for a second or two, and at least two birds appeared to be watching the vulture. When the vulture had soared to about 50 m away from the quail, it suddenly turned, dropped to an elevation of about 20 m (just above the treetops), and approached the vicinity of the quail, flapping it wings three times. Two quail flew about 30 m; the remaining ten ran rapidly some 3 or 4 m from the driveway into the adjacent open oak forest, crouched and "froze." The vulture turned overhead, again flew about 50–70 m away and returned. The vulture repeated the performance five more times, and the quail remained motionless during the entire episode. The quail were so cryptic among the leaf litter that I was able to locate only three of the ten that were less than 15 m from my window. I noted the first movement of quail approximately 40 sec after the last pass of the vulture. Within another 30 sec all quail appeared to resume movement, although I had the impression that the activity was more hesitant than before and that the quail were more alert. I heard no vocalizations during the encounter but the closed double window would have prevented my hearing faint sounds.

I doubt that the vulture was interested in the quail; I believe the attraction was the odor from the remains of a large fish that my neighbor had thrown out for his cat.

Turkey Vultures roost about two miles from my home and many times each day fly along the ridge on which my house is situated. In the next few days I observed four more incidents of vultures flying over the vicinity while quail were feeding near my house. In all four cases the vulture was at least 70 m from the quail, and I noted no reaction.

These observations suggest that the quail were habituated to distant overflights of vultures, while a near overflight elicited a brief freezing response, and direct approach by the vulture, similar to an "attack," elicited fleeing responses followed by prolonged immobility. In my 25 years of watching and trapping hawks, I often have been impressed with the lack of overt reactions by birds to hawks unless the hawk appears to be attacking. Whenever I was able to observe closely the behavior of birds used as lures in hawk traps, it seemed to me that the birds were watching the hawk, but overt reactions were rare unless the hawk approached directly and rapidly.

Laboratory experiments by Melzack (J. Comp. Physiol. Psychol. 52:694, 1961) have shown that young Mallards (*Anas platyrhynchos*) continue to watch models of hawks after habituation has eliminated overt fear responses. He suggested that birds may escape direct attack by hawks by maintaining a "state of vigilance" and by reacting to "swooping, change of speed compared with size . . . and the like." My natural observations appear to be in general agreement with the inferences of Melzack.

Willis (Condor 65:313, 1963) suggested that the Zone-tailed Hawk (*Buteo albonotatus*) is an aggressive mimic of the Turkey Vulture and that the similarity between the two species permits the hawk to approach prey that are habituated to the vulture. I (Condor 74:221–222, 1972) have suggested that the similarities in shape and manner of flight are due to aerodynamic requirements, not mimicry. My observations, and those of Melzack, suggest that habituation may not play a significant role in reactions to predators and thus add further doubt that the Zone-tailed Hawk is a mimic of the Turkey Vulture.

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EXISTENCE METABOLISM

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Existence metabolism is the energy required by birds for "normal" (non-flying, non-breeding, non-molting) activities over at least one 24-hr period under air temperatures which are controlled but which do not necessarily lead to minimum (basal) energy requirements. Its prediction for birds of different weights under different conditions of photoperiod and temperature is of interest to ecologists who might use such relationships to estimate energy intake by correcting these estimates for activities and for assimilation efficiency. This paper identifies limitations of previous analyses and presents an analysis of the functional relationship between existence metabolism and the variables of body weight, ambient temperature and photoperiod, using regression techniques on data from the literature. The importance of these are evaluated using an analysis of variance.

MATERIALS AND METHODS

Data on existence metabolism at various temperatures were obtained from a variety of sources. All were used in a previous analysis by Kendeigh (1970) and many were undertaken by his students; this probably indicates a certain consistency in the data and the definition of "existence metabolism" used. These sources were: Yellow-bellied and Variable seedeaters (*Sporophila nigricollis* and *S. minuta*), Blue-black Grassquit (*Volatinia jacarina*) and Green-backed Sparrow (*Arremonops conirostris*) from Cox (1961), Zebra Finch (*Taeniopygia castanotis*) from El-Wailly (1966), Common and Hoary redpolls (*Acanthis flammea* and *A. hornemanni*) from Brooks (1968), Tree Sparrow (*Spizella arborea*) from West (1960), House Sparrow (*Passer domesticus*) from Kendeigh (1949) and Davis (1955), White-throated Sparrow (*Zonotrichia albicollis*) from Kontogiannis (1968), Dickcissel (*Spiza americana*) from Zimmerman (1965) and Evening Grosbeak (*Hesperiphona vespertina*) from West and Hart (1966). With only a few exceptions, observed values of existence metabolism could be related to specific observations of body weight (or the mean of a small group of individuals) and air temperature; data above 30° C were excluded.

I analyzed data using methods of linearizable and intrinsically non-linear multiple regression as described by Draper and Smith (1966). The computer programs used were those of the University of California (Biomedical Computer Programs, BMDO2R and BMDO7R), (Dixon 1973). Lack of fit statistics were calculated by hand. Initially a linearizable model was analyzed. This was the form:

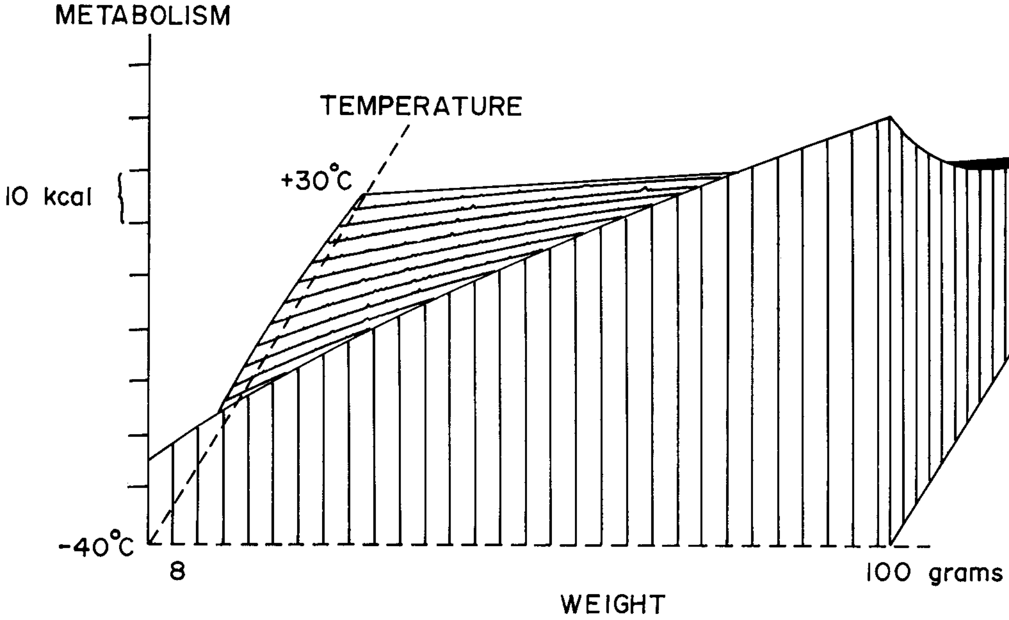

FIGURE 1. Existence metabolism as a function of temperature and body weight for an arbitrary photoperiod.

$M_e = B_0 + B_1T + B_2T^2 + B_3T^3 + B_4P + B_5W^{0.67} + B_6TW^{0.67} + B_7T^2W^{0.67}$, where M_e = existence metabolism, T = air temperature, P = photoperiod, W = weight and B_0 through B_7 are coefficients to be estimated. The exponent of 0.67 was chosen as an arbitrary constant statistically indistinguishable from observed values, and not because of some a priori acceptance of the form of the M_e-weight relation. All but the last term were included by the stepwise procedure. Analysis of the residual plots suggested that five data points out of a total of 146 were sufficiently remote from the regression surface to be considered outliers and to be excluded from subsequent analysis. Inspection of the original data showed that these points were a considerable distance from the remainder of the observations made under similar conditions. Their exclusion improves the percentage of the total variability explained by the model ($R^2 \times 100$), decreases the pure error mean square but leaves the values of the parameters essentially unchanged.

The statistical model used so far can be expressed in the form: $Y = X\beta + \epsilon$, where Y is the vector of dependent variable values, β, the vector of parameters to be estimated, X contains the matrix of independent variable values (which may include known nonlinear functions of the other columns; e.g. column two may be the values of column one squared), and ϵ allows random deviation of the observed values of Y from that given by the model. In this case it is possible to derive directly an expression for the coefficients which minimizes the sum of the squares of the deviations. However, when X contains terms that are functions which need to be estimated, for example X_1^c, where c is unknown, this approach cannot be used. To estimate the exponent of the weight parameter it was necessary to use an intrinsically non-linear approach. This, from assigned starting values, explores the multidimensional response surface of the residual mean sum of squares from the regression analysis in relation to the values of the parameters to be estimated. The program returns a set of parameter values which represent a minimum residual mean sum of squares.

The analysis used as initial conditions, the values for the parameters determined by the previous analysis, which assumed a linearizable model. The intrinsically non-linear analysis did not result in a significant improvement of the regression sums of squares. Thus, without loss of generality, the discussion can be limited to the linearizable model. Furthermore, this limitation allows a critical analysis of residuals.

RESULTS

The least squares fit to predict existence metabolism (M_e) results in the following equation:

$M_e = 0.37 - 0.11T - 0.00011T^3 + 1.9W^{0.67} - 0.043W^{0.67}.T + 0.53P$, where T is the air temperature in degrees centigrade, P is the photoperiod in hours, W the weight in grams; the units of M_e are kcal per bird per day. This surface is shown in figure 1. Table 1 gives an anlysis of the variance of the model and the values and standard errors of the coefficients. The ratio of the lack of fit mean square to the pure error mean square is less than one, implying that the model has no prominent bias. Inspection of the residual plots against all the variables suggests neither heterogeneity of variance nor marked trends in the magnitude and direction of the deviations from the model.

DISCUSSION

Kendeigh (1970) presented an analysis of weight against existence metabolism for two temperatures, 0° C and 30° C. For each of the species a linear relation was established between metabolism and temperature and the values for metabolism at 0° C and 30° C were obtained by interpolation. This may produce only an approximate model and the subsequent analysis might miss important effects such as those of photoperiod. Weight was presumed to be

TABLE 1. Analysis of variance of factors affecting existence metabolism.

Source		Mean square	df	F	
	Constant = B				
Reduction	T given B.	5652	1	737	*
Reduction	$W^{0.67}$ given T,B.	4284	1	559	*
Reduction	$W^{0.67}$.T given $W^{0.67}$,T,B.	1044	1	136	*
Reduction	P given $W^{0.67}$.T,$W^{0.67}$,T,B.	328	1	43	*
Reduction	T^3 given P,$W^{0.67}$.T,$W^{0.67}$,T,B.	96	1	12	*
	Total regression	2281	5	298	*
	Residual	7.66	135		
	Lack of fit	7.55	99	F<1	
	Pure error	8.12	36		

Variable	Coefficient	Standard error
Constant	0.36938	
Temperature	0.11420	0.04724
Temperature cubed	–0.00011	0.00003
Weight to the 0.67 power	1.90391	0.07211
Weight to the 0.67 power × temperature	–0·04255	0.00362
Photoperiod	0.52753	0.07946

* Reject null hypothesis (that variable is insignificant) with at least 99.5% confidence.

constant for all temperatures, for a particular species (though sexual differences were taken into account). The original data show that in at least one case (Brooks 1968), the air temperature of the experiment was correlated with body weight. The temperature-metabolism relationship was assumed to be linear. If this were incorrect the estimates of metabolism might be biased at either or both of the two temperatures. Brooks presented curvilinear fits for two species of redpoll.

My analysis overcomes these difficulties and provides a better predictive equation. This analysis still needs to address the question of the biological significance of the four types of terms included.

The relation of metabolism to weight by the "power law" has been discussed by Schmidt-Nielsen (1970). There is no evidence in the present analysis to reject the value of 0.67 for the exponent on the weight term.

This analysis includes a weight-temperature interaction term. This was obtained implicitly by Kendeigh (1970); though the slopes of the log metabolism-log weight relations did not differ at 0° C and 30° C their intercept did. This will give rise to an interaction on the detransformed scale. The interaction is such that the slope of the metabolism-temperature relation is more negative at higher body temperatures, a fact that is clear from an examination of the data presented in table 1 of Kendeigh's analysis. The slope of the metabolism-temperature relation—where metabolism is measured over the short term by oxygen consumption—is considered a measure of thermal conductivity. The relation of thermal conductivity to body weight and thus the interaction term in his analysis are, despite the different methods of measurement, probably due to the same phenomena. The variation of thermal conductivity to body weight was discussed by Lasiewski et al. (1967).

Increased photoperiod may increase the amount of time the birds are active and hence increase energy costs. Less clear are the presence of non-linear terms in the temperature effects. In addition to linear terms, a cubic term was found to be statistically significant. Though these terms themselves may have no particular biological significance, they represent the first terms of a Taylor polynomial expansion about some point of the function which expresses the true relation. The estimated relation is almost linear over most temperatures. At low temperatures the inclusion of a cubic term indicates that there is an upward curl to the line. A reason for this upward curl at low temperatures may be that at these temperatures the thermal insulation of a bird decreases as it shivers to produce more heat (E. Pivorum pers. comm.).

The present model is not only statistically more defensible but also provides a better predictive equation for existence metabolism than previous attempts. More terms are included but all may be interpreted biologically. The new equation should provide a better basis for calculating the energetic impact of birds.

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ENERGETICS OF GROWTH FOR BLACK-BELLIED TREE DUCKS

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Ricklefs (1969) postulated that the rate at which food can be processed and utilized is a physiological constraint that limits the growth rates of birds. The brood size of altricial birds is known to be limited by the ability of the adults to feed their young (Lack 1954, Royama 1966, and Ricklefs 1968) but the energy required for their growth is not known. This subject has been much studied in domestic animals (Kleiber and Dougherty 1934, Brody 1945, Hill and Anderson 1958, Scott et al. 1959, and Hijikuro and Morimoto 1969), but has received little attention in wild birds (Stivens 1961, Brisbin 1965, Sugden 1969, Penny and Bailey 1970). This study is an attempt to determine the energy cost for growth in Black-bellied Tree Ducks (*Dendrocygna autumnalis*) and the ecological efficiency of that growth.

The precocial young of the Black-bellied Tree Duck acquire their own food. The amount that a duckling eats should be limited only by its ability to find food. These ducklings are brooded by the adults for a time but begin the energy-demanding process of thermoregulation around the ninth day of age (Cain 1972). Their growth rate is highest between the ages of 4 to 33 days (Cain 1970).

METHODS

Black-bellied Tree Duck eggs were collected in San Patricio County, Texas, transported to the University of Illinois, and incubated at 39°C in a forced-air incubator at 85–90% relative humidity. Ducklings were brooded in these incubators for 48 hr after hatching and then placed in a 10 m × 10 m room at 32–38°C with a 15-hr photoperiod.

Ducklings used in the metabolism and growth determinations were placed in metabolism cages like those described by Owen (1970) but larger, 54 × 43 × 48 cm. They were fed chick startena for 21 days and milo (*Sorghum vulgare*) thereafter. All the food was oven-dried (65°C) to a constant weight. Temperature was kept at 32°C and the photoperiod at 15 hr during the tests, approximately the conditions normally encountered during the nesting season in south Texas. During intervals between tests, the ducklings were fed a mixture of chick startena, milo, and cracked corn. Duckweed, aquatic invertebrates, and small fish (*Gambusia affinis*) were placed in the water pans daily to insure a balanced diet.

At 3-day intervals the ducklings were weighed to the nearest 0.1 g on a triple-beam balance. The unused food and excreta were collected, oven dried, and homogenized with a Waring Blender. Their caloric value was determined with a Parr oxygen bomb calorimeter.

The relationships among photoperiod, temperature, metabolism, and growth were determined by Kendeigh's (1949) method, which involves subtracting the caloric value of the excreta (excretory energy) from the caloric value of the food eaten (gross energy intake). The remainder is the amount used (metabolized energy), and during a period of constant weight (change within ±1.5%) is called existence energy. Productive energy is the amount metabolized above that needed for existence at a particular temperature.

To calculate the existence requirements for the growing ducklings, I plotted the metabolized energy against weight gained. From the resulting regression lines at weekly intervals the existence energy was the metabolized energy with no gain in weight (i.e. $X = 0$). I calculated the energy cost per gram of dry weight increase by multiplying the metabolized energy required per gram of wet weight increase (the slope of the regression line) by the percent of wet weight that was dry weight. This product, divided by the calories per gram of dry matter and multiplied by 100 yielded the productive efficiency.

RESULTS

Body weight. Growth of body weight for 26 ducklings (fig. 1) followed closely my data for more than 100 pen-raised ducklings (Cain 1970). My previous study showed the growth of pen-raised ducklings to resemble that of wild ducklings. The dry weight of 1-day-old ducklings in this study averaged 31.9% of the wet weight and increased to 43.0% at six weeks of age, remaining constant thereafter (table 1). These values are similar to those reported by Sugden (1969) for Lesser Scaup (*Aythya affinis*) ducklings.

Caloric values per gram dry weight of the duck-

TABLE 1. Weights and caloric values of ducklings sacrificed at weekly intervals.

Age in weeks	N	Wet weight (gram)	Dry weight (gram)	Percent dry weight	Caloric value (kcal/gram) dry weight	Caloric value (kcal/gram) wet weight
pipped	3	30.8	9.8	31.9	6.0	1.9
2	4	45.0	11.2	24.9	5.5	1.4
3	5	59.8	19.7	33.0	4.8	1.6
4	1	85.6	29.5	34.5	5.4	1.9
5	1	166.6	62.6	37.6	5.6	2.1
6	1	257.0	110.4	43.0	5.7	2.4
7	1	405.5	167.1	41.2	5.6	2.1
9	1	440.0	184.4	41.9	5.3	2.2