ENERGY REQUIREMENTS FOR EGG-LAYING AND INCUBATION IN THE ZEBRA FINCH, *TAENIOPYGIA CASTANOTIS*

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The energy required for nesting activities, particularly egg-laying and incubation, has seldom been determined quantitatively for wild birds. Riddle *et al.* (1934) studied food consumption and weight variation of common pigeons at the various stages of the reproduction cycle. Kendeigh (1941) indicated that the initial development of the gonads does not demand great energy expenditure and that the principal energy drain comes in the female with the formation of the eggs. Kendeigh *et al.* (1956) developed the hypothesis that the size and number of eggs are influenced by the energy resources of the bird during the three days immediately preceding laying.

Kendeigh (1963) has also shown that incubation requires an expenditure of energy in the form of heat in excess of that normally lost in the birds' metabolism. An equation was derived for calculating the amount of heat applied to the eggs during incubation. The equation includes several empirical constants, values for which are given for the House Wren, *Troglodytes aedon*, but the equation may be applied to any other species if the constants for that particular species are determined.

In the above studies, estimations of the energy requirements for egg-laying and incubation were based on indirect measurements. In the present work, the energy cost of egg-laying and incubation has been measured by a direct experimental procedure using the Zebra (or Chestnut-eared) Finch, *Taeniopygia castanotis* ($=$ *Poephila guttata*).

A knowledge of this energy cost is important. If a species is unable to mobilize sufficient energy in any region to carry on reproduction, then the species will be excluded from that region, except as a transient. Likewise, the timing of reproduction will be regulated to conform with the time of the year when energy is sufficient.

For these experiments, advantage was taken of the egg-laying productivity and the readiness of the Zebra Finch to incubate in captivity. Some of the birds used in the experiments had been kept previously for about two months in a cage 124 cm wide, 185 cm high, and 306 cm long. Several extra pairs were bought from dealers in Topeka, Kansas, and in Chicago, Illinois. All the birds were put together in the large cage for at least three weeks before they were placed in the experimental cages.

The Zebra Finch is distributed throughout Australia. The species inhabits dry areas but not deserts (Marshall, 1959), where there is shrubby vegetation for cover and nesting. It is well known (Frith and Tilt, 1959) that Zebra Finches breed after a period of rainfall. Robinson (1956) also claims that in northwestern Australia there are breeding peaks in both spring and autumn. In southwestern Australia the failure of winter rains and the low temperatures prevent winter reproduction not only in Zebra Finches but also in most other birds (Serventy and Marshall, 1957). The wet season (White, 1924) coincides with the period of highest temperatures and longest days. This is the summer period which starts in October and ends in March. June, July, and August, when the Zebra Finch stops breeding, are the coldest months (Frith and Tilt, 1959).

PROCEDURE

Experimental cages. Fourteen pairs of Zebra Finches were placed in experimental, bottomless metal cages measuring 32.5 cm wide, 37.5 cm high (the lower 27.5 cm

of metal, the upper 10 cm of wire mesh), and 46 cm long. The cages rested on metal trays. Each cage was provided with a nest box, 15 × 15 × 15 cm, made of wire mesh. The nest box was placed on the outside at the back of the cage; the birds could enter the nest box by passing through an opening in the side wall. Food and water were accessible from two containers placed outside on the front of the cage. Two wooden perches were provided in each cage.

The nest material provided during the nesting stage consisted of excelsior (fine-shredded wood) and down feathers, mostly from chickens. However, in these experiments, the nest built by the bird was replaced by artificial ones at intervals during the incubation period. Zebra Finches, unlike most birds, defecate in the nest, and the feces had to be collected for caloric measurement. A new nest was inserted each time an old one was removed. The birds would accept the new nest but only after some reconstruction of it.

Food. Zebra Finches are basically seed-eaters. However, because of the difficulty in separating the feces from unused seed, the birds were given a commercially mixed chicken feed which was ground fine enough to pass through a 0.06-cm mesh screen. The feed was a complete ration for laying chickens. It consisted of crude protein 16%; crude fat 3.5%; crude fiber 4.5%; calcium 2.8%; phosphorus 0.6%; iodine 0.00008%; and salt 0.3% with supplements of vitamin A and B_{12}. The caloric value of the food ranged from 4.035 to 4.120 kcal/g dry weight.

Metabolism measurements. The amount of food metabolized by each pair of birds was measured before, during, and after egg-laying and incubation. One hundred grams of ground food were placed in the food containers at the beginning of each four- or five-day period. The same amount of food was placed in the oven for three days to measure the dry weight of the food supplied. At the end of each period the feces and unused food were separated and placed in the oven to measure their dry weights. Caloric determinations were then made of representative samples, using a Parr adiabatic oxygen bomb calorimeter. The metabolized energy of the birds for the period was calculated by subtracting the caloric value of the excreta from the caloric value of the food consumed.

The males and females were first tested separately in order to detect possible differences in their energy metabolism. They were then placed together to measure their metabolized energy when not nesting; this served as the control. In both instances, they were tested for a sufficient number of periods, usually three or four, until it was evident that they were maintaining a constant weight. Under these conditions the energy they metabolize is what they require for existence. Nesting material was then provided; this usually induced the birds immediately to start building the nest. The energy spent for nest-building and egg-laying, which progressed simultaneously, was calculated from the difference between the metabolized energy during the control stage and this stage. The energy required for incubation was calculated from the difference in metabolized energy between this stage and the control. Egg production causes rapid changes in body weight for which no allowances could be made; but during incubation, metabolized energy was averaged only for those periods when the birds maintained a constant weight. This was necessary in order to avoid making arbitrary corrections for the energy being stored in the bird when there was a gain in weight or for the additional energy becoming available when there was a loss in weight.

Temperature measurements. Separate experiments were run at several controlled air temperatures, which were recorded at 24-minute intervals with copper-constantan

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TABLE 1
DATA ON EGGS AND INCUBATION

Tem-pera-ture	Mean wt of eggs		Mean size of clutch		Extent of laying		Extent of incubation		Success of hatching		Incubation period	
	N	g ± SD	N	Eggs	No. of pairs	Per cent	No.	Per cent	No. of eggs	Per cent	No. of eggs	Mean days
14.5° C	16	0.98 ± 0.12	4	4.0	4	100	4	100	16	0	9	Failed to hatch
20.9	18	1.01 ± 0.12	5	3.8	8	62	5	100	19	42	8	15.1
24.4	36	0.97 ± 0.08	8	4.0	12	67	8	62	20	45	9	15.3
29.1	31	0.96 ± 0.09	5	3.6	6	83	5	80	14	86	12	14.6
34.4	9	0.86 ± 0.04	3	4.0	4	75	3	100	12	67	9	13.1

thermocouples and a recording potentiometer. Mean values (± SD) were: 38.7° ± 0.5°, 34.4° ± 0.9°, 29.1° ± 1.6°, 24.4° ± 1.5°, 20.9° ± 1.3°, 14.5° ± 0.9°, 12.3° ± 0.3°, 6.9° ± 0.4°, 3.3° ± 0.6°, and −1.3° ± 0.1° C. All experiments were run under a 12-hour photoperiod (12L : 12D).

Egg and nest temperatures during incubation were measured using the procedure of Baldwin and Kendeigh (1932). A small hole was bored in the middle of the egg, and a thermocouple was inserted through the hole which was then sealed with collodion. The egg was placed in the nest so that the thermocouple passed through the nest material and out of the bottom of the nest to an indicator potentiometer. The nest temperature was measured by stretching the thermocouple through the nest cavity so that the sensitive junction lay just above the nest lining and under the eggs. The thermocouple wires were then passed through the bottom of the nest to the potentiometer.

RESULTS

REPRODUCTIVE BEHAVIOR OF THE ZEBRA FINCHES

Egg-laying and clutch size. The experiments started with six pairs at an air temperature of 29.1° C and eight pairs at 20.9° C. Four pairs in each experiment completed the reproductive cycle, that is, they laid eggs, incubated, and the eggs

TABLE 2
MEAN (± SD) BODY WEIGHT (G) AT VARIOUS STAGES OF THE NESTING CYCLE

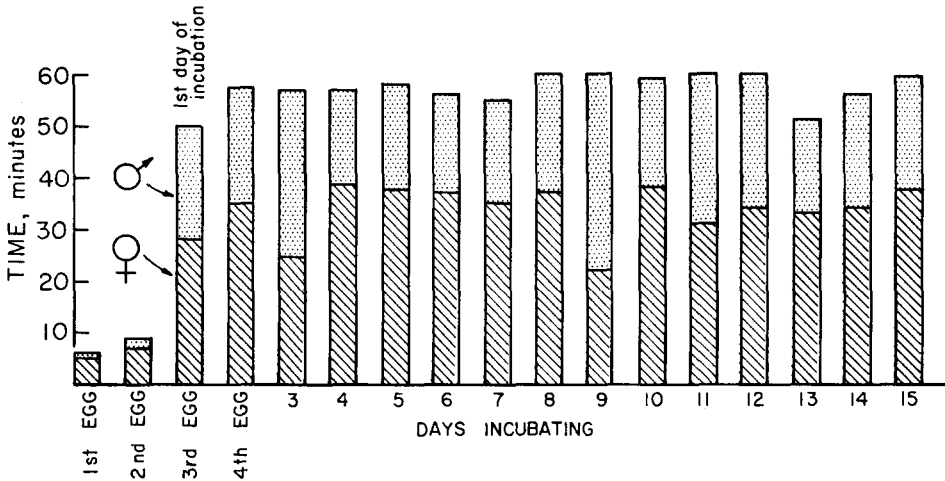| Temperature	Sex	No. of birds	Before nesting	During nest-building and egg-laying	During incubation
14.5° C	M	4	12.7 ± 0.59	12.5 ± 0.71	12.9 ± 0.71
	F	4	12.6 ± 0.77	13.3 ± 0.64	12.8 ± 0.65
20.9	M	5	12.0 ± 0.68	12.0 ± 0.33	12.2 ± 0.29
	F	5	12.2 ± 1.18	12.6 ± 1.24	12.3 ± 1.18
24.4	M	5	12.2 ± 0.88	12.1 ± 0.92	12.1 ± 0.86
	F	5	12.0 ± 0.52	12.2 ± 1.27	12.0 ± 0.94
29.1	M	4	12.4 ± 1.42	11.9 ± 0.99	11.9 ± 1.05
	F	4	10.7 ± 0.96	10.9 ± 0.88	11.3 ± 0.87
34.4	M	3	11.7 ± 1.17	12.2 ± 1.06	12.1 ± 1.06
	F	3	12.1 ± 0.74	13.4 ± 1.04	12.5 ± 0.72

Figure 1. The attentive time of male and female Zebra Finches on the eggs, in minutes per hour.

hatched. After the completion of these two experiments, two pairs died. The remaining 12 pairs were put together in an experiment at 24.4° C, but only five pairs completed the nesting cycle. Four pairs were then placed at 34.4° C, with three pairs completing the cycle, and four pairs also at 14.5° C.

The mean (± SD) length and breadth of Zebra Finch eggs are 15.8 ± 0.8 and 11.9 ± 0.5 mm, respectively. The percentage moisture in the egg and the caloric values of eggs and embryos (kcal/g dry wt) are 75.4 ± 1.7, 5.0 ± 0.08, and 4.1 (one measurement only), respectively. The mean weight of eggs tends to increase from high to low temperature (table 1), although the change is not statistically significant ($P > 0.05$).

Incubation. Both sexes participate in incubation. In this study the incubation period was generally 15 days but became reduced to about 13 days (12 to 14) at 34.4° C. Both males and females develop brood patches and apply an equal amount of heat to the eggs. Egg temperatures were measured at five different nests, one at 29.1° C, one at 20.9° C, and three at 24.4° C. The means (± SD) of 132 egg temperatures and of 111 nest temperatures during the female attentive period were 35.4° ± 1.39° C and 32.6° ± 1.42° C, respectively. The means of 82 egg temperatures and of 59 nest temperatures during the male attentiveness were 35.1° ± 1.36° C and 32.4° ± 1.28° C, respectively.

The mean duration of the attentive periods of females and males was calculated on the basis of daily one-hour observations from a blind at each of four nests (fig. 1). It appears that incubation begins after the laying of the third egg, even when four eggs are laid. The average time that the females spent sitting on eggs was 33.4 ± 5.1 minutes per hour, or 56 per cent of the time. The average time that the males spent sitting on the eggs was 24.2 ± 5.9 minutes per hour, or 40 per cent of the time. The difference in attentiveness is significant ($P < 0.05$).

Weight changes. The body weights of individual Zebra Finches lie between 9.55 and 14.29 g. There was no difference in the average weights of the two sexes except at 29.1° C, where the males were significantly heavier (table 2). During nest-
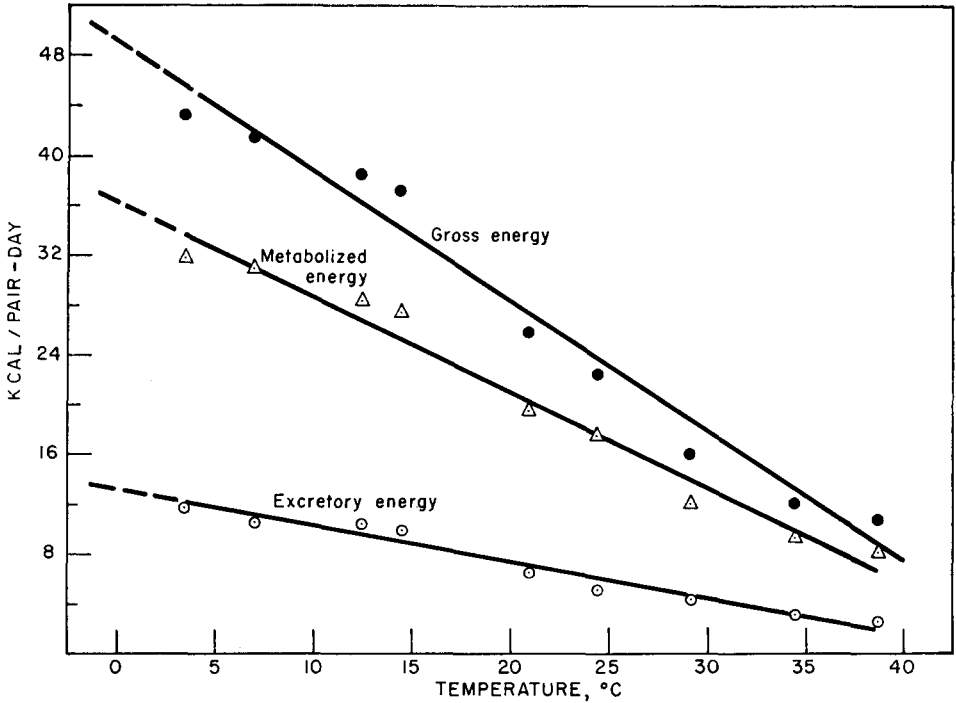
Figure 2. Energy partition of Zebra Finches in relation to air temperature. Measurements were made on the sexes separately, but the data are combined for expression as kcal/pair-day. Regression lines were fitted by the method of least squares.

building and egg-laying the slight increase in the body weight of all the females is probably due to the growth of the oviduct and eggs. Riddle *et al.* (1934) found that the body weight of adult doves and pigeons increased also during incubation, but in the present investigations there was no consistent tendency to do so.

ENERGY INTAKE

Gross energy intake. There is general agreement that food intake in homeotherms is an inverse linear function of air temperature. It has been confirmed by the present work (fig. 2). The gross energy intake of males and females in separate cages was not significantly different, nor was their energy intake when separated different from what it was when together as pairs during the control runs (table 3).

Riddle *et al.* (1934) have shown that the increase in weight of pigeons during incubation is very frequently accompanied by less food consumption than in the resting stage. This was attributed to the fact that the pigeon wastes less energy because it is relatively inactive. In Zebra Finches the gross energy intake during nest-building and egg-laying and during incubation was significantly higher ($P <$ 0.05) than during the control. Gross energy intake during nest-building and egg-laying was not significantly different from that during incubation (table 3).

Excretory energy. The calories lost in the excreta, that is, undigested food and digested but unabsorbed food and wastes from the kidneys, did not differ between sexes and increased linearly with decreasing temperature (table 3, fig. 2).

Category	Sexes separated	Sexes together in pairs		
		Control	Nest-building and egg-laying	Incubating
Gross energy, kcal/pair-day =	$49.03 - 1.05\,X$	$47.89 - 1.07\,X$	$48.51 - 1.04\,X$	$49.71 - 1.10\,X$
Excretory energy, kcal/pair-day =	$12.96 - 0.29\,X$	$12.07 - 0.28\,X$	$10.36 - 0.22\,X$	$10.23 - 0.22\,X$
Metabolized energy, kcal/pair-day =	$36.07 - 0.76\,X$	$34.88 - 0.76\,X$	$38.49 - 0.83\,X$	$42.41 - 0.98\,X$

Kendeigh (1949), Seibert (1949), and Zimmerman (1965) working with song birds and Williams (1964) working with the Canada Goose noted that the energy value of excrement per unit weight varied with air temperature. Davis (1955), West (1960), and Cox (1961), however, found no significant variation of calories per gram excrement with temperature. In the present investigation no significant variation of calories per gram excreta in relation to temperature was detected. Likewise, the caloric value of the excreta was not appreciably different between males and females. The average value of the excreta at all temperatures was 3.063 ± 0.010 kcal/g. There was no significant difference between the energy loss in the excreta of bird pairs during the control stage and the combined losses of males and females when separated.

In spite of the greater amount of food intake during nest-building and egg-laying and during incubation, compared with that during the control stage, the total calories lost in the excreta were not significantly different than those during the control stage (except at 14.5° C where the eggs failed to hatch). Likewise, there was no significant difference between the caloric value per gram excreta during incubation and that during nest-building and egg-laying.

Efficiency of food utilization. Kendeigh (1949), Seibert (1949), and West (1960) have previously reported increases in the efficiency of food utilization from low to high temperatures. Davis (1955) found a peak of efficiency at 18° C in summer-acclimatized House Sparrows, *Passer domesticus.* Zimmerman (1965), in his investigation of Dickcissels, *Spiza americana,* described one peak at the higher temperatures and another peak associated with the period of reduced excretory energy at lower temperatures. Williams (1964) working with the Canada Goose, *Branta canadensis,* found that efficiency tended to be increased toward both low and high temperatures.

In Zebra Finches the food-utilization efficiency is maximum at 24.4° C for all stages of the cycle (table 4). The efficiency was significantly higher during nest-building and egg-laying and during incubation at all temperatures (except 34.4° C for incubation) than during the control stage or for the males and females when separated.

Metabolized energy. Metabolized energy of separated males and females did not differ significantly at any temperature. Likewise the sums of the metabolized energy of the two sexes measured separately did not differ significantly from that of males and females together in the control stage. Metabolized energy during nest-building
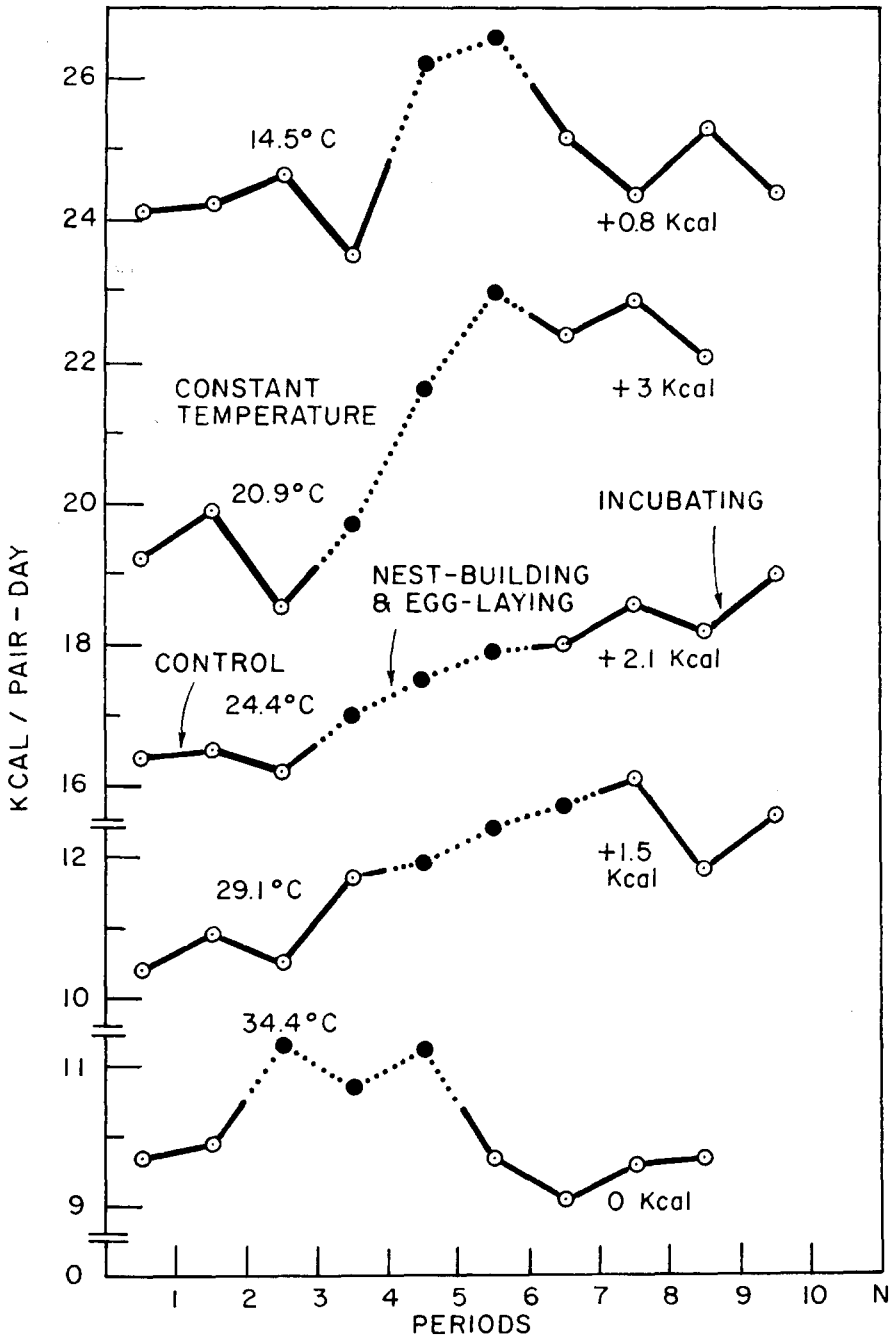
Figure 3. Metabolized energy in relation to air temperature in various stages of the nesting cycle. The experimental periods were usually three or four days in length.

TABLE 4

COEFFICIENTS OF UTILIZATION[a]

| | Males and females alone | | | Nest-building and | |
Temperature	M	F	Control	egg-laying	Incubation
3.3° C	73.7	73.2	–	–	–
6.9	75.0	74.4	–	–	–
12.3	73.1	73.0	73.0	–	–
14.5	73.8	73.5	73.6	78.8	75.4
20.9	75.8	75.2	74.4	77.6	78.4
24.4	77.3	78.8	77.8	81.2	81.1
29.1	73.8	76.0	75.9	76.9	78.1
34.4	76.3	76.7	77.8	77.8	76.0
38.7	74.1	77.4	–	–	–

[a] (Metabolized energy/gross energy) $\times$ 100.

and egg-laying was significantly higher ($P < 0.05$) than during the control at each experimental temperature (fig. 3). Metabolized energy during incubation was significantly higher than the control only at the three intermediate temperatures (29.1°, 24.4°, 20.9° C). The difference between the metabolized energy during nest-building and egg-laying and that during incubation was not significant at the same intermediate temperatures. At 14.5° C, where the eggs failed to hatch, the rate of metabolized energy during incubation was nearly the same as the control. At 34.4° C the ambient temperature nearly equalled the incubation temperature. Metabolized energy increased linearly with decreasing temperature at all stages of the nesting cycle (table 3, figs. 2, 4).

The goodness-of-fit, using chi-square test, shows that the data for metabolized energy in relation to air temperature fit a cubic regression a little better than a linear regression. The cubic regression line suggests a possible zone of thermal neutrality between 29° and 38° C. However, this zone is not well defined, and there was no statistically significant difference between the cubic and linear regressions. Until more evidence accumulates, we prefer to consider the data as following the linear regression.

Lethal temperatures. Five out of eight birds died at a mean air temperature of −1.3 ± 0.1° C, although they tolerated +3.3° C (fig. 2). A temperature of −1.3° or slightly above, therefore, constitutes the lower limit of temperature tolerance. During an attempt to determine the upper limit of tolerance, eight birds tolerated 42° C, but when the temperature was accidentally raised to 45° C, six birds died. When the temperature was lowered to 43°, one of the remaining two birds died after one day and the other after three days. The upper limit of tolerance must then be between 42° and 43° C.

DISCUSSION

Energy requirement for egg-laying. The minimum energy required to sustain the essential body processes without gain or loss in weight is called *existence energy* (Kendeigh 1949). Any energy assimilated in addition to what is required for existence may be used for growth, storage, or various activities and is referred to as *productive energy*. It has been recognized for a long time that a fixed amount of feed is required per day for the maintenance of a laying chicken, no matter what its rate of egg production may be (Titus, 1939).
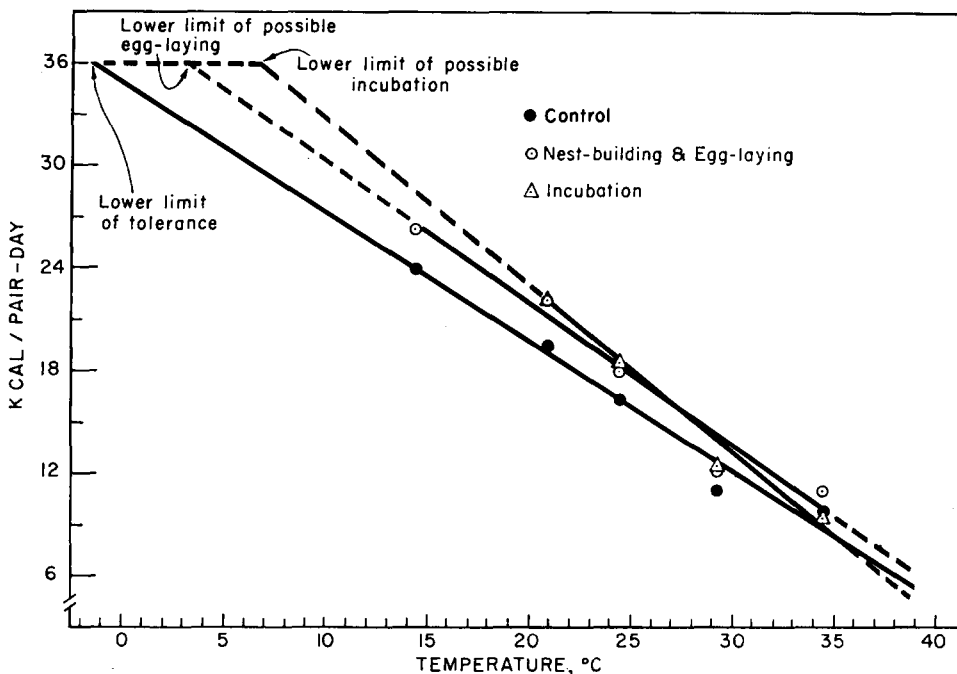
Figure 4. Metabolized energy in relation to air temperature in various stages of the nesting cycle. Measurements were made on pairs together in the same cage. The regression lines were fitted by the method of least squares.

In the Zebra Finch productive energy that is used for nest-building and egg-laying has been calculated as the difference between the energy metabolized during this stage and that metabolized during the control when the birds were maintaining an existence level. The amount of this energy used is greater at the lower temperatures (figs. 3, 4).

Waite (1929) and Brody (1945) found for the domestic fowl that 54 and 77 per cent, respectively, of the energy consumed above maintenance and corrected for live weight changes was recovered in the eggs. Kendeigh et al. (1956) calculated that the energy incorporated in the eggs of the House Wren was 1.572 kcal per egg, and assumed that the total energy of a six-egg clutch was deposited over a nine-day period or at a daily rate of 1.048 kcal. To determine how the percentage of the productive energy incorporated into the eggs of the Zebra Finch would vary at different temperatures, we may assume an efficiency of egg production of 77 per cent at high temperatures, especially at 34.4° and 29.1° C, where the birds spend a minimum of energy on other activities (table 5). The mean calculated energy converted into eggs at these two temperatures would be: $[(1.3 + 1.4)/2]0.77 = 1.040$ kcal per day. The energy incorporated into the eggs subtracted from the total productive energy gives the energy cost of producing eggs, nest-building, and the heat applied to the eggs during the laying period (0.310 kcal/pair-day). This increases at low temperature, probably because more heat is lost from the body during nesting activities and more heat is applied to the eggs during the laying period. The efficiency of egg production therefore also decreases at low temperatures. Because of the assumption made above,

TABLE 5
ENERGY (KCAL/PAIR-DAY) USED FOR EGG PRODUCTION

Air temper-ature	Grams of eggs produced per clutch	Existence energy during control (a)	Metabolized energy during nest-building and egg-laying (b)	Total produc-tive energy (b − a = c)	Productive energy incorpor-ated into eggs corrected for weight of eggs (d)	Productive energy used for egg formation, nest-building and heat applied to eggs (c-d)	Efficiency of egg forma-tion (d/c × 100)
14.5° C	3.92	24.0	26.4	2.4	1.186	1.214	49
20.9	3.84	19.5	22.2	2.7	1.144	1.556	42
24.4	3.88	16.4	18.0	1.6	1.165	0.435	73
29.1	3.46 ⎱	11.0	12.3	1.3 ⎱	1.040	0.310	77
34.4	3.44 ⎰	9.8	11.2	1.4 ⎰			

the actual energy and efficiency figures are only approximations, but the manner in which temperature influences the efficiency of egg production should be qualitatively correct.

Energy requirement for incubation. The productive energy used for incubation has been calculated from the difference between the energy metabolized during this stage and that metabolized during the preliminary control period. The Zebra Finch incubated at temperatures ranging from 34.4° through 14.5° C. The eggs hatched at all temperatures within the above range except at 14.5° C, where 12 of the 16 eggs were fertile but had dead embryos of various ages. However, the calculated produc-tive energy used for incubation at this temperature was low (0.8 kcal/pair-day), and failure to hatch may be attributed to insufficient application of heat to the eggs. At 34.4° C there was no productive energy used for incubation (table 6). The amount of energy spent for incubation increased at lower temperatures since the bird must compensate for the greater rate of heat loss from the eggs.

The calculated percentage of productive energy used for incubation seems to be low compared with 28 per cent calculated by West (1960) for the Tree Sparrow, *Spizella arborea*, and 17–51 per cent calculated by Kendeigh (1963) for the House Wren. The reason for this is that both sexes share in the incubating duties in the Zebra Finch but only the female in the Tree Sparrow and House Wren.

In his work with the House Wren, Kendeigh (1963) derived an equation for calculating the amount of heat applied by the bird to the eggs during incubation, when the nest temperature is known and one assumes that the rate of heat applica-tion must equal the rate of heat lost. This equation is modified for the Zebra Finch as follows:

$$kcal = n \cdot w \cdot h \cdot b \cdot (t_e - t_a) \cdot i \cdot (1 - c \cdot a)$$

where

n = number of eggs in the clutch (4),
w = mean weight of the eggs (0.96 g),
h = specific heat of eggs (assumed to be 8×10^{-3} kcal/g-°C),
b = rate of cooling of the eggs (4.04°/°C-hr),
t_e = egg temperature (35.2° C),
t_a = ambient or room temperature,
 i = interval in hours (24, if computations are made on a daily basis),
c = percentage of total surface of eggs covered by attentive bird (assumed to be about 25),
a = percentage of total 24 hours that the adults are attentive (approximately 96).

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TABLE 6

ENERGY USED FOR INCUBATION

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		Indirect procedure (cooling rate method)			Direct procedure (food intake method)		
Mean air temperature, t_a	Mean No. of eggs per clutch	Mean weight of eggs, g	Difference between mean egg temperature and t_a $(35.2 - t_a)$	Calculated energy for incubation kcal/pair-day	Calculated energy for incubation kcal/pair-day	Productive energy available kcal/pair-day	Per cent used for incubation
14.5° C	4.0	0.98	20.7	4.78	0.8	12.0	39.9[a]
20.9	3.8	1.01	14.3	3.24	3.0	16.5	18.2
24.4	4.0	0.97	10.8	2.47	2.1	19.6	10.7
29.1	3.6	0.96	6.1	1.24	1.5	25.0	6.0
34.4	4.0	0.86	0.8	0.16	0	26.2	0

[a] Calculated from amount needed (4.78) but not actually used.

The cooling rate of eggs of the Zebra Finch was not directly determined but may be calculated. The cooling rate of the House Wren's eggs, weighing 1.40 g, is 5.2°/ °C-hr. The mean weight of the Zebra Finch's egg is 0.96 g, and the cooling rates are probably proportional to the surface areas. Using Meeh's formula $(S = 10W^{2/3})$, where S is the surface area in square centimeters and W is the weight in grams, the ratio of the surface area of House Wren's egg to that of the Zebra Finch is 1.251/ 0.973. The calculated cooling rate of Zebra Finch's eggs would then be 4.04°/°C-hr.

It was not necessary to measure the nest temperature throughout incubation, as was done by Kendeigh with the House Wren, since the Zebra Finch, with both adults alternating at incubation duties, maintains relatively constant nest and egg temperatures. Furthermore, the nest structure was open and loose, not enclosed in a wooden box as with the House Wren, so that the eggs were almost directly exposed to room temperature. The rate of cooling would be more directly affected by ambient temperatures, and the equation was solved by using ambient rather than nest temperature. Results obtained by this indirect calculation agreed well with the direct measurements at moderate temperatures although they averaged somewhat higher (table 6).

One would expect the indirect procedure to give higher values than the direct procedure, since the latter measures only the heat derived from productive energy that is applied to the eggs. The eggs also receive some of the normal heat loss from existence energy, and this is included in the indirect procedure. However, this normal heat loss is only a small fraction of the total amount of heat that is required (Kendeigh, 1963). It appears obvious that the eggs did not hatch at 14.5° C because the actual amount of heat applied (0.8 kcal/pair-day) was substantially less than that estimated as necessary for normal embryonic growth (4.78 kcal/pair-day).

The lower limits of temperature at which egg-laying and incubation occur. Zebra Finches laid eggs and incubated at all temperatures between 34.4° and 14.5° C, although at 14.5° C incubation was not normal and did not result in hatching of eggs. The lower limits of air temperature at which they should just be able to lay eggs and incubate, as calculated from the regression line in figure 4, are 3.2° C and 6.8° C, respectively. Actually one female out of four laid two eggs at 3.3° C. The

calculated limit for egg-laying was almost identical with the observed value and indicated that the maximum potential of the species for metabolizing energy under stress of extreme cold is also reached at higher temperatures under stress of egg-laying. It is not clear, however, why incubation became unsuccessful at 14.5° C, well above the theoretical limit of 7° C. This will require further study. At 14.5° C, theoretically only 39.9 per cent of the potentially available productive energy would be needed for incubation. Apparently this could not be spared.

SUMMARY AND CONCLUSIONS

Zebra Finches in captivity are able to produce clutches of eggs throughout the year. The clutch size in these experiments was 3 or 4 eggs. The eggs measured 15.80 × 11.90 mm. The average egg's weight was 0.96 g. Both sexes incubated and had a brood patch. Egg temperatures while being incubated averaged 35.2° C. The incubation period was generally about 15 days, but was reduced to 13 days at high ambient temperatures.

The body weight of the Zebra Finches ranged between 9.55 and 14.29 g. There was no significant difference between the sexes in body weight except at 29.1° C, where the males weighed more than the females. During nest-building and egg-laying there was a slight increase in the body weight of all the females.

Efficiency of food utilization was maximum at 24.4° C for all stages of the cycle and was higher during nest-building, egg-laying, and incubation than during the control period.

Metabolized energy was an inverse linear function of air temperature at all stages of the nesting cycle. Metabolized energy of separated males and females did not differ significantly at any temperature. Metabolized energy during nest-building and egg-laying was significantly higher than during the control period at each experimental temperature. Metabolized energy during incubation was significantly higher than during the control period except at 14.5° and 34.4° C.

The lower and upper limits of temperature tolerance for existence were −1.3° and 43° C, respectively.

Zebra Finches laid eggs and incubated at all air temperatures from 34.4° to 14.5° C but not successfully at the latter temperature. Some egg-laying occurred at 3.3° C.

The efficiency of egg-production decreased at low air temperatures.

The energy cost of incubation increased with decrease of air temperature. Direct and indirect methods of estimating the energy cost of incubation gave similar results.

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