computer facilities and nonlinear multiple regression analyses (Zar 1969) it is now possible, as shown in this paper, to make detailed studies of caged birds held out-of-doors and to assign relative importance to each of the pertinent variables. These experiments better approximate field conditions and permit the study of variables rarely measured in the laboratory. The similarity in the effects of temperature, body weight, and weight change on metabolism under controlled and outdoor conditions in this study supports the use of outdoor experiments. Helms (1968) used a multiple regression analysis to study the metabolism of White-throated Sparrows (*Zonotrichia albicollis*) under outdoor conditions and came to a similar conclusion. When energy studies are made of free-living birds, this will be one way to partition the effects of the many variables occurring in the field.

With the aid of regression models, the yearly energy budget of an individual under natural conditions can be estimated. This is the ultimate aim of this general research program in bioenergetics. Obviously, when the energy budgets of individuals are known, this can be projected into energy budgets of whole populations to provide important information on the role of the species in the energy flow of the ecosystem.

SUMMARY

The bioenergetics of caged Blue-winged Teal were studied under controlled and outdoor conditions with special emphasis on the effects of different variables on metabolism. At temperatures above 0°C there was no difference in the existence metabolism of ducks held under 12- and 15-hr photoperiods. Existence metabolism was different for males and females and was associated with the differences in weight of the two sexes.

Excretory energy varied curvilinearly and inversely with temperature, leveling off at temperatures below -20°C. This relationship was due to a drop in the amount of fecal material voided and to a decrease in the caloric value of the feces at these temperatures. The coefficient of food utilization increased at both high and low temperatures, and opposite changes occurred in the caloric value of the feces. The nitrogen content of the feces increased both above and below 30°C.

Upper and lower lethal temperatures were not reached, but teal withstood ambient temperatures of -48 and +50°C.

The caloric equivalent of a gram change in weight was 5.0 kcal/bird-day for indoor birds. For outdoor birds the value varied between 2.9 and 7.0 with a yearly average of 5.3 kcal/bird-day.

A modified method for determining existence metabolism was developed which enables the use of birds that are not maintaining constant weight. Multiple linear and nonlinear regression analysis was used to determine the effects of different variables on the metabolism of caged teal kept out-of-doors. Body weight, change in body weight, and molt correlated positively with metabolism, while temperature and photoperiod exhibited a negative correlation with metabolism. Existence metabolism out-of-doors was the same during the autumn, winter, and spring but different during the summer. The slope for existence metabolism vs. temperature out-of-doors was flatter than indoors; the difference may be associated with the birds' inability to adjust completely to rapidly fluctuating temperatures.

Changes in body weight were positively correlated with changes in available productive energy. The coefficient of utilization and caloric value of the feces out-of-doors showed similar but opposite seasonal changes. The body weights of caged teal held out-of-doors increased about 25 per cent in the fall, decreased during the winter, and increased slightly at the end of April during the premigratory period.

Three molts occurred during the year: an extended prenuptial molt which peaked in April, a postnuptial molt of body feathers during July, and a delayed postnuptial molt of flight feathers during August and September. Total daily activity decreased during periods of molt and was lowest during the winter. Nocturnal activity increased sharply during premigratory periods.

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