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Ronald M. Case

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ENERGETIC REQUIREMENTS FOR EGG-LAYING BOBWHITES

Ronald M. Case,^a Division of Biological Science, University of Missouri, Columbia

Abstract:

As part of an extensive bioenergetics study of bobwhite quail (*Colinus virginianus*), energy requirements for egg laying were determined. Caloric values for eggs averaged 5.489 kcal/g. Net energetic efficiency of converting productive energy into eggs was conservatively estimated to be 54% for quail laying at a rate of 0.45 egg/bird-day at 25 C. Assuming that those values were the same for quail laying a 10-g egg at a rate of 1 egg/bird-day resulted in an energy requirement of 69.645 kcal/bird-day. This is an energy demand equivalent to that of existence alone at about -3.3 C.

Bioenergetic studies of a species contribute to the understanding of factors limiting the number of individuals on a given area and the species' geographic distribution. They also contribute to a broader knowledge, namely, the flow of energy through an ecosystem. The primary objective of this study was to quantify energy expended by bobwhites for laying eggs. These data will supplement knowledge of basic energy requirements of bobwhites (2) and energy conserved by huddling (3). When integrated with field data on food habits, weight dynamics, and mortality (15,16,17,18), it may be possible to determine the critical season for the regulation of numbers of bobwhites.

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Materials and Methods

Ten adult, game-farm-raised, females were placed in individual, polypropylene, 48 X 25 X 13 cm cages with 0.5-inch mesh bottoms and sliding, 0.25-inch mesh, hardware cloth tops. Caged birds were kept in a walk-in environmental chamber under controlled temperature, photoperiod, and relative humidity and were provided ad libitum feed (a balanced mash of 20.5% protein, 2.7% fat, and 3.6% crude fiber) having a caloric value of 4.250 ± 0.030 kcal/g (mean $\pm$ SE), and water.

Data were collected at 3-day intervals for a 12-day period at each temperature treatment. Feed and feces were separated and oven-dried at 65 C to a constant weight. Weight of birds, feed, and excreta were to the nearest 0.1 g.

Feed and excreta were prepared for calorimetric analysis by

^aPresent address: Department of Poultry Science, University of Nebraska, Lincoln 68503

grinding in a Wiley Model micro mill. Samples were weighed to the nearest 0.1 mg before being analyzed in a Parr oxygen-bomb calorimeter.

Energy requirements were determined using the feeding method, i.e., calculating gross energy intake, excretory energy, and metabolized energy (see Cox (4) for definitions) for each bird. If constant body weight were maintained (weight change of 1% or less), metabolized energy was termed existence energy for nonlaying birds--the energy required by quail to subsist under caged conditions.

Birds were previously kept under a 10-hr photoperiod and it was desired to have all of them in reproductive condition before the start of this 15-hr photoperiod experiment. From results of others (7,8,11) I decided to allow a minimum of 60 days for acclimation, and actually allowed 83 days.

Temperature treatments were at 10-C increments from 5 to 35 C. A minimum of 2 weeks of acclimation was allowed after conditions were changed. Eggs were punctured with a dissecting needle and oven-dried at 65 C to a constant weight. They were analyzed calorimetrically by the same method used for excreta and feed, except they were ground by hand in a mortar after drying. See Case (2) for greater detail on methods.

Results and Discussion

Gross energy intake, metabolized energy, and excretory energy varied significantly ($P < 0.005$) at different temperatures. Figure 1 depicts the significant ($P < 0.005$) quadratic effect of temperature on those variables.

Case (2) reported that body weight differences accounted for less than 1% of the total variation about energy variables in male and female bobwhites under a 10-hr photoperiod. Also, a significant difference was not detected for existence requirements neither between males and females under a 10-hr photoperiod nor between males and nonlaying females under a 15-hr photoperiod. Thus, assuming that egg-laying females had the same existence requirement as males and nonlaying females, it was possible to determine the productive energy (Figure 1). Productive energy is the difference, in kcal/bird day, between metabolized energy and existence energy.

Eggs from birds maintained at 25 C were heaviest and had greatest caloric value (Table 1). Greatest caloric value/g and ash-free caloric value/g were for eggs laid at 35 C. Ash percentage was lowest at 35 C.

Productive energy and egg calories/bird-day were 13.800 and 7.438 kcal/bird-day, respectively, at 25 C, and those were highest of the 4 temperature treatments (Table 2). The highest egg-laying rate (0.452 egg/bird-day) was at 15 C.

Wilson (24) found that egg production of domestic chickens declined above 26.5 C, that some hens quit laying at 38 C, and that shell thickness

decreased as temperature increased above 21 C. Although caloric value of eggs did not decrease significantly at 35 C in my experiment, rate of laying decreased drastically.

At temperatures higher than 25 C, excessive body heat may be generated by a high level of feeding. This hypothesis seems to account for the following observations: (A) energy intake and productive energy decreased at temperatures warmer than 25 C, (B) ash percentage of eggs decreased with increasing temperature, and (C) 2 birds laid eggs at 35 C with shells so thin they broke and could not be collected. DeWitt, Nestler and Derby (5) concluded that bobwhites required 2.3% calcium in their diet for egg production. The feed I used had sufficient calcium for egg laying below 35 C. It was either deficient or not used at 35 C, as evidenced by thin-shelled eggs. Payne (14) observed that when feed consumption is low, higher concentration of minerals in the diet may be necessary to sustain egg production in domestic hens.

Net efficiency of egg laying was maximum at 5 C. Wilson (25), using temperatures ranging from 5 to 40 C, reported lowest conversion of feed to eggs at 5 C for domestic hens. Net efficiency for egg formation in the zebra finch (*Taeniopygia castanotis*) was 49% at 14.5 C and 77% at 34.4 C (6). The high net efficiency at 5 C in my experiment seems spurious. This may be due, in part, to the small number of eggs (8 from 4 birds for 48 possible bird days). My other net efficiencies were comparable to those of El-Wailly (6) and Brody (1).

If existence energy of laying birds is equal to that of nonlaying birds, and caloric value, percent dry weight, and net energetic efficiencies remain the same as egg size and rate of laying increase, then it is possible to calculate the energy requirement for egg laying in bobwhites. Using the data from Tables 1 and 2 and assuming a 10-g egg is laid each day at 25 C, then $5.489 \text{ kcal/g} \times 10 \text{ g} \times 0.3371 = 18.503 \text{ kcal/egg}$. Since the net efficiency of egg formation is 54%, a productive energy ($18.503 \text{ kcal}/0.54$) of 34.265 kcal/bird day is required to form a 10-g egg. Adding productive energy to existence energy at 25 C (35.380 kcal/bird-day), it is then possible to calculate the temperature-equivalent existence energy. That is, from Figure 1, laying an egg at 25 C requires as much metabolized energy as existence alone at -3.3 C ($65.630 - 1.210T = 69.645$; $T = -3.3 \text{ C}$).

It must be stressed that this is probably an overestimate. For example, a net efficiency of egg formation of 70% (commensurate with values in literature and my data at other temperatures) results in a temperature-equivalent existence energy of about 3 C. Smaller eggs (representative bobwhite egg weights: 9 g, (21); 9.6 g (20); 8.8 g, this study) and possibly still higher efficiencies (perhaps as great as 77%) would lower the energy requirement further.

Speculation

There exists considerable evidence that food resources limit bird populations. In bobwhites, this seemingly would be in late winter when seed abundance has diminished and low temperatures are maintaining a

high demand for food. Lack (12) and Fretwell (9) have discussed the role of dominance in winter survival of birds when food may be limiting. Perhaps a similar explanation exists for the low survival rate of juvenile bobwhites from September to April noted by Robel (16) and by Robel and Fretwell (19). The latter study showed a significant decrease in the proportion of juvenile bobwhites from fall to late winter and early spring over an 8-year period. Indirect evidence for food limitation of bobwhites in late winter is provided by decreased weights from December-January through March (10,18). One must also consider the importance of weather, namely snow cover, on limiting food availability (22).

Could food also account for differential sex mortality? Sex ratios of juvenile bobwhites are about equal (10,13), but that of adults is generally in favor of males. This differential sex ratio is usually attributed to high mortality of females during the nesting season. Rosene (23) suggested that possibly the physical strain imposed on females during egg laying and incubating is greater than that on males and thus females may die faster because they are weaker. My data on energy demands for egg laying indicate that at 25 C the productive energy required for egg formation (34.265 kcal/bird day) is nearly equal to that required for existence (35.380 kcal/bird day) at the same temperature. Apparently those data could be interpreted as supporting Rosene's hypothesis. I think that is not true. Adult quail weights increase in April and this is attributed to the increased weight of females (18). One could surmise that food must not be critical at this time because body weights increase, and the increased food is probably due to the increased availability of animal food. This is supported by Robel (17) finding an increase in volume of animal matter of 15% or more in bobwhite crops in April over that for December-March. An elevated metabolism, necessitated by egg laying, is not deemed to impose a physical strain on females. Since both males and females can readily sustain themselves at an equivalent winter-level of existence (about -3.3 C), strain could result only if food is in short supply.

If there is an energetic basis for a differential sex ratio it would probably be effective in late winter. Robel (1965) did find a difference in females:males from 1.28:1 in September-December to 0.96:1 in January-April, although this difference was not statistically significant. Regressions of existence energy on temperature for male and female bobwhites at 10 hr, not statistically different from each other, do indicate a steeper slope and a higher intercept for females (2). If this divergence is not due to random scatter and if it continued at colder temperatures (females requiring more energy), then energy demands may influence the sex-related survival of bobwhites during late winter when food is in short supply.

Two major gaps in information are brought out in regard to those statements, 1) existence energy requirements of quail of each sex at colder temperatures and 2) the availability of food in late winter and early spring. Especially lacking is information on the abundance and utilization (foraging and metabolic efficiency) of animal food by bobwhites in the wild.

Conclusion

Using estimates obtained in this experiment on metabolized energy, productive energy, caloric value of eggs, and efficiency of converting metabolized energy into eggs, it was possible to estimate the energy requirement for producing a 10-g egg at the rate of 1 egg/bird day at 25 C. This resulted in an energy requirement of 34.265 kcal/bird day, nearly equal to that of existence alone (35.380 kcal/bird day) at 25 C. This was judged to be a maximal estimate since average egg weights may be less and conversion efficiencies are likely higher.

The energy requirement for egg laying plus existence at 25 C is about equal to that for existence alone at -3.3 C. This was not judged to impose a physical strain on females. The observed increase in body weight prior to egg laying must reflect adequate food (at least calories) availability.

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Table 1. Weight, caloric content, and ash percentage of eggs laid during four indicated temperature treatments.

MEAN $\pm$ SE								
Temp (C)	N	Fresh weight (g)	Dry weight (g)	Percent dry weight	Caloric value (kcal/g)	Ash-free caloric value (kcal/g)	Total kcal/egg	Percent ash
5	8	8.19 $\pm$ 0.21	2.74 $\pm$ 0.08	33.42 $\pm$ 0.31	5.429 $\pm$ 0.056	6.610 $\pm$ 0.037	14.882 $\pm$ 0.477	17.87 $\pm$ 0.44
15	38	8.69 $\pm$ 0.10	2.94 $\pm$ 0.04	33.81 $\pm$ 0.15	5.442 $\pm$ 0.027	6.578 $\pm$ 0.018	16.054 $\pm$ 0.233	17.28 $\pm$ 0.22
25	43	8.79 $\pm$ 0.09	2.97 $\pm$ 0.04	33.71 $\pm$ 0.14	5.489 $\pm$ 0.025	6.585 $\pm$ 0.016	16.379 $\pm$ 0.210	16.67 $\pm$ 0.19
35	11	8.32 $\pm$ 0.19	2.77 $\pm$ 0.07	33.23 $\pm$ 0.28	5.862 $\pm$ 0.050	6.730 $\pm$ 0.033	16.200 $\pm$ 0.429	12.99 $\pm$ 0.40

Table 2. Productive energy, efficiency of egg production, and rate of lay at indicated temperature treatments.

Temp C	N ^a	Metabolized ^b energy (a)	Existence ^{b,c} energy (b)	Productive ^b energy (a-b=c)	Egg kcal/bird-day (d)	Net energetic efficiency (d/c) $\times$ 100	Rate of egg laying (egg/bird-day)
5	4	62.406	59.581	2.825	2.802	99.2	0.167
15	7	60.380	47.484	12.896	7.304	56.6	0.452
25	8	49.180	35.380	13.800	7.438	53.9	0.448
35	5	28.804	23.290	5.514	4.149	75.2	0.250

^an is the number of birds laying eggs at each treatment.

^bvalues in kcal/bird-day.

^cexistence requirement of males, see text for rationale.

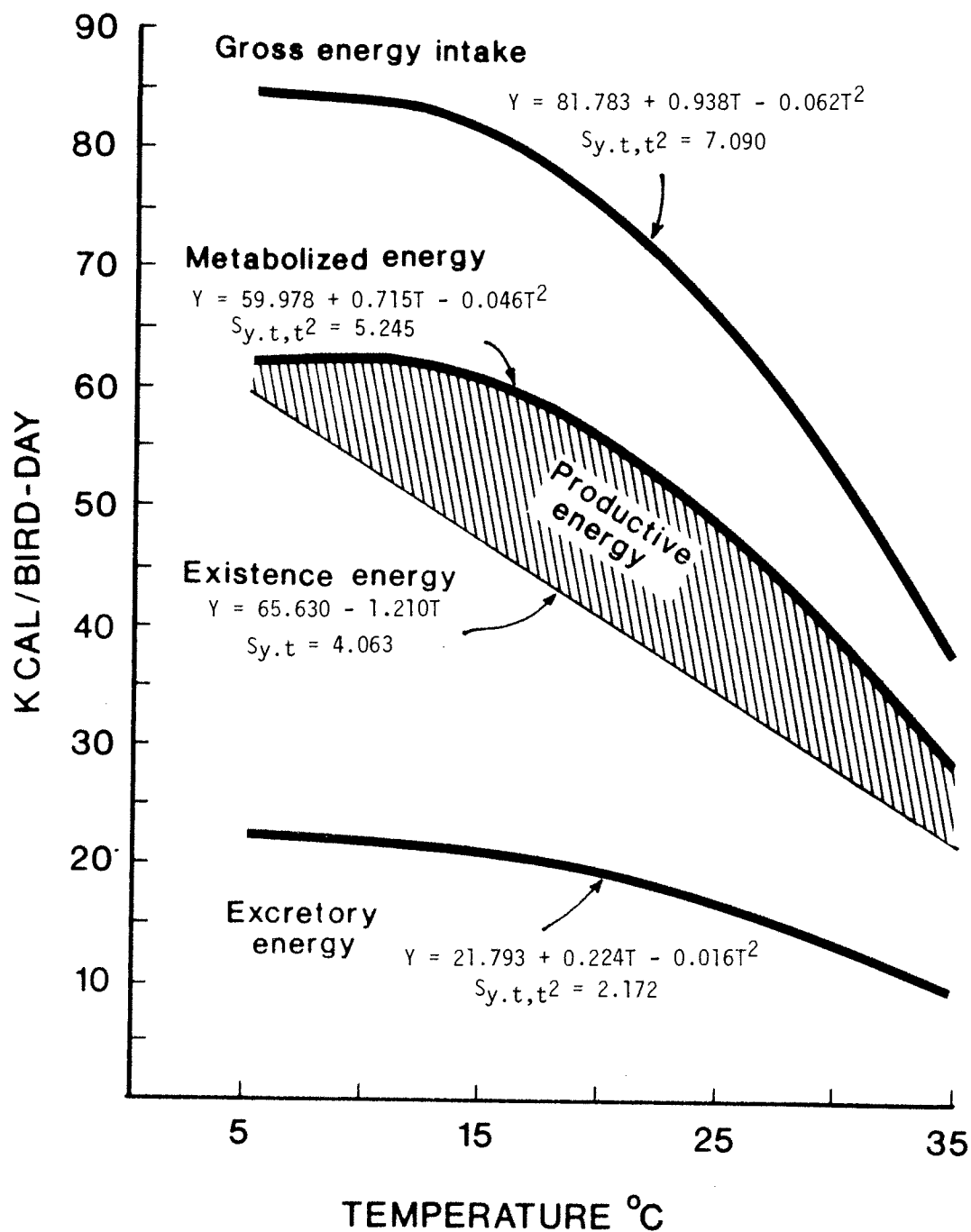


Figure 1. Gross energy intake, metabolized energy, productive energy, existence energy, and excretory energy as a function of ambient temperature for egg-laying bobwhites under a 15-hour photoperiod.