

# THE EFFECT OF TEMPERATURE AND CLUTCH SIZE ON THE ENERGETIC COST OF INCUBATION IN A FREE-LIVING BLUE TIT (*PARUS CAERULEUS*)

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**ABSTRACT.**—The energetic cost of incubation of a free-living Blue Tit (*Parus caeruleus*) female was studied during two breeding seasons by measuring the rate of oxygen consumption in a nest box converted into a metabolic chamber. Like its congeners, only the female Blue Tit incubates and during that time is fed by the male. Just before and during the egg-laying period the female spends the night in the nest. Because of the progressive development of incubation behavior during this period, it is possible to measure the oxygen-consumption rate of a nonincubating female (resting metabolism) and to compare it with values obtained later when the bird is incubating a full clutch under otherwise similar conditions. The air temperature in the metabolic chamber was regulated experimentally. The results show that the energy cost of incubation is relatively important below the lower critical temperature (about 15°C). With a fall in the air temperature, energy expenditure increased in relation to that of the resting metabolism. The energy cost of incubation also increased with clutch size, by about 6–7% for each additional egg. At air temperatures around 0°C, which are frequent under natural conditions in Fennoscandia, the female must increase her metabolic rate by 50–90% to keep the eggs in a normal-size clutch (10–13 eggs) warm. During the last days of incubation we accounted for the metabolism of the embryos, which on the day before hatching contributed about 15% of the total oxygen consumption when the female was incubating a clutch of 13 eggs. Received 30 May 1984, accepted 16 November 1984.

THE evaluation of the energy cost of incubation by birds has been a subject of some controversy (e.g. Vleck 1981, Walsberg 1983). Based on heat-flow models, Walsberg and King (1978a, b) claimed that the resting metabolism of three passerine species, the Red-winged Blackbird (*Agelaius phoeniceus*), the Willow Flycatcher (*Empidonax traillii*), and the White-crowned Sparrow (*Zonotrichia leucophrys*), averaged about 15–18% less than that of nonincubating birds. Biebach (1979) and Vleck (1981) found from measurements of the rate of oxygen consumption in the Zebra Finch (*Poephila guttata*) and the European Starling (*Sturnus vulgaris*) that the metabolic rate of the female while incubating was 20–30% greater than that of nonincubating birds. Mertens (1980) estimated the energy requirement by measuring the heat loss from a Great Tit's (*Parus major*) nest and found that a considerable energy expenditure was involved in incubating. Using heat-flux disks mounted in the walls of a nest box occupied by a female Great Tit, Mertens concluded that the heat loss during incubation, at an air temperature of 8°C, was roughly 3 times greater than the heat loss

incurred at the resting metabolic rate of a non-incubating bird.

Titmice are ideal subjects for an evaluation of the energy cost of incubation because it is possible to measure the metabolism of individual birds in both an incubating and a nonincubating situation. Because they are hole-breeders, it is possible to measure the rate of gas exchange directly. Furthermore, free-living birds can be studied outside the laboratory, thus avoiding errors due to stress arising from the conditions of captivity. Because of the female's behavior pattern during the egg-laying period, the energy expended during incubation can be calculated simply by subtracting the oxygen-consumption rate of the bird when standing above the eggs in a resting, nonincubating posture from the oxygen-consumption rate while incubating, in both cases under the same environmental conditions.

A description of the female's behavior during the egg-laying period illustrates the last point. In general, eggs are laid in the early morning on consecutive days, and the female starts to incubate after the first egg has been

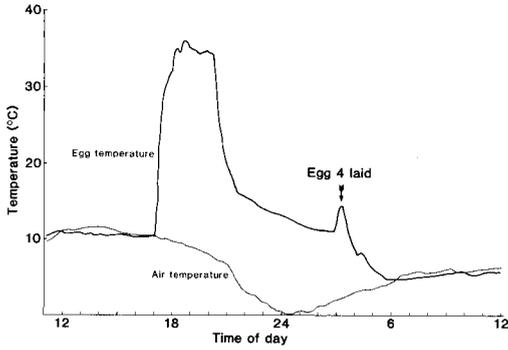


Fig. 1. Typical nightly pattern of the changes in egg temperature during the early part of the egg-laying period in a titmouse nest, in this case the Coal Tit (*Parus ater*).

laid (Haftorn 1966, 1983). This pattern occurs in combination with the nightly stay of the female in the nest (Fig. 1). When she enters the nest in the evening, she immediately removes the nesting material that usually covers the eggs during the daytime. She then sits down in a normal incubating posture, causing the temperature of the eggs to increase abruptly. During the early part of the egg-laying period, however, the female incubates for a short time only. After a while she stands up and spends the rest of the night standing in the nest cavity, in the usual sleeping posture. Because there is now no direct contact between her brood patch and the eggs, the temperature of the eggs falls. Just before she leaves the nest the following morning, a slight peak in her oxygen consumption and body temperature, and in the temperature of the eggs, indicates when an additional egg was laid. Thereafter she covers the eggs with nesting material and departs. The nightly incubation time increases more or less regularly throughout the egg-laying period, and during the final few nights the female incubates continuously all night long (Fig. 2; Haftorn 1979, 1983).

The male tit never takes part in incubation. During the early part of the egg-laying period, therefore, there is an excellent opportunity to study the metabolism of an individual bird both in an incubating position and in a resting, non-incubating position (to obtain her resting metabolism) under controlled environmental conditions. Data for the female's resting metabolic rate also can be obtained just prior to egg-lay-

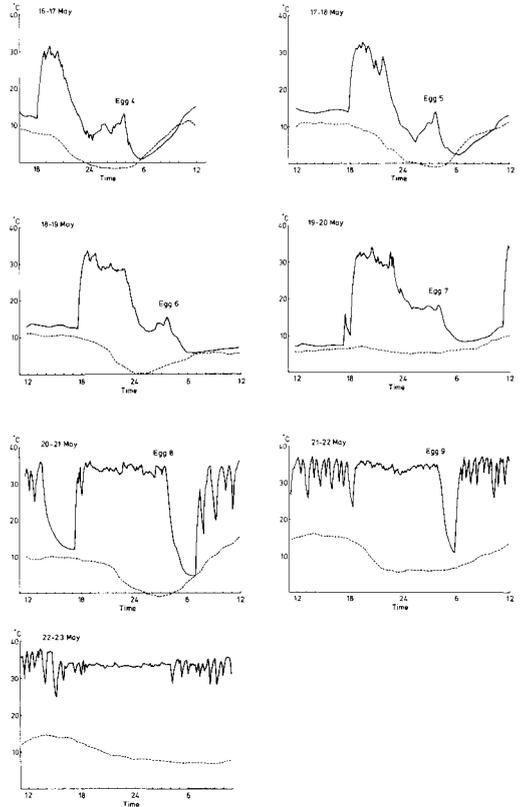


Fig. 2. The course of egg temperature (solid lines) and the corresponding air temperature outside the nest (dotted lines) during the egg-laying period (after the laying of the third egg) and on the first day of the incubation period, for a Great Tit's nest (final clutch of 9 eggs). After Haftorn (1981).

ing, when she spends the whole night in the finished nest.

In this paper we present the results of a study of the metabolism of a free-living female Blue Tit (*Parus caeruleus*) during the egg-laying and incubation periods. The main aim was to investigate whether the rate of oxygen consumption by the Blue Tit during incubation differs from that during nonincubation. Because the data obtained showed that a significant difference exists, we then investigated the influence of clutch size on the energy expenditure involved in incubation.

#### METHODS

A pair of color-banded Blue Tits that bred successfully in nest boxes erected at Målsjöen, Klaebu in

Norway (63°N) was studied during two successive years (1982–1983). Clutch sizes were 10 eggs in 1982 and 13 eggs in 1983. The eggs were laid on consecutive days, starting on 26 and 20 May, respectively.

Before the experiments were started, a normal nest box was converted to a metabolic chamber (net volume 1 l in 1982 and 2.3 l in 1983). The oxygen-consumption rate was measured by an open-circuit system using a S-3A oxygen analyzer (Applied Electrochemistry Inc.). Dry air was pulled into the nest through an inlet tube placed in one of the upper corners of the nest box, at a rate of 200 ml/min in 1982 and 300 ml/min in 1983, causing the oxygen extraction to be below 1%. During the experiment, the entrance hole was closed off by a transparent piece of plexiglass. The outcoming air was dried with silica gel, and CO<sub>2</sub> removed with Ascarite, before the air was passed into the analyzer for continuous analysis of its O<sub>2</sub> content. All oxygen-consumption values were corrected to STP and calculated according to the equations of Depocas and Hart (1957).

To increase the temperature in the nest box, the air within a plastic tent placed above the nest box was warmed by means of an electric heater beneath the box. To lower the air temperature, cold antifreeze solution was run through a spiral of thin copper pipe fitted to the nest cup and hidden in the nesting material.

The oxygen-consumption rate of the female was measured at air temperatures that ranged from -5° to 25°C.

Contrary to the situation in 1982, in 1983 we also measured the metabolic rate during the last three days before the eggs hatched. This has the following implications:

During most of the incubation period the rate of oxygen consumption by the embryos is negligible compared to that of the incubating female. However, oxygen consumption is known to increase exponentially during the course of the incubation period, and just prior to hatching it is many times greater than during the early part of the incubation period (Vleck et al. 1979). For a bird that lays a clutch of many eggs, oxygen consumption by the embryos thus may contribute substantially to the overall rate of oxygen consumption measured during the later part of the incubation period. Therefore, using the method described above, we measured the rate of oxygen consumption of the whole clutch (13 eggs) during an experimentally prolonged period-off of the female on the day before the eggs hatched, at an egg temperature equivalent to the normal incubation temperature (36–37°C, as measured in the air above the uncovered eggs). The eggs consumed 19.7 ml O<sub>2</sub> per hour. This means that the embryos accounted for about 15% of the total oxygen consumption recorded when the female was incubating at this advanced stage of embryo development. Although this oxygen consumption by the embryos is of relatively minor

importance, we have allowed for this and corrected the values for the oxygen consumption obtained on the last three days of the incubation period.

All oxygen-consumption rates presented in this paper were measured during the nightly stay of the female in the nest box from two days before the start of egg-laying up to the last day before hatching occurred. Her last excursion (period-off) away from the box during the incubation period usually took place around 1800, and she then left the box next morning for the first time at about 0330–0430.

Egg temperature was measured by inserting a thermocouple into one of the freshly laid eggs (the T-egg), so that the recording point was situated about 1 mm beneath the upper side of the eggshell (i.e. approximately at the site of the blastoderm). The air temperature was recorded in the nest box at a point just above the sitting bird. In both the T-egg and the nest box the temperature was recorded at 1–5-min intervals. Because no embryonic development took place in the T-egg, the temperature measurements were not influenced by any embryonic heat production.

The posture of the attentive female could be checked through a small transparent part of one of the sidewalls of the nest box. The peephole usually was covered by a piece of cardboard.

*Statistics.*—To test the significance of differences between the oxygen-consumption values for the female measured while not incubating and while incubating, we used Student's *t*-tests for air temperatures below the lower critical temperature of the thermoneutral zone. Symbols used are: *r* = Pearson product-moment correlation coefficient, *r<sub>s</sub>* = Spearman rank correlation coefficient, and *r<sub>p</sub>* = partial correlation coefficient.

## RESULTS

*Resting metabolism and the energy cost of incubation.*—Figure 3 provides an example of the data obtained during the female's nightly stay in the nest box during the egg-laying period. At the stage shown, the female had laid 6 eggs, and the seventh egg followed the next morning. The female incubated the eggs from the time she entered the nest in the afternoon until about 2020. For the rest of the night she stood inactively above the eggs with no direct contact between her body and the eggs. As is clearly shown, the female's oxygen-consumption rate was higher when she was sitting on the eggs than after she rose from the eggs, despite the progressive decrease in air temperature.

Figure 3 also shows the changes in the rate of oxygen consumption during the female's gradual transition from a sitting to a permanent standing posture.

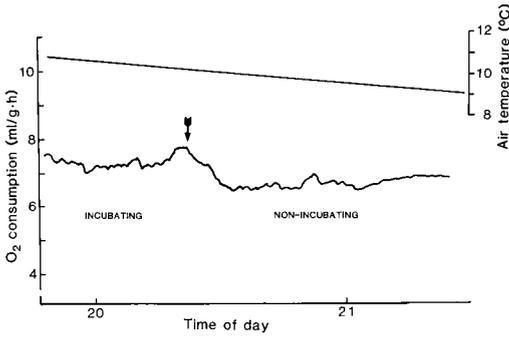


Fig. 3. Changes in the oxygen-consumption rate of a female Blue Tit during one night in the egg-laying period, covering the period between sitting on the eggs and standing above them in a nonincubating posture. The end of incubation is indicated by an arrow. See text for further explanation.

The oxygen-consumption data obtained in 1982 were similar to those obtained in 1983 (Figs. 4, 5). Above an air temperature of 15°C, which apparently is close to the lower critical temperature, the difference in the energy cost while incubating compared to that while not incubating was negligible. Below 15°C, however, the oxygen-consumption rate increased linearly and was significantly higher than the

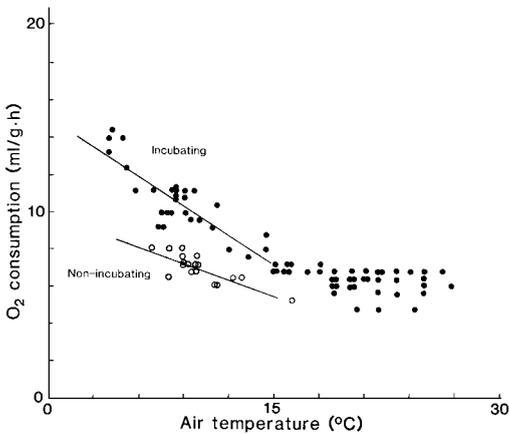


Fig. 4. The relationship between the female Blue Tit's oxygen-consumption rate and the air temperature, when standing above the eggs in a resting (non-incubating) posture (open circles) and when incubating her 10 eggs (solid circles). Each record represents the stable value of oxygen-consumption rate at a stable air temperature. Upper regression line ( $n = 32$ ):  $y = 15.17 - 0.54x$ . Lower regression line ( $n = 18$ ):  $y = 9.85 - 0.29x$ . Data from 1982.

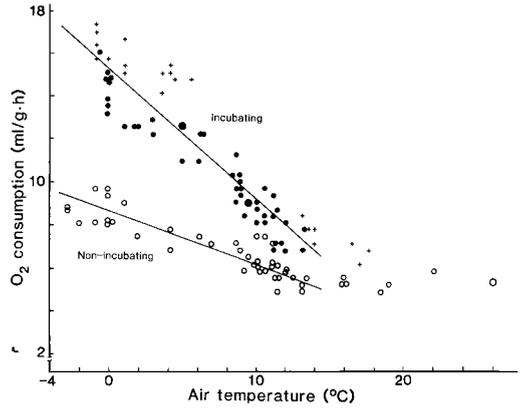


Fig. 5. The relationship between the female Blue Tit's oxygen-consumption rate and the air temperature, when standing above the eggs in the nest without incubating (open circles) and when incubating 13 eggs (solid circles). Crosses represent the oxygen-consumption rate on the day before hatching. Each record represents the stable value of oxygen-consumption rate at a stable air temperature. Large circles represent several equal records. Upper regression line ( $n = 71$ ):  $y = 15.35 - 0.62x$ . Lower regression line ( $n = 41$ ):  $y = 8.45 - 0.22x$ . Data from 1983.

resting metabolic rate at a corresponding air temperature ( $P < 0.001$ ).

To investigate the effect of clutch size on the energy cost of incubation, we temporarily reduced the clutch from 13 to 8 eggs on day 8 of incubation [the removed eggs were placed in nests belonging to incubating female Pied Flycatchers (*Ficedula hypoleuca*) and returned to the Blue Tit's nest after the experiment]. The female Blue Tit's oxygen-consumption rate decreased significantly by about 18% ( $P < 0.001$ ) after the 5 eggs were removed (Fig. 6).

The female's oxygen-consumption rate was significantly higher ( $P < 0.001$ ) on the day before hatching than earlier in the incubation period, even though we allowed for the proportion related to embryonic metabolism (Fig. 5). This increase in oxygen consumption is also clearly seen in Fig. 7. Each regression line in this figure refers to data obtained while the female was incubating a constant number of eggs at a constant air temperature. The same positive trend throughout the incubation period is seen in each case. Again, the observed increase in oxygen consumption is solely that of the incubating female, since allowance was made for the proportion due to embryonic metabolism.

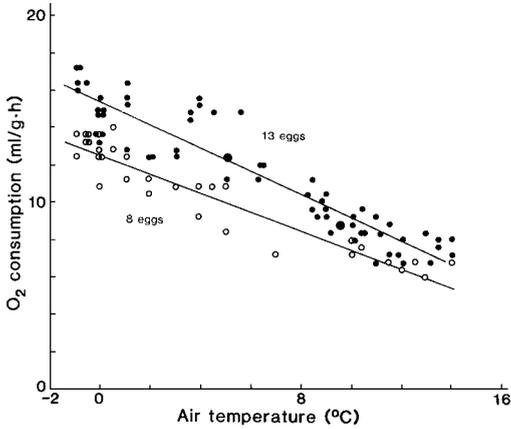


Fig. 6. The relationship of the female Blue Tit's oxygen-consumption rate to the air temperature, when incubating 13 eggs (solid circles) and after the clutch was temporarily reduced to 8 eggs (open circles). Each record represents the stable value of oxygen-consumption rate at a stable air temperature. Large circles represent several equal records. Upper regression line ( $n = 71$ ):  $y = 15.35 - 0.62x$ . Lower regression line ( $n = 32$ ):  $y = 12.55 - 0.51x$ .

*Egg temperature.*—Due to equipment malfunctions in 1983, egg temperature data are available only for 1982, when the clutch consisted of 10 eggs.

The relationship between egg temperature and air temperature was studied by comparing data for the nighttime incubation, including those occasions when the nest temperature was raised experimentally. Although the female incubated steadily, egg temperature decreased significantly with decreasing air temperature, in a curvilinear fashion (Fig. 8). Below an air temperature of 10°C, egg temperature varied more widely and the mean was significantly lower ( $35.35 \pm 1.27^\circ\text{C}$  SD,  $n = 183$ ) than that recorded at temperatures above 10°C ( $36.88 \pm 0.75^\circ\text{C}$ ,  $n = 156$ ;  $t$ -test,  $P < 0.001$ ). When the air temperature was lowered from 10° to 4°C, egg temperature also fell significantly [from 35.66°C at 8–10°C ( $n = 81$ ) to 35.07°C at 4–6°C ( $n = 80$ );  $t$ -test,  $P < 0.005$ ]. A regression analysis for the data obtained within the air temperature range of 4–10°C yielded a correlation coefficient of 0.15 ( $P < 0.05$ ) and an egg temperature intercept of 34.55°C (air temperature 0°C).

Egg temperature increased significantly throughout the incubation period, even when the air temperature was kept constant ( $r_p = 0.34$ ,  $P < 0.001$ ).

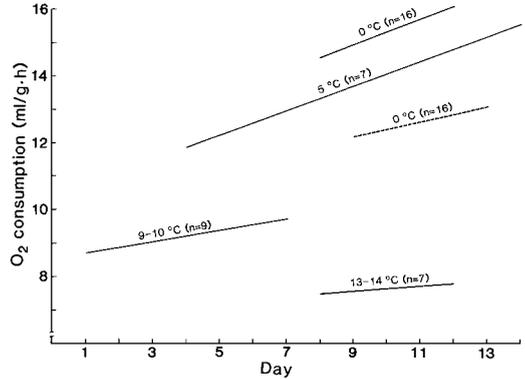


Fig. 7. Regression lines obtained for the relationship between oxygen consumption and progression of the incubation period for the female Blue Tit while incubating. Day 1 is the first day of the incubation period (complete clutch). Solid lines: female incubating 13 eggs; dotted line: female incubating 8 eggs. Ambient temperatures and number of records are specified. All regression coefficients, except the one related to the lowermost line, differ significantly from zero ( $P < 0.05$ ).

#### DISCUSSION

Our data on the energy cost of incubation by a free-living female Blue Tit support the view of Kendeigh (1963, 1973), Ricklefs (1974), Mertens (1977), Biebach (1979, 1981, 1984), and Vleck (1981) that incubation, at least by small birds, requires the production of additional heat when the air temperature falls below the lower

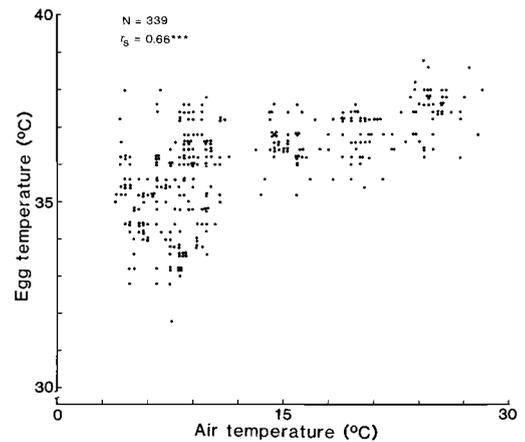


Fig. 8. The relationship between egg temperature and air temperature during the continuous nighttime incubation for the female Blue Tit sitting on a clutch of 10 eggs. \*\*\* =  $P < 0.001$ .

critical value of the thermoneutral zone. According to our results, this critical value for the Blue Tit is about 15°C.

To arrive at a reliable estimate of the sole energy expenditure for incubation, the metabolism of incubating and nonincubating birds under otherwise identical conditions must be compared (cf. Vleck 1981). For birds with large clutches, embryonic metabolism also must be accounted for during the last few days before hatching. Both requirements were fulfilled by the present study.

The oxygen-consumption rate during incubation depends on the clutch size. Thus, below the lower critical temperature, the larger the clutch the more the female Blue Tit increased her metabolic rate. A significant increase was found between clutches of 8 and 10 eggs and between clutches of 10 and 13 eggs ( $P < 0.05$ ). When a 13-egg clutch was temporarily reduced to 8 eggs, the female's oxygen consumption during incubation decreased by about 18% ( $P < 0.001$ ). Biebach (1981, 1984) also found a positive correlation between the energy output of incubating female European Starlings and clutch size. For each additional egg the cost of nighttime incubation increased by about 4% in the European Starling, compared to about 6–7% in the Blue Tit.

At air temperatures ranging from  $-10^{\circ}$  to  $10^{\circ}\text{C}$  the energy expenditure of a European Starling incubating 6 eggs was 25–30% greater than that of a nonincubating bird (Biebach 1981), a result similar to that obtained for the Zebra Finch (Vleck 1981). While  $10^{\circ}\text{C}$  is considered to be the lower critical temperature for the European Starling (Biebach 1981), for the Zebra Finch the value is as high as  $28^{\circ}\text{C}$ . Over the entire temperature range from  $10^{\circ}$  to  $28^{\circ}\text{C}$ , Vleck (1981) found that the cost of incubating 4 eggs was a constant proportion (about 20%) of the metabolic rate of nonincubating birds. Above  $28^{\circ}\text{C}$  the energy cost of incubation was negligible. Vleck suggested that the relative cost of incubation for starlings was slightly higher because of the relatively larger clutch size (equivalent to 58% of the adult body weight of a starling compared to only 33% for the 4-egg clutch of a Zebra Finch).

The relative cost of incubation for the Blue Tit was much higher than for the European Starling and Zebra Finch, a result of the much larger clutch size (an 8-egg clutch represents about 90% of the adult female's body weight,

and a 13-egg clutch about 146%). In contrast to the Zebra Finch, for the Blue Tit the cost of incubation represented an increasingly greater proportion of the metabolic rate of the nonincubating bird at decreasing air temperatures. At  $10^{\circ}\text{C}$  the estimated proportion was 20% for an 8-egg clutch and 47% for a 13-egg clutch, compared to values of 49% and 82% at  $0^{\circ}\text{C}$ .

In the Great Tit, Haftorn (1983) found that egg temperature tended to increase during the incubation period. He suggested that this increase was due to the progressive development of the brood patch, which possibly did not attain its maximum efficiency of heat transfer until well into the incubation period. The present findings provide further support for this hypothesis. At air temperatures between  $-1^{\circ}$  and  $5^{\circ}\text{C}$  on the day before hatching, the metabolic rate of the incubating Blue Tit was significantly higher ( $P < 0.001$ ) than the value recorded over the same temperature range earlier in the incubation period (Fig. 5).

This trend is also evident in Fig. 7. The general picture indicates that the female's oxygen consumption increases during the course of the incubation period. The level of the  $0^{\circ}\text{C}$  regression line shows a distinct change after the clutch of 13 eggs was reduced to 8 eggs. The gradual increase in the metabolic rate of the female during the incubation period coincided with a significant increase in egg temperature.

In Scandinavia the Blue Tit and its congeners frequently are exposed to nighttime air temperatures of around  $0^{\circ}\text{C}$  during the incubation period (see Haftorn 1983: Table 2). According to our results, when incubating a normal-size clutch (10–13 eggs) under such conditions, the female Blue Tit must increase her resting metabolism by 50–90% to keep the eggs warm (see Figs. 4, 5).

When evaluating our results for the energy cost of incubation, it is important to bear in mind that they were obtained during a period of steady-state incubation at night and do not take into account the additional energy cost in rewarming the eggs after the female's regular periods-off. These excursions occur about 28 times during the daytime incubation (although some rewarming also takes place during the night in connection with egg shifting). During the daytime, on the other hand, the prevailing air temperature usually is considerably higher than during the night. This difference partly compensates for the additional energy cost of

TABLE 1. Mean sizes of first clutches laid in different parts of the Blue Tit's European breeding area. [Data from Berndt et al. (1983), which indicate that clutch size in West Germany increases with latitude (provided the data were corrected for diminishing clutches with the advance of the breeding season), are not included.]

	Latitude	Mean clutch size	SE	Number of clutches	Source
Norway	63°20'N	11.0	0.24	35	This study
Sweden	60°19'N	9.3		7	Johansson 1972
	59°03'N	11.35	0.35	20	Källander 1976
	59°11'N	10.58	0.30	38	Källander 1976
	58°04'N	11.85		13	Jansson 1960
	57°30'N	9.8 <sup>a</sup>	0.26	29	Enemar 1981
	57°30'N	11.6 <sup>b</sup>	0.40	25	Enemar 1981
	55°58'N	10.86	0.31	22	Källander 1976
	Unspecified	11.64	0.16	94	Källander 1976
	Unspecified	10.2		45	Durango 1944
	Unspecified	9.88		80	Lack 1950
Finland	Unspecified	10.89 <sup>c</sup>	0.40	19	Haartman 1969
Denmark	Ca. 55°30'N	10.7		143	Frederiksen et al. 1972
	Ca. 55°30'N	10.6		205	Larsen 1974
	55°55'N	11.85		54	Beck 1937
West Germany	52°27'N	10.04	0.36	24	Winkel 1975
Holland	Unspecified	10.65		3,455	Lack 1950
Switzerland	Unspecified	10.3		125	Glutz von Blotzheim 1962
Scotland	Unspecified	9.54		50	Lack 1950
South England	Unspecified	11.64		312	Lack 1950

<sup>a</sup> In small nest boxes constructed for the European Tree-Creeper (*Certhia familiaris*).

<sup>b</sup> In larger nest boxes.

<sup>c</sup> Laid before 15 May.

rewarming the eggs. However, adequate data for the daytime energy cost of incubation, including rewarming the eggs, are still needed.

Although no information about the productive energy (as defined by Kendeigh 1973) of the female Blue Tit exists, the quantity of energy invested in incubation at air temperatures around 0°C must represent a substantial part, perhaps almost all. The lowest air temperature for successful incubation by tits is still unknown. It is certainly variable and depends on a series of circumstances, such as the female's body condition, the clutch size, the efficiency of nest insulation, the duration of sudden cold periods, and the quantity of food supplied by the male. The male's contribution to the food requirements of his mate during the egg-laying and incubation periods may be of vital importance (cf. Royama 1966, Krebs 1970).

When the air temperature fell below approximately 14°C during the period of continuous incubation at night, the egg temperature also showed a distinct decrease (Fig. 8). This tendency also was found in the Great Tit, the Willow Tit (*Parus montanus*), and the Goldcrest (*Regulus regulus*; Haftorn 1978, 1979, 1983). It is

noteworthy that the air temperature at which the egg temperature started to decrease coincides with the lower limit of the zone of thermoneutrality (TNZ), indicating a possible limit to the heat transfer of the brood patch.

Because the metabolic rate, and probably also the body temperature, is constant within the TNZ, the conductance must decrease with the decrease in air temperature according to the equation  $\dot{Q} = C(T_b - T_a)$ , where  $\dot{Q}$  = metabolic rate,  $C$  = conductance,  $T_b$  = body temperature, and  $T_a$  = air temperature. If this change in the Blue Tit's conductance also applied to the brood patch, one would expect a slight decrease of egg temperature within the TNZ when the air temperature approached the lower limit of the TNZ. There is no evidence of such a trend, however.

We therefore suggest another model that implies an uncoupling of the regulation of the conductance in the brood patch from the rest of the body. According to this hypothesis, the conductance in the brood patch increases with falling air temperature and reaches its maximum value at the lower limit of the TNZ. At the same time, the normal decrease of conduc-

tance at falling air temperature within the TNZ takes place in the rest of the body. At a constant metabolic rate and constant body temperature, this system would facilitate heat transfer to the eggs and thereby explain the fact that the egg temperature remains at a constant level within the TNZ. According to the model, however, the heat transfer to the eggs at temperatures below the TNZ cannot be improved by a further increase of conductance in the brood patch. Consequently, the average egg temperature decreases more or less linearly with decreasing air temperature, as we observed.

However, at the lowest air temperatures (4–6°C) for which relevant data are available, egg temperature was still relatively high (mean = 35.1°C). This value exceeds the temperature (25–27°C) below which no embryonic development occurs (Drent 1975). Even when the air temperature temporarily fell quite a bit below 0°C, we did not detect anomalies in incubation behavior, and the eggs hatched normally.

Above an air temperature of 23°C the average egg temperature seemed to increase (Fig. 8). This may indicate that the incubating Blue Tit had reached its upper limit of the TNZ and that the conductance of the brood patch had obtained a minimum value. More data are needed to clarify this point.

Having found that it costs more to incubate a large clutch than a small one, Biebach (1981) posed the question of whether this additional cost may have some effect on clutch size under certain circumstances. In general, tits lay large clutches, and the Blue Tit lays the largest of all (Perrins 1979). According to Lack (1950), the clutch size of the Blue Tit tends to decrease from central Europe northward. He cited mean clutch sizes (first broods) of 10.65 eggs in Holland and 9.88 eggs in Sweden. More recent data, however, render this conclusion somewhat doubtful (Table 1). Our study area at Trondheim (63°N) is situated close to the northern limit for regular breeding by this species in Fennoscandia (about 64°30'N), and yet the mean clutch size for the Trondheim district is one of the highest recorded anywhere in Europe.

The fact that clutch size is highest in early spring, at a time when the air temperature is relatively low, and thereafter declines as the breeding season progresses (Lack 1955, 1958; Haartman 1969) and the weather ameliorates, further supports the view that the incubation capacity of the Blue Tit is well adapted to the

seasonal temperature regime that prevails in southern Fennoscandia. The data thus indicate that to breed successfully at a site near the northern limit of its breeding range, the Blue Tit apparently need not save energy by decreasing its clutch size.

#### ACKNOWLEDGMENTS

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#### LITERATURE CITED

- BECK, H. 1937. Biologiske studier vedrørende Mejserne paa Strødam. *Danske Fugle* 4: 147–154.
- BERNDT, R., W. WINKEL, & H. ZANG. 1983. Über Legebeginn und Gelegestärke von Kohl- und Blaumeise (*Parus major*, *P. caeruleus*) in Beziehung zur geografischen Lage des Brutortes. *Vogelwarte* 32: 46–56.
- BIEBACH, H. 1979. Energetik des Brütens beim Star (*Sturnus vulgaris*). *J. Ornithol.* 120: 121–138.
- . 1981. Energetic costs of incubation on different clutch sizes in starlings (*Sturnus vulgaris*). *Ardea* 69: 141–142.
- . 1984. Effect of clutch size and time of day on the energy expenditure of incubating starlings (*Sturnus vulgaris*). *Physiol. Zool.* 57: 26–31.
- DEPOCAS, F., & J. S. HART. 1957. Use of the Pauling oxygen analyzer for measurement of oxygen consumption of animals in open-circuit systems and in a short-lag, closed-circuit apparatus. *J. Appl. Physiol.* 10: 388–392.
- DRENT, R. 1975. Incubation. Pp. 333–420 in *Avian biology*, vol. 5 (D. S. Farner and J. R. King, Eds.). New York, Academic Press.
- DURANGO, S. 1944. Några jämförelser rörande tallitans, *Parus atricapillus borealis* Selys, och kärrmesens, *Parus palustris palustris* L., *biologi. Ornis Fennica* 21: 33–42.
- ENEMAR, A. 1981. Försök med holkar för trädkrypare *Certhia familiaris*. *Vår Fågelvärld* 40: 233–238.
- FREDERIKSEN, K. S., M. JENSEN, E. HØJKJAER LARSEN, & V. HØJKJAER LARSEN. 1972. Nogle data til belysning af yngletidspunkt og kuld størrelse hos mejser (*Paridae*). *Dansk Ornithol. Foren. Tids.* 66: 73–85.
- GLUTZ VON BLOTZHEIM, U. N. 1962. *Die Brutvögel der Schweiz*. Aarau, Verlag Aargauer Tagblatt AG.
- HAARTMAN, L. VON. 1969. The nesting habits of Finnish birds. I. Passeriformes. *Commentationes Biologicae* 32: 1–187.

- HAFTORN, S. 1966. Egglegging og ruging hos meiser basert på temperaturmålinger og direkte iakttagelser. [Egg-laying and incubation in tits based on temperature recordings and direct observations.] *Sterna* 7: 49-102.
- . 1978. Egg-laying and regulation of egg temperature during incubation in the Goldcrest *Regulus regulus*. *Ornis Scandinavica* 9: 2-21.
- . 1979. Incubation and regulation of egg temperature in the Willow Tit *Parus montanus*. *Ornis Scandinavica* 10: 220-234.
- . 1981. Incubation during the egg-laying period in relation to clutch size and other aspects of reproduction in the Great Tit *Parus major*. *Ornis Scandinavica* 12: 169-185.
- . 1983. Egg temperature during incubation in the Great Tit *Parus major*, in relation to ambient temperature, time of day, and other factors. *Fauna norv. Ser. C, Cinclus* 6: 22-38.
- JANSSON, K.-E. 1960. Några siffror och rön från sju års studier av småfåglar heckande i holkar. *Vår Fågelvärld* 19: 127-136.
- JOHANSSON, H. 1972. Clutch size and breeding success in some hole nesting passerines in Central Sweden. *Ornis Fennica* 49: 1-6.
- KÄLLANDER, H. 1976. Några häckningsdata för blåmes *Parus caeruleus* och entita *P. palustris* i Sydvästskåne. *Vår Fågelvärld* 35: 1-7.
- KENDEIGH, S. C. 1963. Thermodynamics of incubation in the House Wren, *Troglodytes aedon*. *Proc. 13th Intern. Ornithol. Congr.*: 884-904.
- . 1973. Monthly variations in the energy budget of the House Sparrow throughout the year. Pp. 17-44 in *Productivity, population dynamics and systematics of granivorous birds* (S. C. Kendeigh and J. Pinowski, Eds.). Warsaw, Polish Sci. Publ.
- KREBS, J. R. 1970. The efficiency of courtship feeding in the Blue Tit *Parus caeruleus*. *Ibis* 112: 108-110.
- LACK, D. 1950. Family-size in titmice of the genus *Parus*. *Evolution* 4: 279-290.
- . 1955. British tits (*Parus* spp.) in nesting boxes. *Ardea* 43: 50-84.
- . 1958. A quantitative breeding study of British tits. *Ardea* 46: 91-124.
- LARSEN, V. H. 1974. En analyse af yngleresultater hos mejser *Paridae* i Danmark. *Dansk Ornithol. Foren. Tids.* 68: 49-62.
- MERTENS, J. A. L. 1977. The energy requirements for incubation in Great Tits, *Parus major* L. *Ardea* 65: 184-196.
- . 1980. The energy requirements for incubation in Great Tits and other bird species. *Ardea* 68: 185-192.
- PERRINS, C. M. 1979. British tits. London, Collins.
- RICKLEFS, R. E. 1974. Energetics of reproduction in birds. Pp. 152-297 in *Avian energetics* (R. A. Paynter, Ed.). Cambridge, Massachusetts, Nuttall Ornithol. Club.
- ROYAMA, T. 1966. A re-interpretation of courtship feeding. *Bird Study* 13: 116-129.
- VLECK, C. M. 1981. Energetic cost of incubation in the Zebra Finch. *Condor* 83: 229-237.
- , D. F. HOYT, & D. VLECK. 1979. Metabolism of avian embryos: patterns in altricial and precocial birds. *Physiol. Zool.* 52: 363-377.
- WALSBERG, G. E. 1983. Avian ecological energetics. Pp. 161-220 in *Avian biology*, vol. 7 (D. S. Farner, J. R. King, and K. C. Parkes, Eds.). New York, Academic Press.
- , & J. R. KING. 1978a. The heat budget of incubating Mountain White-crowned Sparrows (*Zonotrichia leucophrys oriantha*) in Oregon. *Physiol. Zool.* 51: 92-103.
- , & ———. 1978b. The energetic consequences of incubation for two passerine species. *Auk* 95: 644-655.
- WINKEL, W. 1975. Vergleichend-brutbiologische Untersuchungen an fünf Meisen-Arten (*Parus* spp.) in einem niedersächsischen Aufforstungsgebiet mit Japanischer Lärche *Larix leptolepis*. *Vogelwelt* 96: 41-63, 104-114.