

ENERGETIC COST OF INCUBATION IN THE ZEBRA FINCH

CAROL M. VLECK

ABSTRACT.—At temperatures below 28°C, rate of oxygen consumption (\dot{V}_{O_2}) of Zebra Finches (*Poephila guttata*) incubating eggs averaged 20% higher than the \dot{V}_{O_2} of non-incubating Zebra Finches sitting in a nest at the same temperature. This increase represents the energetic cost of incubation. The \dot{V}_{O_2} of non-incubating birds sitting in a nest was lower than values reported for birds perched in the open at the same temperature. In the Zebra Finch, the ameliorating effects of the nest microclimate approximately compensate for the increment in metabolic rate due to incubation. The energetic cost of incubation increased when birds had to rewarm cold eggs. Incubating birds responded to artificially cooled eggs by elevating their metabolic rate and increasing heat flow to the clutch. The pattern of adult attentiveness at the nest determines the number of times and amount by which the eggs must be rewarmed. Because it is energetically more expensive to rewarm eggs than to maintain temperature once the eggs are warm, the cost of incubation depends in part on the attentiveness pattern.

Reproduction, especially the care of eggs and young, places special demands on the way birds allocate available energy. Various techniques have been used to estimate the energetic costs associated with territorial defense (Stiles 1971, Wolf and Hainsworth 1971), nest building (Collias and Collias 1967, Withers 1977a), egg production (King 1973), and the feeding of nestlings (Utter and Lefebvre 1973). These activities, together with incubation of the eggs, include most of the time and energy that birds devote to reproductive activities. However, the costs of incubation, an activity that takes up a significant portion of the reproductive cycle, are difficult to measure and have been the subject of controversy (Kendeigh 1973, King 1973).

Linear heat flow models have been used to make indirect estimates of the energetic cost of incubation based on the assumption that heat loss from eggs must be balanced by extra heat production by the parent (Kendeigh 1963, Ricklefs 1974). For example, Drent (1970) found that Kendeigh's (1963) model accurately described the heat input required to keep the eggs of Herring Gulls (*Larus argentatus*) warm. However, not all of this input necessarily represents an additional cost to an incubating adult. King (1973) pointed out that heat produced as a by-product of metabolism could substitute for at least part of the heat needed to maintain egg temperature. This would be particularly effective if heat were preferentially shunted to the eggs, e.g., through an incubation patch, while heat loss from other re-

gions was minimized. Kendeigh's (1963) model was used by Siegfried and Frost (1975) and Ricklefs (1974), while King's view was accepted by White and Kinney (1974) and Walsberg (1977).

Measurements of oxygen consumption during incubation in the wild have been made for the Great Tit (*Parus major*; Mertens 1977) and Baird's Sandpiper, (*Calidris bairdii*; Norton 1973). However, neither author compared the oxygen consumption of incubating and non-incubating birds, and consequently it is impossible to estimate the energy expended solely for incubation. In contrast, Biebach (1977, 1979) measured the oxygen consumption of both incubating and non-incubating Starlings (*Sturnus vulgaris*) and calculated the energetic cost of incubation at several nest temperatures. Gessaman and Findell (1979) measured CO₂ production of three incubating and non-incubating American Kestrels (*Falco sparverius*) but their results are ambiguous. Mertens (1980) measured heat loss from the nest of a Great Tit, using heat flux disks mounted in the nestbox walls, and found that heat loss from the bird and nest increased considerably during incubation.

The energetic cost of warming cooled eggs "to the incubation temperature" has not been determined. Kendeigh et al. (1977) suggested that energy expended to rewarm eggs could be calculated from estimates of the heat needed to rewarm eggs, but this procedure ignores the inefficiency of heat transfer from the parent to the eggs. If a bird increases its heat production in order to re-

warm eggs, its heat loss by other avenues will also increase. Consequently, the energy expended to rewarm the clutch is probably greater than the increase in heat content of the eggs.

The Zebra Finch (*Poephila guttata*) is an excellent subject for studies of incubation because it will nest readily in the laboratory. In an earlier study, El-Wailly (1966) estimated the energetic costs of incubation by measuring the food consumption of incubating pairs of Zebra Finches. His measurements were necessarily integrated over several days and were not sensitive to changes in the birds' behavior. I have determined the energetic cost of incubation in the Zebra Finch directly by measuring the rate of oxygen consumption of individuals during incubation at several nest temperatures. In addition, I have estimated how much it costs the bird to warm its eggs by measuring the oxygen consumption of birds incubating artificially cooled eggs.

METHODS AND MATERIALS

BIRDS

Pairs of Zebra Finches from a captive breeding colony were kept in small cages and provided with seed, water, grit, green vegetation, and nesting material (dry grass, burlap string, coconut fibre, and cotton). The cages were placed in a walk-in constant temperature cabinet where lights were on 14 h of the day and temperatures could be regulated within $\pm 0.2^\circ\text{C}$ from about 8° to 35° . The nest container was a metal can (diameter, 10 cm; length, 13.5 cm) with a plastic, snap-on lid containing a circular entrance hole, 3 cm in diameter (Fig. 1). The long axis of the can was horizontal. Each pair of birds built a loosely woven domed nest filling the container except for a small cavity near the rear of the container and a tunnel from the nest cavity to the entrance hole. Three to five eggs were laid in the cavity. Wild Zebra Finches in Australia build very similar nests that are usually situated on the terminal twigs of bushes or trees, but may be on the ground, in tree hollows, fence posts, or even in rabbit burrows (Immelmann 1965).

I monitored temperature in one of the bird's own eggs by inserting a thermocouple, made from 40-gauge copper and constantan wire, into the center of the egg and gluing it in place with epoxy. This will be referred to as the "thermocouple egg." Nest air temperature was measured with a 24-gauge thermocouple situated in the entrance tunnel leading to the nest cavity. In some nests, temperature beneath the eggs was measured with a 40-gauge thermocouple placed just below the eggs. Air temperature outside the nest box was also monitored. All temperatures were recorded on a Honeywell multichannel potentiometric recorder.

Zebra Finches of both sexes share almost equally in incubation. The sex of the incubating bird was determined either by observing the nest through a window of the chamber, or by removing one member of the pair from the cage. I weighed the birds after 2 h without food, both before they nested and after the incubation period, and assumed that each bird's mass during incubation was the mean of these values.

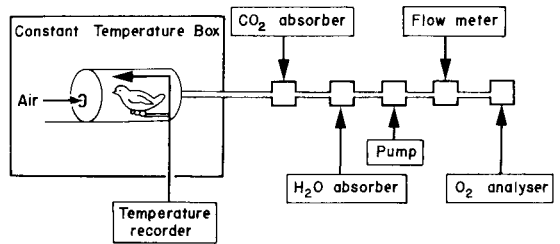


FIGURE 1. Experimental system used to measure oxygen consumption and egg temperature during normal incubation in the Zebra Finch. Nest and egg temperatures were measured with thermocouples.

OXYGEN CONSUMPTION

Oxygen consumption of incubating birds was measured in an open-flow system using the nest container as a metabolic chamber (Fig. 1). Air was pulled into the nest through the entrance hole, past the bird, and out of the rear of the nest container with a peristaltic pump. Carbon dioxide and water vapor were removed with Ascarite and Drierite, respectively. Flow rates were measured with a Brooks rotameter calibrated against a Brooks thermal mass flow meter. Flow rates used were between 550 and $770\text{ cm}^3/\text{min}$ (STP).

The fractional concentration of oxygen in the samples of air was measured with a Beckman G-2 paramagnetic oxygen analyzer and recorded continuously. Rate of oxygen consumption (\dot{V}_{O_2}) was calculated using Eq. 4a of Withers (1977b). The lowest rate of oxygen consumption maintained for at least 3 min in any 20-min interval was assumed to be the incubating \dot{V}_{O_2} at that temperature. The \dot{V}_{O_2} of non-incubating, non-reproducing birds was measured in the same way. For these measurements, birds were placed in a nest in a container like that used in the incubation experiments.

In this system, in which the metabolic chamber is open to the atmosphere, errors are possible due to (1) the diffusion of oxygen down its partial pressure gradient into the chamber, and (2) the leakage of expired air out of the chamber. Both of these would lead to underestimates of \dot{V}_{O_2} . Therefore, to test the accuracy of the method, I also measured the oxygen consumption of non-incubating Zebra Finches in another type of open-flow system where rate of flow into the chamber was measured. Birds were placed in a nest in a sealed plexiglass chamber and supplied with air at flow rates of about $500\text{ cm}^3/\text{min}$ (STP). \dot{V}_{O_2} was calculated using Eq. 2 of Hill (1972). The \dot{V}_{O_2} measurements of non-incubating birds in the two types of open-flow systems did not differ ($P > 0.6$). This indicates that the two previously mentioned problems were not significant in the system that I used with incubating birds. Consequently, I combined the measurements obtained with both systems. All measurements of oxygen consumption were made between 08:00 and 20:00 when the lights were on.

The oxygen consumption of the eggs did not contribute significantly to the measured oxygen consumption. At most there were two developing eggs in the nests. The oxygen consumption of embryonic Zebra Finches rises exponentially during incubation, but even just prior to pipping it is only about $0.85\text{ cm}^3/\text{h}\cdot\text{egg}$ (Vleck et al. 1979). It is less than half this rate during 80% of the incubation period. Because the total oxygen consumption of adults was between 35 and $100\text{ cm}^3/\text{h}$, embryonic \dot{V}_{O_2} was never more than 5% of the total and was usually much less.

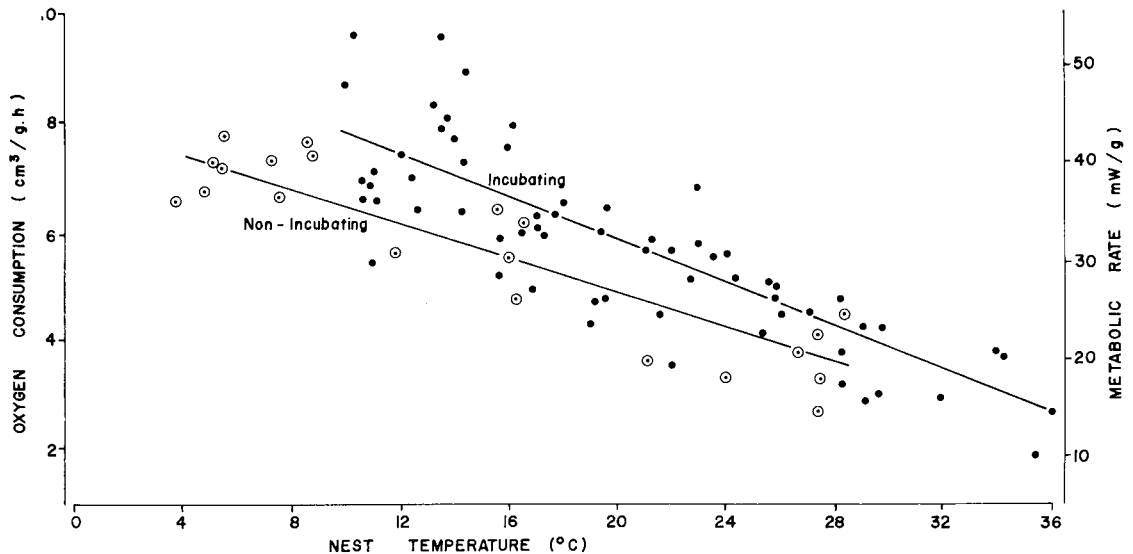


FIGURE 2. Relationships between mass-specific energy metabolism and nest temperature in Zebra Finches incubating eggs (closed circles) or resting in a nest, but not incubating (open circles). Regression equations for the two lines are given in the text (Eq. 3 and 4).

EGG TEMPERATURE AND METABOLISM

In order to determine the effect of egg temperature on the metabolic rate of incubating birds, I artificially changed the temperature of the clutch by putting a hollow glass egg of the same size and color as a Zebra Finch egg into the nest between the natural eggs of the clutch. The glass egg had two ports through which water from a controlled temperature bath was circulated. I measured the temperature of the artificial egg with a 40-gauge thermocouple glued to the upper surface. Rates of water flow through the artificial egg were high enough to change the surface temperature as much as 20°C even when a bird was incubating.

The incubating bird's behavioral responses to changes in egg temperature in the closed nest container were not visible. However, I also put a similar artificial egg into open cup-shaped nests of two other pairs of Zebra Finches and watched their behavior as the temperature of the artificial egg was changed.

To measure the metabolic response of the incubating bird to controlled egg temperatures between 10 and 46°C, I (1) monitored the \dot{V}_{O_2} of an incubating individual for at least 20 min at a given ambient temperature; then (2) turned on the pump of the water bath so that the artificial egg was cooled or warmed; and (3) re-measured the \dot{V}_{O_2} of the bird for another 20 min and then turned the pump off. I then calculated the mean \dot{V}_{O_2} for the 15-min interval before the pump was turned on and the mean \dot{V}_{O_2} during the 15-min interval just before it was turned off.

STATISTICS AND ENERGY EQUIVALENCE

I calculated regression equations by the method of least squares. The coefficient of determination (r^2) is reported as an indication of goodness of fit. All coefficients in the regression equations presented below are significantly different from zero ($P < 0.05$).

In converting from units of oxygen consumption to energy I have assumed an energy equivalent of 20.1 kJ/l O_2 which exists in a bird with a respiratory quotient of 0.8.

RESULTS

NEST ENVIRONMENT AND METABOLIC RATE

The nest of the Zebra Finch provides a sheltered microclimate for incubation. Air temperature in the nest was higher than the temperature in the constant temperature cabinet and can be described by the following equation:

$$T_N = 2.98 + 0.93 T_{\text{chamber}} \quad (1)$$

($n = 55$ measurements on 3 nests, $r^2 = 0.99$)

where " T_N ," the temperature in the tunnel leading to the nest cavity, and chamber temperature are in °C. The temperature measured directly below the eggs was higher than the air temperature in the nest tunnel and can be described by the following equation:

$$T_{\text{beneath egg}} = 16.07 + 0.64 T_N \quad (2)$$

($n = 28$ measurements of 3 nests, $r^2 = 0.78$).

Mass-specific \dot{V}_{O_2} of non-incubating birds at rest increased linearly with decreasing nest temperature between 4 and 28°C (Fig. 2) and is described by the following equation:

$$\dot{V}_{O_2} = 8.16 - 0.17 T_N \quad (3)$$

($n = 21$ measurements on 10 birds, $r^2 = 0.83$)

where \dot{V}_{O_2} is in $\text{cm}^3/\text{g}\cdot\text{h}$.

Mass-specific \dot{V}_{O_2} of incubating Zebra Finches increased when nest temperature

dropped from 36° to 10°C. For birds that were maintaining egg temperature constant:

$$\dot{V}_{O_2} = 9.77 - 0.20 T_N \quad (4)$$

($n = 68$ measurements on 12 birds, $r^2 = 0.69$).

Analysis of covariance (Dunn and Clark 1974) shows that the slopes of Eq. 3 and 4 are not significantly different ($F = 1.33$, $P > 0.25$), but that the Y-intercepts are ($F = 22.4$, $P < 0.01$). The average mass of the birds was 11.6 g (SD = 0.79, $n = 12$). The total \dot{V}_{O_2} of an 11.6 g bird can be calculated by multiplying Eq. 3 and 4 by 11.6:

$$\text{(non-incubating)} \dot{V}_{O_2} = 95 - 1.99 T_N \quad (5)$$

$$\text{(incubating)} \dot{V}_{O_2} = 113 - 2.32 T_N \quad (6)$$

where \dot{V}_{O_2} is in cm^3/h .

EGG TEMPERATURE AND INCUBATION BEHAVIOR

The mean temperature at the center of the egg during normal incubation is about 37°C. When egg temperature was altered by pumping water through the artificial egg in the clutch, the incubating birds' responses were such that in a natural situation, they would tend to return the eggs to the normal temperature. Zebra Finches continued to incubate regardless of the temperature of the eggs. When the surface temperature of the artificial egg was below 30°C, the incubating bird responded by settling on the eggs, sitting deeper in the nest, and turning the eggs with its bill. At temperatures below 20°C, the birds often shivered and erected the feathers on the head, neck, back, and scapular region. At moderate temperatures (30 to 40°C) they responded with only a few settling and turning motions, whereas at temperatures above 40°C they also panted and erected the head feathers.

The incubating bird appeared to sense the temperature of the artificial egg and to adjust its position and contact with the eggs in order to increase heat transfer to cold eggs and possibly conduct heat away from hot eggs. In one case when the artificial egg was cooled, the temperature of another egg that was not in contact with it rose about 3°C as a result of the thermoregulatory response of the incubating bird (Fig. 3). The bird's body temperature was also probably affected by the artificial egg, because shivering or panting occurred when the temperatures of the artificial egg were extreme. Similar behavioral responses to variations in egg temperature have been described in

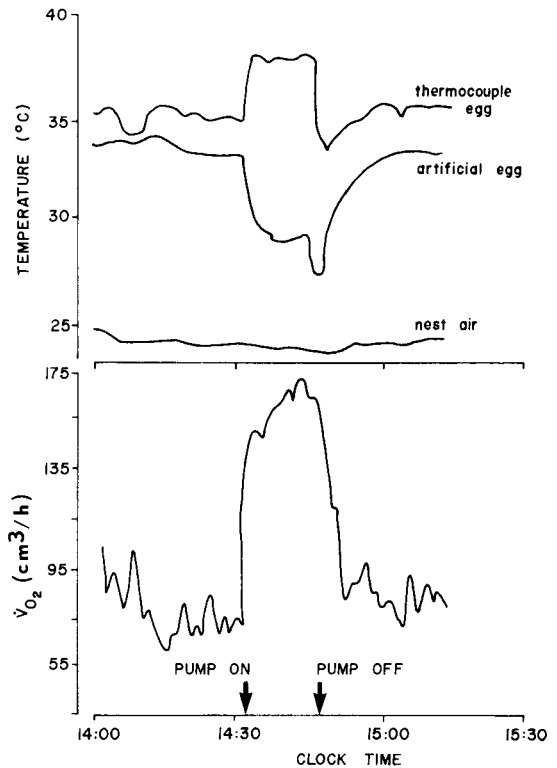


FIGURE 3. Record of oxygen consumption and egg temperatures during egg temperature manipulation. During the time the pump was on, indicated by arrows, cold water was circulated through the artificial egg. The bird increased its metabolic rate and heat transfer to the clutch, thereby raising the temperature of a natural egg containing a thermocouple.

the Ringed Turtle Dove (*Streptopelia risoria*; Franks 1967) and in the Herring Gull (Drent et al. 1970).

METABOLIC RESPONSE TO EGG TEMPERATURE

When egg temperatures were below normal incubation temperature, \dot{V}_{O_2} of incubating adults increased significantly ($P < 0.05$). When cold water was pumped through the artificial egg in a clutch, \dot{V}_{O_2} was sometimes more than double the rate measured just before the egg was cooled (Fig. 3). The average \dot{V}_{O_2} usually decreased when the artificial egg was warmed.

However, the temperature of the artificial egg was not a good predictor of the metabolic response of the incubating bird, because the position of this egg relative to the rest of the clutch and to the incubating adult was not constant. Metabolic rate was more closely correlated with the temperature of a natural egg in the clutch, possibly because this temperature more nearly approximated mean clutch temperature. The temperature of the thermocouple-containing natural egg

was normally about 37°C, but varied between 28.5 and 40°C when the artificial egg in the clutch was cooled or warmed. When the egg temperature was manipulated, mean \dot{V}_{O_2} varied with nest air temperature and the temperature of a normal egg. Multiple regression of \dot{V}_{O_2} on T_N and T_{egg} yields:

$$\dot{V}_{O_2} = 412 - 0.859 T_N - 8.55 T_{egg} \quad (7)$$

($n = 33$ measurements on 6 birds, $r^2 = 0.57$)

where \dot{V}_{O_2} is in cm^3/h .

The mean \dot{V}_{O_2} before manipulation of egg temperature varied with nest temperature:

$$\dot{V}_{O_2} = 128 - 2.45 T_N \quad (8)$$

($n = 33$ measurements on 6 birds, $r^2 = 0.69$).

The mean \dot{V}_{O_2} predicted from Eq. 8 is higher than the minimum \dot{V}_{O_2} at the same T_N predicted from Eq. 6, but the two do not differ significantly ($P > 0.05$) in either slope or intercept. Mean \dot{V}_{O_2} over a 15-min interval is higher than minimum \dot{V}_{O_2} because it includes the metabolic costs of activities associated with incubation, such as settling on the eggs and turning them, in addition to the metabolic costs of just keeping the eggs warm.

DISCUSSION

ENERGETIC COST OF INCUBATION

The energetic cost of incubation is the cost to an adult bird of keeping a clutch of eggs at incubation temperature, over and above costs for maintenance and other activities. The average cost of incubation is given by the difference between Eq. 6 and 5 at a given nest temperature (Fig. 2). This cost is about $9 \text{ cm}^3\text{O}_2/\text{h}$ or 49 mW at 28°C and increases to $15 \text{ cm}^3\text{O}_2/\text{h}$ or 82 mW at 10°C. Over this range of temperatures, incubation cost is a constant fraction (about 20%) of the metabolic rate of non-incubating birds.

The energetic cost of incubation is negligible above 28°C, which is near the lower critical temperature of the Zebra Finch (Calder 1964, Cade et al. 1965). \dot{V}_{O_2} was not measured in non-incubating birds above 28°C, but is unlikely to differ much from that of incubating birds.

These results are similar to those obtained by Biebach (1979) in the Starling. The \dot{V}_{O_2} of incubating and non-incubating Starlings is not significantly different above 10°C, which is the lower critical temperature for this species, but below 10°C, is 25 to 30% higher in incubating birds than in non-incubating birds. The slightly higher relative cost of incubation in Starlings is probably due to a relatively larger clutch

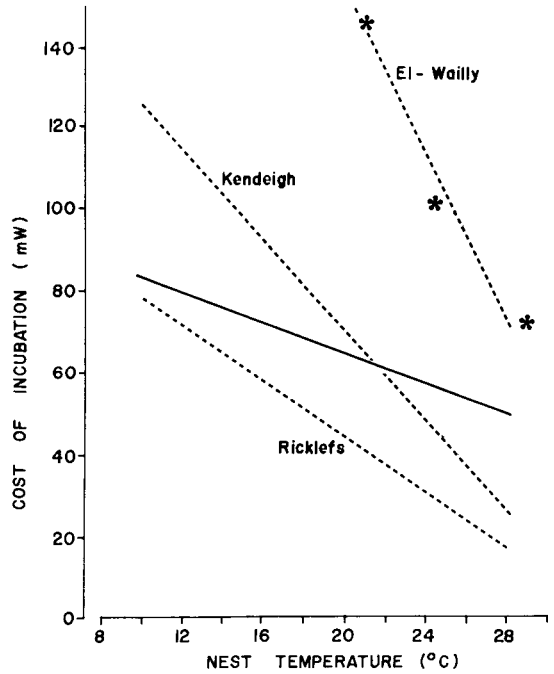


FIGURE 4. Cost of incubation in the Zebra Finch measured in this study (solid line) between nest temperatures of 10 and 28°C, compared with that computed by other methods (hatched lines). Asterisks are data from El-Wailly (1966) to which the line was fitted by least squares regression. The other two lines are based on the linear heat flow models of Kendeigh (1963) and Ricklefs (1974) and estimate the energy needed to maintain incubation temperature in four 1-g Zebra Finch eggs (see text).

(58% of the adult mass vs. 33% for a four-egg clutch of the Zebra Finch).

Within the thermal neutral zone of the birds, heat needed for incubation can come from the bird's normal heat production and there is no energetic cost of incubation. Below the thermal neutral zone, the eggs can be viewed as a poorly insulated extension of the bird's own body that usually does not contribute significantly to heat production. It follows that the conductance of the bird-egg complex exceeds that of non-incubating birds and metabolic rate must be higher to maintain homeothermy.

COMPARISON OF METHODS

The energetic cost of incubation that I report in this paper can be compared with El-Wailly's (1966) estimates for the Zebra Finch (Fig. 4). His values are based on food consumption and metabolized energy of pairs of incubating birds and the cost of incubation calculated as the difference in metabolized energy of incubating and non-incubating pairs. The metabolic costs associated with incubation are lower when

calculated from \dot{V}_{O_2} rather than from food consumption. El-Wailly's method probably overestimates the cost of incubation because it cannot distinguish costs of incubation from other changes in the birds' behavior and energy balance. El-Wailly replaced nests periodically in order to collect excreta. New nests were usually modified to some extent by the birds so that energy devoted to nest building was included in the total cost. In addition, birds with an incubation patch are likely to have a higher rate of heat loss from this vascularized and defeathered area, even when not incubating. This increased cost to the non-incubating member of a pair would also be included in El-Wailly's estimate.

The energetic cost of incubation measured as oxygen consumption can also be compared with that calculated from the heat flow models of Kendeigh (1963) and Ricklefs (1974). Both models assume that the energy expended by the adult is equal to the rate of heat loss from the eggs, and are based on estimates of the thermal conductance of the clutch, and the temperature gradient across the eggs. Kendeigh's (1963) model estimates thermal conductance from the heat capacity of the clutch, a correction factor for the portion of the egg covered by the adult bird, and the cooling rate of the eggs. I used Kendeigh's model to estimate the cost of incubation in the Zebra Finch, employing the same numbers as El-Wailly (1966) with the following exceptions. I measured the cooling rate of eggs in unattended nests by the method of Morrison and Tietz (1957) (cooling constant = 3.02/h, SD = 1.05, n = 3), and used the temperature gradient measured from the center of incubated eggs (37°C) to nest air below the eggs (Eq. 2), rather than to air outside the nest.

The calculated costs of incubation using Kendeigh's (1963) model are higher than measured values at nest temperatures below 22°C, but lower at high nest temperatures (Fig. 4). I interpret these differences to mean that at least some of the heat necessary to maintain egg temperature does come from the bird's normal heat production as suggested by King (1973). This may include as much as one-third of the heat required because Kendeigh's method predicts values at nest temperatures of 10 and 15°C which are 30% above resting rates rather than the 20% difference that I measured. The measured cost of incubation does not decrease with temperature as quickly as Kendeigh's method predicts, indicating that

there may be some cost associated with incubation in addition to warming eggs. Perhaps there is a cost for increased alertness of the incubating bird or perhaps this is an effect of reproductive hormones.

Ricklefs's (1974) model for estimating the energetic cost of incubation involves calculating the mass-specific heat conductance of the adult bird from equations in Lasiewski et al. (1967), assuming the conductance of the eggs is the same, and then multiplying the conductance value by the mass of the eggs and the temperature gradient. Using this method, the predicted cost of incubation is less than the observed cost at all temperatures (Fig. 4). Ricklefs's model fails because the average thermal conductance of an adult Zebra Finch is a poor index of the conductance of a clutch in a nest. Simple heat loss models for estimating the energetic cost of incubation cannot accurately substitute for direct measurement because of the complexities of the thermal environment of an egg in contact with a bird, other eggs in the clutch, and the nest itself.

COST OF INCUBATION AND OTHER ACTIVITIES

The \dot{V}_{O_2} of non-incubating Zebra Finches in a nest (Eq. 3) averages 18% lower than the values for non-nesting Zebra Finches reported by Calder (1964). This difference is to be expected because birds in a nest have reduced radiative and convective heat loss. There should also be some postural savings because the birds were sitting in a nest, not perched on a bar. Similarly, Mertens (1980) found that the heat loss of a Great Tit in a nest box was smaller when the box contained a nest than when it did not. Walsberg and King (1978a, b) estimated that the resting energy expenditure of three species that nest in open bowls should be 15–18% less when they are in a nest than when they are perched in the open because of the increased thermal resistance of the nest. Sitting quietly in a nest is not as energetically expensive as many other activities. However, for the Zebra Finches I studied, the energy that the bird saved because it was in a nest was more than offset by the energy it expended to maintain the eggs at incubation temperature. This was also true in the Great Tit studied by Mertens (1980). We cannot assess the ecological importance of the energetic costs of incubation without a complete time and energy budget for a given species. It is likely that the major cost of incubation is not the energy expended dur-

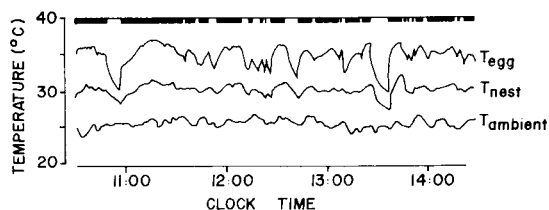


FIGURE 5. Record of egg, nest, and ambient temperature for the nest of a Zebra Finch in which only the female was incubating. Female attentiveness is represented by the shaded bars at the top of the figure; open bars represent absences from the nest.

ing incubation, but the time committed to incubation that is no longer available for foraging and other activities (Vleck, in press).

THE ENERGETIC COST OF WARMING EGGS

An additional cost of incubation, which must be included in the total, is that of re-warming eggs after absence from the nest. Zebra Finches greatly increased their expenditure of energy when attempting to warm cool eggs. They may have been cooled by the cold artificial eggs and hence increased \dot{V}_{O_2} as a thermoregulatory response. However, the result, increased heat flow to the eggs, is the same whether the bird raises its metabolic rate in response to lowered egg temperature or to lowered body temperature or both. Under natural circumstances, the eggs would quickly warm as heat was transferred from parent to egg, and these periods of elevated heat production would be brief. My findings are similar to those of Biebach (1979). He lowered the temperature of a clutch of copper eggs under an incubating Starling and found that the bird's metabolic rate increased more than threefold as it attempted to warm the cold eggs.

ATTENTIVENESS PATTERNS AND ENERGETIC COSTS

Since it costs less to keep eggs warm than it does to rewarm them, the total cost of incubation is influenced by the pattern of nest attentiveness, which determines the number of times eggs must be rewarmed to the incubation temperature. In the Zebra Finch, both sexes incubate; consequently, attentiveness is close to 100% and eggs almost never cool. I monitored egg temperatures in one case in which the male had been killed and the female alone incubated the eggs. This bird left the nest frequently, usually to defend it from other Zebra Finches in the flight cage. Because egg tempera-

TABLE 1. Energy expenditure of incubating Zebra Finches and mean egg temperature for two patterns of nest attentiveness (see text). Energy is expressed first as the energy used per hour of attentiveness and secondly as the energy used when incubating during a given hour.

	Attentiveness	
	80%	100%
Energy used/h of attentiveness (kJ)	1.49	1.38
Energy used in incubation/h (kJ)	1.19	1.38
Mean egg temperature (°C)	34.5	37.0

ture fluctuated depending on the presence or absence of the bird, her attentiveness could be determined from the record of egg temperature (Fig. 5). In one 12-h period, at an average ambient temperature of 24.2°C, the female left the nest a mean of 5.3 times/h (SD = 1.77) and was absent a mean of 13.75 min/h (SD = 4.88) or 23% of the time. Egg temperature dropped an average of 2.7°C (SD = 1.46) during these absences and the bird was re-warming the eggs 22% of the time she was incubating.

Using the appropriate equation for mean oxygen consumption, either for incubating at a constant egg temperature (Eq. 8) or for re-warming eggs (Eq. 7), I calculated the mean energy expenditure during incubation for this pattern of attentiveness. The energy required for 1 h of interrupted attentiveness was about 8% more than the energy required for 1 h of continuous attentiveness (Table 1). The difference would be even greater at lower ambient temperatures because the eggs would cool faster during the bird's absences and the cost of re-warming them would be greater. Because this female incubated only about 80% of the time, however, the energy she used in incubation during any given hour was actually less than if she had incubated constantly (Table 1). Because of her reduced attentiveness, mean egg temperature was only about 34.5°C, whereas egg temperature when eggs are incubated by both parents is about 37.0°C. Laboratory experiments (Vleck, unpubl. data) indicate that embryonic Zebra Finches do not develop properly if eggs are incubated artificially at 35°C, and none of the eggs in the nest of this lone female hatched.

Because the Zebra Finch is not normally a single-sex incubator, I cannot say that the increased metabolic rate in response to low egg temperature that I observed is the normal response of species that regularly leave the nest and then return to incubate cooled eggs. However, Gabrielsen and Steen

(1979) demonstrated that those incubating Willow Ptarmigan (*Lagopus lagopus*) who show pronounced tachycardia when they return to a cold nest, rewarm their clutches more quickly than birds with normal heart rates. Such tachycardia is presumably associated with increased heat flow to the incubation patch, and must entail the expenditure of energy by the adult. Furthermore, the metabolic rate of embryos, and thus growth and development, are slowed by a decrease in temperature in most avian species (Kendeigh 1940, Khaskin 1961, Hoyt et al. 1978, Vleck and Kenagy 1980) and rewarming the eggs to incubation temperature as quickly as possible may have adaptive value because it shortens the incubation period.

The energetic cost of incubation increases as the attentiveness of birds is fragmented by many periods off the nest. Drent (1973) suggested that birds ideally should take one long bout off the eggs, rather than several shorter bouts, in order to maximize mean egg temperature. This is probably the most energy-efficient pattern of attentiveness for a single parent as well. However, attentiveness patterns may be a compromise between the neglect that an embryo *in ovo* can tolerate and the energy balance of the adult. The many species that have evolved cooperative incubation behavior, with one member of the pair feeding the other or taking a turn on the eggs, are an indication of the special demands that incubation can place on energy balance.

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Department of Biology, University of California, Los Angeles, California 90023. Present address: Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721. Accepted for publication 28 October 1980.

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RECENT PUBLICATION

Birds of Prey of the World.—Friedhelm Weich, in collaboration with Leslie H. Brown. 1980. Verlag Paul Parey, Hamburg and Berlin. 159 p. \$48.00. This book is an illustrated manual for the identification of all living falconiform birds, modelled after Peter Scott's colored key to the waterfowl of the world (1957. Wildfowl Trust, Slimbridge). Written in both German and English, it first gives a key to species, using characters of size, proportions, color of soft parts, and feathering. A compendium of the Order then characterizes the morphology of every genus with a paragraph of text and a fine pen-and-ink drawing. The heart of the work is a series of 40 color plates that depict all species and all distinctive races, adult and immature plumages, males

and females, and unusual color phases. All the birds are shown in a standardized side view so as to display field marks and permit comparison. A table facing each plate gives the scientific, German, and English names; characteristics of appearance; distribution; and several measurements. Although the book is intended as a field guide for worldwide use, it would seem to be of limited practicality because of its size. Also, problems of identification can usually be simplified by considering only those species that are known to occur within one's region. On the other hand, it will be useful for its all-inclusive set of illustrations, unmatched by any other reference on these birds. Indexes, bibliography.