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Ecological energetics of nestling growth in the willow warbler Phylloscopus trochilus

Juha Tiainen

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The daily and cumulative allocation of energy to biomass production, maintenance, and faecal output was studied in nestling willow warblers *Phylloscopus torchilus* L. from hatching to fledging. The daily energy consumption of a willow warbler nestling increases from a minimum of 3.3 kJ on the first day of life to a maximum of about 39 kJ during the last six days of the nestling period. At the same time, the daily gross production efficiency declines from 0.77 to 0.08, the net production efficiency from 0.77 to 0.13, and the assimilation efficiency from over 0.90 to 0.61. Correspondingly, the cumulative energy consumption increases from the initial 3.3 kJ to about 370 kJ at the time of fledging. The gross production efficiency of the cumulative energy budget of a fledgling willow warbler is 0.17, the net production efficiency 0.26, and the assimilation efficiency 0.67. Some comparative data on the wood warbler *Ph. sibilatrix* L. suggest that the assimilation efficiency of this species may be slightly lower than that of the willow warbler.

Physiological thermoregulation is fully developed in willow warbler nestlings at the age of 7 days, but effective thermoregulation is already developing at the age of 4 days. Only males fed the nestlings of two nests before they became able to thermoregulate, the females being concerned with brooding at this time. Later both parents fed the nestlings.

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1. Introduction

In recent years, it has been emphasised that the growth and energy allocation of bird chicks are important components of reproductive strategies (e.g. King 1973, 1974, Ricklefs 1974, O'Connor 1980, Dunn 1980). The energetics of avian offspring are an integral part of the energetics of parent birds until independence of the young. Depending on the mode of development of the chicks, the energetic commitment by parents to their young varies a great deal during the breeding cycle. Precocial chicks require of their parents a larger energetic commitment to the eggs, while altricial chicks require a more extensive energy input from their parents in the form of feeding and brooding (e.g. Lack 1968, Dunn 1980). Dunn (1980) advanced the hypothesis that if the allocation of energy by chicks to basal metabolism, thermoregulation, activity, growth and excrements is variable and "modifiable within a developmental mode, implying variation within species that has been acted upon by selection to produce differences between species, then the evolution of reproductive strategies can involve subtle modifications of nestling energy allocation, and energy budgets of young should be closely adapted to the prevailing ecological and demographic environment".

In this paper, I construct daily and cumulative energy budgets for nestlings of the willow warbler *Phylloscopus trochilus* from hatching to fledging. The nestlings of the willow warbler, a small passerine species, are altricial. They depend on parental feeding, and, before they develop the ability to thermoregulate themselves, on brooding, too. The development of thermoregulation and its consequences on parental behaviour are also described. Some comparative data are presented for components of the energy budgets for two related species, the Chiffchaff *Ph. collybita,* and the wood warbler *Ph. sibilatrix.* The energy budgets of the willow warbler nestlings are compared with those of the altricial nestlings of some other passerine species described in the literature.

2. Material and methods

2.1. Notation

An energy budget can be expressed in terms of consumption (*C*, ingested energy), production (*P*, energy used for tissue growth, fat storage, propagules, etc.), respiratory heat loss (*R*, energy required to perform the internal work necessary to maintain life), faecal waste egestion energy (F), and urinary waste energy (which is included into the faecal sacs in birds, and is not separately indicated here) (see Kleiber 1961, Klekowski & Duncan 1975, Wiegert 1976). These can be summed, as follows:

$$C = P + R + F. \tag{1}$$

The sum of production and respiratory heat loss gives the energy flow or assimilation (A, the metabolisable part of the ingested energy):

$$A = P + R. \tag{2}$$

The proportion of consumption used for assimilation, or $U^{-1} = A/C$, is called the assimilation efficiency, and the proportion used for production, $K1 = P/C$, the gross production efficiency. The proportion of assimilation used for production, $K2 = P/A$, is in turn, called the net production efficiency. The energy budget can be studied, e.g., on a daily basis (with a subscript d in the following), or as cumulative from a defined starting point, which may be the beginning of the year, or from birth or hatching (subscript c in the following).

2.2. Field observations

The nestlings studied were from 102 willow warbler, 17 wood warbler, and 6 chiffchaff nests found in the vicinity of the Lammi Biological Station (61° 03′ N, 25° 03′ E), southern Finland, in 1972–1977.

The field work consisted of daily weighing of the nestlings and any droppings, and nest observations of both the parental and nestling behaviour. The live weight increase of the young has been described in an earlier paper (Tiainen 1978), from which the necessary data will be taken. The droppings were weighed using 5 or 10 g Pesola spring balances to an accuracy of 0.01 or 0.05 g, respectively. Some faeces samples were also collected, and weighed and analysed in the laboratory as described below.

The nestling defaecation rate and parental behaviour were studied from underground hides dug at a distance of 30 cm from the nests. The hide construction was tried at 5 nests, but two nests were destroyed by predators before observations could be made, in one of them the hatching failed because of nonfertilization or early death of the embryo, and the last two were destroyed when the nestlings were 3 and 10 days old, respectively.

The development of endothermy was briefly examined by exposing 4 broods of the willow warbler, 1 brood of the chiffchaff, and 1 brood of the wood warbler at different ages to the ambient temperature (nestlings of willow warblers and chiffchaffs to 24 °C, and of wood warblers to 14 °C). The nestlings were laid on the ground, thus eliminating the insulation of the nest, but they were in slight contact with each other. Body temperatures were measured with a thermoelement inserted deep into the gut.

2.3. Laboratory measurements

Respiratory metabolism and thermoregulation

Measurements of oxygen consumption were started as soon as possible after taking the brood from the nest in order to obtain non-postabsorptive results, matching the ”natural” respiration as well as possible. After tests, the broods were returned to the nests.

An open flow system with a paramagnetic oxygen analyser (Beckman, Model E2) was used for the tests. The analyser was calibrated against a gas mixture of 16 % 0_2 and 84 % N_2, and compressed atmospheric air, which was also used as the oxygen source for the birds. The respiratory CO_2 output was removed from the respiration chamber by soda lime to prevent formation of high CO_2 concentrations. The air flow was kept at about 250 ml/min (the velocity was measured after the chamber), and recorded in connection with each reading of the oxygen analyser. The air was dried before the analyser, but not before the respiration chamber. The relative humidity in the chamber was not controlled. Two 2.7 dm^3 iron chambers were used. They were surrounded by a 3 cm thick space through which water flowed from a water bath of regulated temperature. The whole natural brood was placed in a cup of about nest size lined with soft paper and insulated from the chamber bottom using styrox. It is not known how well the thermal properties of the artificial nest matched those of natural nests. The chamber air temperature was measured with a thermocouple using three measuring points connected in series to give an average. The body temperature of the nestlings was measured before and after each test as described in Sect. 2.2. The chambers were dimmed but not wholly darkened to imitate the natural light conditions.

The measurement periods for young nestlings were only up to about half an hour, but for older birds up to more than two hours. The nestlings could be active during the tests, though not more than naturally when alone in the nest without parental care. The initial water bath temperature was usually 35 °C, and was then gradually lowered. In some cases, the test was begun with an initial low temperature which was then increased. Readings were first recorded 15–30 minutes (sometimes after 10 minutes) after the beginning of the test, as about 10 minutes were needed to washout the chamber air. The results were corrected to standard temperature and pressure (STP). The nestlings were always weighed after the tests, and the data were included in the growth data (see Tiainen 1978). A total of 28 tests were performed on 11 broods (2 broods were used on 5 days, 2 broods on 4 days, 2 broods on 2 days, and the rest once each).

Analysis of carcasses and faeces

Only a few nestlings were killed for the carcass analyses, as it was possible to check the resultant trends by comparison with published information (Ricklefs 1967, 1975, Myrcha & Pinowski 1969, Myrcha et al. 1973, Diehl et al. 1973, O'Connor 1977). The sample consisted of 9 nestlings and 5 juvenile willow warblers, 1 wood warbler nestling, and 1 nestlings and 2 juvenile chiffchaffs. The sample size for faecal analyses (the field collection was supplemented in the laboratory in connection with the respiration measurements) was 96 for the willow warbler, and 9 for the wood warbler nestlings.

All the samples were oven-dried for 3–5 days at 60 °C and then weighed with a Mettler analysis balance, accurate to 1 mg. After homogenization, subsamples were weighed on an electronic microbalance (Cahn, accurate to 1 µg), and incinerated in a muffle furnace for at least 20 hours at 500 °C to obtain the ash percentage. The energy contents were measured by determining the organic carbon contents of the carcasses and faeces using the method of Salonen (1979). The necessary conversion factors from carbon to energy contents were obtained from the relationship between the energy contents Y (kJ/g org. carbon) and carbon percentage X (from the ash-free dry weight) presented by Salonen et al. (1976):

$$Y = 30.67 + 0.29\ X. \tag{3}$$

Five (sometimes only four) replicates were weighed on the Cahn microbalance and combusted at 950 °C under oxygen flow in the presence of a cobalt catalyst. The resultant carbon dioxide was measured with a nondispersive infra-red gas analyser (Hartmann and Braun, Uras 2T). The combustion peak areas shown on a chart recorder were measured using a chart integrator. The carbon analyser was calibrated against oxalic acid. Combustion at 950 °C yields the total carbon of the sample (Salonen 1979). The absence of inorganic

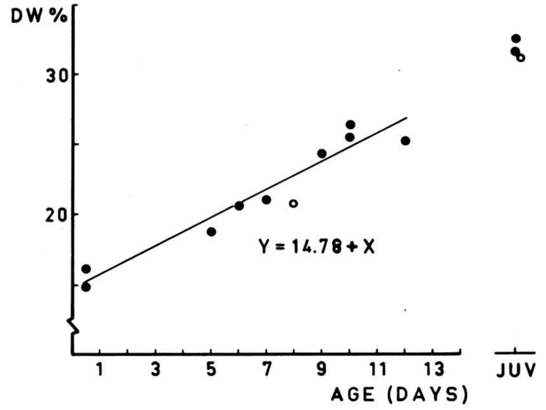

Fig. 1. The dry weight percentage (DW %) of nestling and juvenile willow warblers (black dots) and chiffchaffs (open circles). The regression was calculated only for willow warbler nestlings. $r^2 = 0.942$, the regression coefficient deviates significantly from zero ($p < 0.001$).

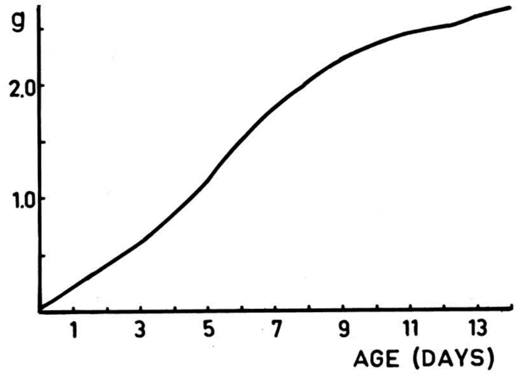

Fig. 2. The dry weight (g) of willow warbler nestlings calculated from the fresh weights (Tiainen 1978) using the regression of Fig. 1.

(carbonate) carbon was proved by combustion of ash from the muffle furnace incineration. The replicates from the faecal material weighed about 1000–2000 μg, and for carcasses about 2000–4000 μg, which normally gave coefficients of variation of less than 2 %, often less than 1 %. Thus, the efficiency of the homogenization was sufficient.

3. Results and discussion

3.1. Production

With the input data of the fresh weight ($W(t)$), the dry weight percentage ($DW\%(t)$), the ash free dry weight, and the carbon contents ($C(t)$), the energy contents ($E(t)$) of a nestling can be calculated from the equation

$$E(t) = W(t) \times DW\%(t) \times 0.01 \times A(t) \times C(t), \quad (4)$$

where $A(t)$ is the conversion factor derived from Eq. (3), and t is the time in days. The daily production can be calculated as the difference between energy contents of an average nestling on two consecutive days:

$$P_d = E(t) - E(t-1), t = 1, 2, \ldots, 14, \quad (5)$$

and the cumulative production since hatching as the difference between the energy contents of a nestling on day t and a newly hatched chick:

$$P_c = E(t) - E(O) \quad (6)$$

The dry matter percentage of the nestlings increases linearly from hatching to the age of 12 days (Fig. 1). Predictions from the fitted regression were inserted into Eq. (4). As the dry weight percentage of the juveniles is higher than that of any nestlings and can be predicted by the regression in a few days after the departure from the nest, the regression was assumed to describe adequately also the dry matter contents of 13–14 day old nestlings, too. Using the live weight data from Tiainen (1978), and the dry weight percentage, the growth of the nestlings can be shown to be continuing at the time of fledging (Fig. 2).

The ash free dry weight percentage of the dry weight shows a slight tendency to decrease between the ages of 5 and 12 days (Fig. 3). Bone ossification is well known to continue for a long time after the birds become independent of their parents (see e.g. Ricklefs 1975), as is also shown by the lower ash free dry weight percentage of juveniles in Fig. 3. The low percentage of 0.5 day old nestlings may, at least partly, be due to their high water content. As R. E. Ricklefs (pers. comm.) points out to me, "The body fluids of birds have about 2 % by weight dissolved salts.

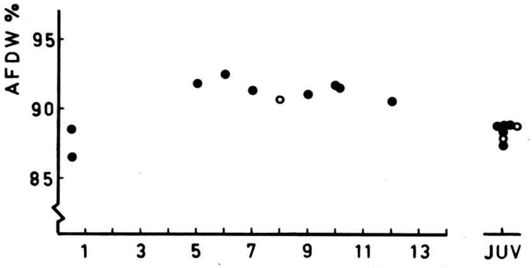

Fig. 3. The ash free dry weight (AFDW) as percentage of the dry weight determined from samples from homogenised carcasses of willow warblers (black dots) and chiffchaffs (open circles) (two replicates for the age 0.5 days, one for the other ages).

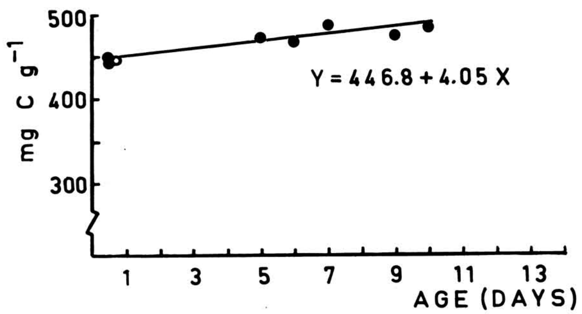

Fig. 4. The carbon contents (mgC g^{-1}) of of willow warbler (black dots) and wood warbler (open circles) nestlings. The regression was calculated only for willow warblers. $r^2 = 0.816$, the regression coefficient deviates significantly from zero ($p < 0.01$).

Before ossification of the bones begins, during the first week or so of the nestling period, changes in body water content could have a marked influence on ash content".

The carbon contents show a slight increase with age (Fig. 4). As a result, the carbon percentage of the ash free dry weights does not show any change, and an average percentage was used to obtain an age-independent conversion factor of 45.7 for Eq. (4). Predictions from the regression (see Fig. 4) were used as the carbon contents in Eq. (4). Thus, the energy contents of a carcass are obtained per dry weight (not per ash free dry weight).

3.2. Development of endothermy and changes in parental behaviour

The development of the endothermy and changes in parental behaviour were studied in order to find out which temperatures would be suitable and ecologically relevant for the measurements of respiratory heat loss.

The youngest nestlings did not yet thermoregulate (Figs. 5 and 6). From the age of 7 days, the body temperature did not decline when the ambient temperature was low. Still at the age of 5 and also 6 days, however, there was a slight decline in the body temperature when the nestlings were taken from the nest and kept apart (Fig. 5). When kept together in the artificial nest in the respiratory chamber, their body temperatures did not decline at the age of 6 days, and they were able to increase their body temperature at the age of 5 days (Fig. 6). The temperature decline in willow warbler nestlings was perhaps not so marked at the age of 4 days as it was in only half a day younger wood warbler nestlings (Figs. 5 and 6).

The 'physiological' age of endothermy, or the age when individual nestlings are fully capable of maintaining their body temperature during exposure to moving air of various temperatures (Dunn 1975, 1976, 1979), is thus about 7 days. The age of 'effective' endothermy, or the age when the brood is capable of thermoregulation in the nest (Dunn 1975, 1976, 1979), is about two

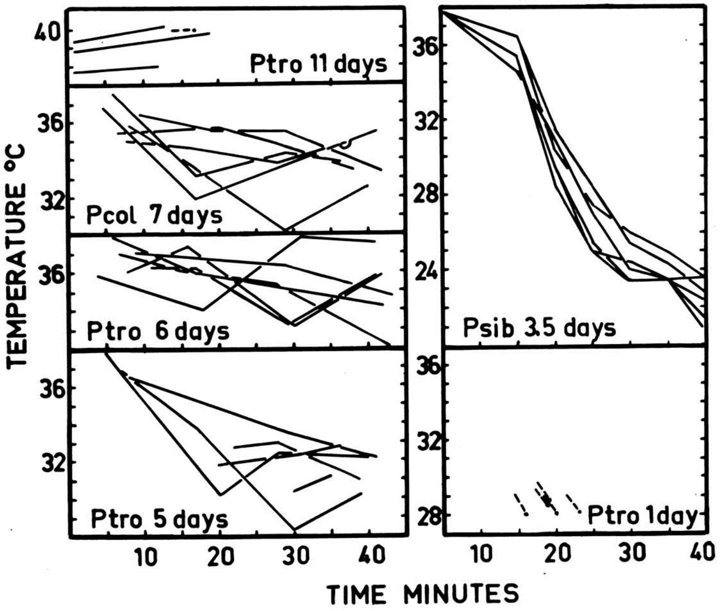

Fig. 5. Changes in the body temperature of willow warbler (Ptro), chiffchaff (Pcol) and wood warbler (Psib) nestlings at different ages (in days) during exposure to low ambient temperatures (24 °C in the case of willow warblers and chiffchaffs, 14 °C in the case of wood warblers). The young were kept individually, but with a slight contact with each other.

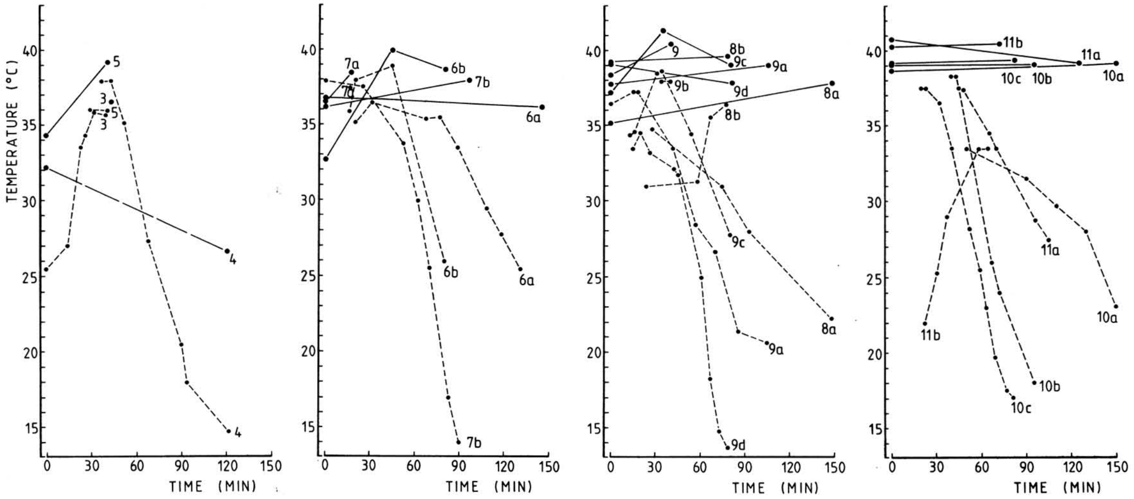

Fig. 6. Changes in the body temperature of willow warbler nestlings (large dots and continuous lines) during the respiration tests with changing ambient (chamber) temperatures (small dots and broken lines). The inserted figures indicate the age (in days) broods used in tests, and lower case letters different broods of the same age. The line of body temperature of the 4 day old brood is interrupted because the initial high ambient temperature is likely to have raised the body temperatures, too. The body temperatures shown are averages of all nestlings of each brood.

days earlier (cf. also Mertens 1969, 1977a, b).

According to the observations at two willow warbler nests, there were clear changes in the parental care of nestlings at the time of development of endothermy in the nestlings (Table 1). Most of the feeding of nestlings was conducted by the male until the age of about 6 days, while the female kept them warm. Afterwards, the female's share in feeding equalled or exceeded that of the male. Brooding was reduced, but the female still brooded for short periods at low ambient temperatures. It also spent the night in the nest at

Table. 1. Share of males and females in feeding at two willow warbler nests. The change in the shares occurst at the time of development of endothermy in the nestlings (see Figs. 5 and 6). There were 6 nestlings in Brood A, and 5 in Brood B. The total feeding rates correspond to those of Kuusisto (1941).

Age of nestlings (days)	Length of the observation period (min)	Feeding visits to the nest					
		No. of visits		Male/ Female	Visits/hour		
		Male	Female		Male	Female	Sum
Brood A							
1	29	4	0	≥4	8.3	0.0	8.3
3	129	11	6[1]	1.9	5.1	2.8[1]	7.9
Brood B							
3	78	13	2	6.5	10.0	1.5	15.5
4	70	12	2	6.0	10.3	1.7	12.0
4	86	14	1	14.0	9.8	0.7	10.5
5	38	8	1	8.0	12.6	1.6	14.2
6	119	22	10	2.2	11.1	5.0	16.1
7	55	4	10	0.4	4.4	10.9	15.3
8	61	9	9	1.0	8.9	8.9	17.7
10	146	11	34	0.3	4.5	14.0	18.5

[1] These observations were made on a very warm day. The female frequently left the nest after having brooded the young for a short time only. It always returned shortly afterwards, but usually without food.

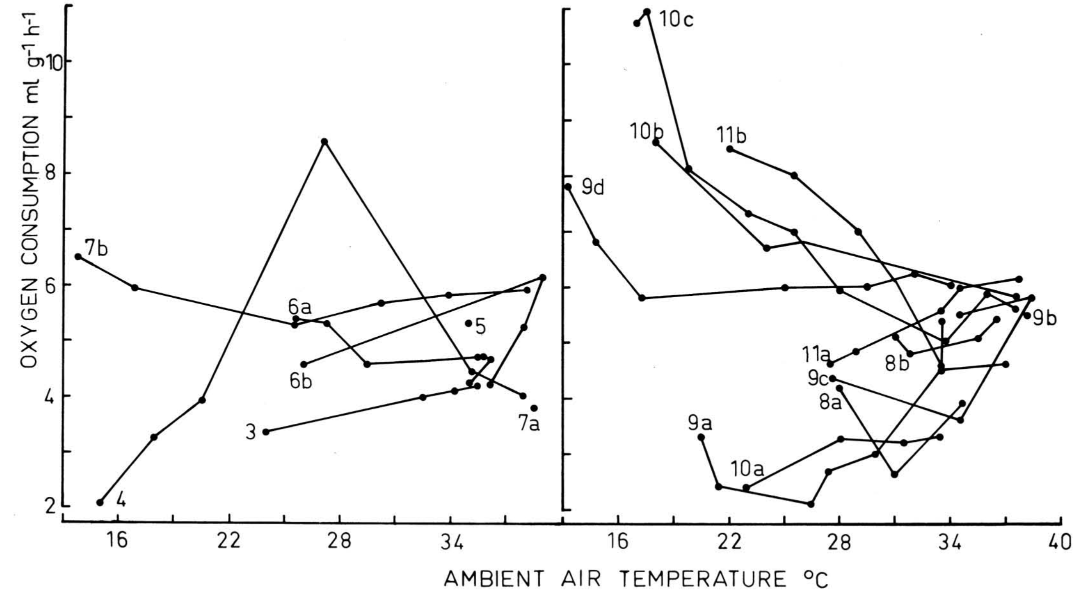

Fig. 7. Oxygen consumption of nestling willow warblers in changing ambient temperatures (see Fig. 6). Ages and broods indicated as in Fig. 6.

least until the young were 9 days old (observations from various nests).

Because of the attentiveness of the female, the temperature experienced by the youngest nestlings may be about the same as that prevailing between the eggs of incubating passerines, i.e. 32–35 °C (Drent 1975). Even after the age of endothermy, they do not experience low temperatures.

3.3. Respiratory heat loss

Measurements of oxygen consumption showed great variation (Fig. 7). This variation was due at least to the following factors.

Age and ambient temperature. Before the age of effective endothermy, the oxygen consumption declined with decreasing ambient temperature. The nestlings were first able to increase their oxygen consumption at the age of 4 days (Fig. 7), but I do not know whether or not their body temperatures remained correspondingly high (Fig. 6). From the age of 6 or 7 days, the nestlings responded to an ambient temperature lower than about 22–30 °C by increasing their internal work and oxygen consumption to compensate for the increased heat loss to the environment (cf. e.g. Dawson & Evans 1957, 1960, Dyer 1968, Dawson & Hudson 1970, Westerterp 1973, O'Connor 1975a, Mertens 1977a). In endothermic nestlings, the highest temperatures caused an increase in the body temperature (Fig. 6), and a thermolytic response could be observed in broods 6b, 7b, 8b, and 9c (Fig. 7).

Locomotory activity and specific dynamic action (SDA). The great differences in the levels of oxygen consumption of different broods were partly due to variable locomotory activity of the nestlings in the respiration chamber. Activity differences may partly have been due to differences in the absorptive state of the nestlings. The nestlings may have been in the postabsorptive state at the end of some long-lasting tests. This may also have increased their locomotory activity. The effect of the locomotory activity and SDA could not be measured with the available equipment.

Brood size. There were four nestlings in broods 10b, 10c, and 11b, and five in 7b, and 9d. The thermoregulatory response of the former three was stronger than that of the latter two (Fig. 7; cf. O'Connor 1975b, Mertens 1977b, Bryant & Gardiner 1979, see also Royama 1966). Due to the small number of tests, the result is not conclusive.

To find the relationship between the oxygen consumption and the age of the young, the lowest values from the thermoneutral zone in Fig. 7 were combined in Fig. 8, where the curve, fitted by eye, was used in the energy budget calculation. In former complete energy budget studies of passerines, with measurements of the respiratory

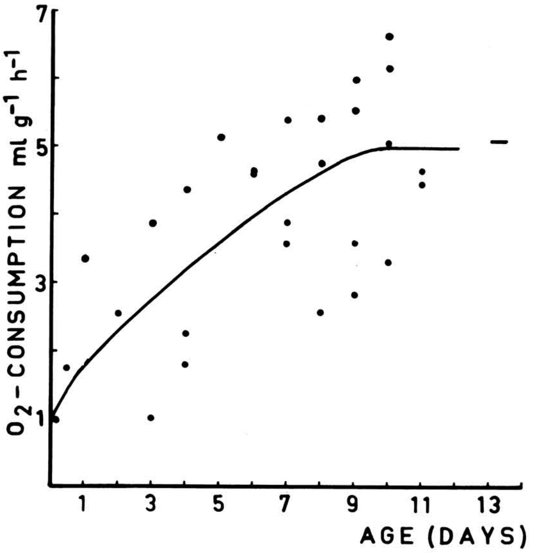

Fig. 8. The dependence of the oxygen consumption of willow warbler nestlings on age. The data were partly derived from Fig. 7 (low values from the thermoneutral zone), and partly from other tests where the birds were kept in constant ambient temperatures at thermoneutrality (about 35 °C, nestling age 0.5–4 days). The curve was fitted by eye. The horizontal bar represents the basal metabolic rate of adult willow warblers during the daytime (from Aschoff & Pohl 1970).

heat loss in the laboratory, Brenner (1968), Myrcha et al. (1972) and Westerterp (1973) used natural nest air temperatures measured above the nestlings, Diehl & Myrcha (1973) a temperature of 25–26 °C (about 6° above the average air temperature at noon), and Blem (1975) 36 °C which was in the thermoneutral zone. Bryant & Gardiner (1979) avoided the problem by making the measurements in field without removing the nestlings from the nest.

I calculated the respiratory heat loss for Eqs. 1 and 2 as follows:

$$R_d = 19.25 \times O_2(t) \times W(t) \times 24, \quad t = 0.5, 1.5, \dots, \ 13.5, \tag{7}$$

and

$$R_c = \Sigma R_d\ , \tag{8}$$

where 19.25 is the conversion factor from oxygen uptake in ml to joules (Petrusewicz & Macfadyen 1970), and $O_2(t)$ the hourly age specific oxygen consumption rate from Fig. 8. Daily changes in the respiratory heat loss were ignored, although preliminary measurements in constant conditions showed a 10 % lower value by night than by day. Blem (1975) and Mertens (1977a) found no such differences in the basal metabolism of house sparrow and great tit nestlings, respectively. In the house martin, the daytime metabolism was 25–99 % higher than night-time metabolism depending on the age of nestlings and the brood size (the difference was greatest in young nestlings and small broods; the significance of external conditions and a probable endogenous rhythm is difficult to interpret) (Bryant & Gardiner 1979). The results of Brenner (1968) on the red-winged blackbird also suggested differences between daytime and night-time metabolism, and Brenner (1964, ref. Bryant & Gardiner 1979) found a 76 % higher metabolic level in the daytime than in the night-time. In adult birds, the basal metabolism is about 25 % higher during the diurnal activity time than during the resting time (Aschoff & Pohl 1970). Ignorance of the diurnal differences in this study should not introduce great errors because the diurnal difference seemed to be small and the night period is short in Lammi (6–7 hours); in addition the oldest nestlings, in which such a rhythm should be most pronounced, also experience low night temperatures when the female no longer remains in the nest at night, and must increase their energy expenditure for thermoregulation. The energy expenditure for metabolism was calculated for the half-day ages (see Eq. 7) to find average values for the daily periods.

3.4. Energy of faecal and urinary waste egestion

The fresh weight of the faeces of the nestlings first increases considerably, but at the age of 8–10 days it decreases due to a decline in the water content (Fig. 9). The dry weight increase is almost sigmoidal, but is adequately described also by two linear regression lines. For the calculation of the waste energy by the equations

$$F_d = DW(t) \times DR(t) \times B(t) \times C(t) \times 17, \quad t = 1.5, 2.5, \dots, 13.5, \tag{9}$$

and

$$F_c = \Sigma F_d\ , \tag{10}$$

predictions for the dry weight ($DW(t)$) were obtained from the regression lines of Fig. 9. The defaecation rate ($DR(t)$) was also found to increase during the first ten days which were covered in the observations (Fig. 10). Predictions from the regression were used for this period. On days 11–14, the rate was assumed to remain unchanged (cf. Lack & Silva 1949, Westerterp 1973, but see also Betts 1955, Gibb & Betts 1963, Royama 1966). The energy contents were determined in a similar way as for carcasses. The carbon contents ($C(t)$) do not change with increasing age of the nestlings (Fig. 11), and neither does the ash-free dry weight, which was an average of 86.45 % of the dry weight. A carbon

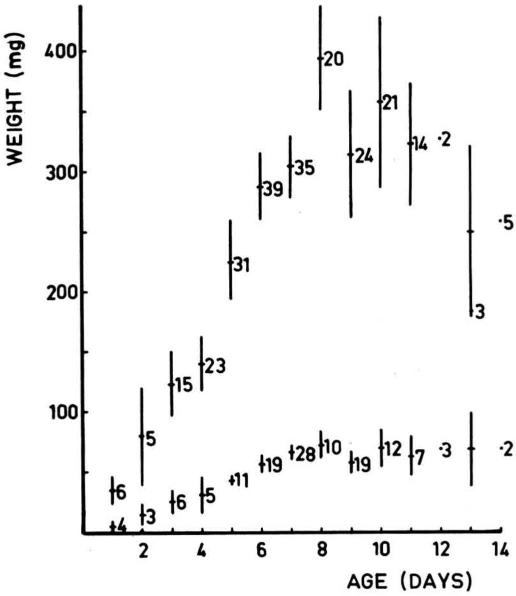

Fig. 9. Fresh and dry weights of faeces of willow warbler nestlings of various ages. Mean, 95 % confidence limits, and number of examined faeces samples given. Lines on day 13 represent means and confidence limits for all the days 12–14 combined. The relationship between the dry weight y and the age x was described by the regression $y = -5.58 + 9.97\,x$ between days 1–8 (calculated from the means, $r^2 = 0.994$, the regression coefficient deviates significantly from zero, $P < 0.001$), and by the mean of 69.20 of weights from days 8–14.

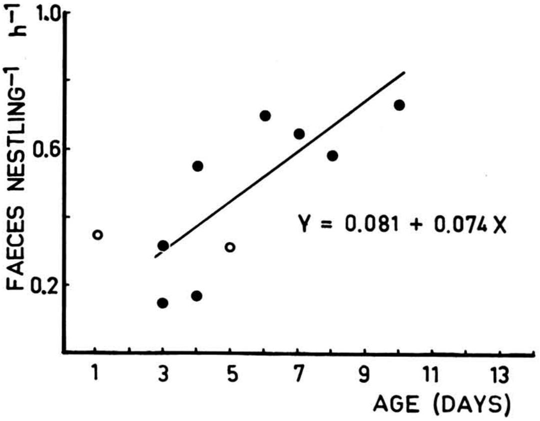

Fig. 10. The defaecation rate of willow warbler nestlings of various ages. Open circles represent observations from short periods of 29 and 38 minutes with only 1 defaecation, and are omitted from the calculation of the regression. $r^2 = 0.832$, the regression coefficient deviates significantly from zero ($P < 0.001$).

percentage of 42.89 % of the ash-free dry weight was thus calculated and inserted into Eq. (3) to obtain a constant conversion factor ($B(t)$) of 43.11. There is some uncertainty in this value, because the carbon percentage is a little outside the range of observations from which Salonen et al. (1976) derived their regression (Eq. (3)). The nestlings were not observed to defaecate between about 20–21.00 hours and before 03–04.00 hours, except for some older nestlings which sometimes defaecated once during the night (cf. Tiainen 1978). Thus, 17 hours were assumed to represent the daily period of defaecation. The faecal waste energy was calculated for half days to get average values to depict the daily values. The nestlings were usually observed to defaecate for the first time at the age of 1 day. The faeces are, of course, generated in the intestine from the beginning of digestion, but this is disregarded in the present energy budget calculations.

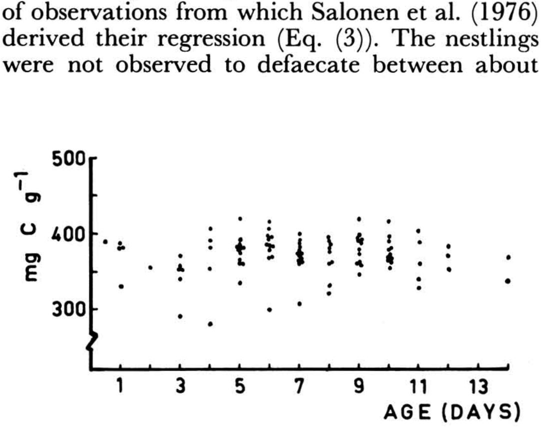

Fig. 11. The carbon contents of the faeces of Willow Warbler nestlings. The dependence on age is described by the mean of 370.8 from all determinations.

3.5. The energy budget

The daily and cumulative energy budgets were constructed using Eq. (1) with the data from Eqs. (5), (7), and (9), and Eqs. (6), (8), and (10), respectively.

The daily energy consumption (Fig. 12) of a nestling increases from about 3.3 kJ on the first day to a maximum of about 41 kJ on the 9th day, and then remains almost unchanged during the rest of the nestling period. Production continues throughout the nestling period, in spite of a levelling off of the live weight at the age of about 11 days (Tiainen 1978), which is due to decreasing water percentage (Fig. 1). The daily gross production efficiency $K1_d$ drops gradually from the initial 0.77 through 0.09 on day 10 to 0.08 at the end of the nestling period. Similarly, the net production efficiency $K2_d$ decreases from the initial 0.77 through 0.15 on day 10 to 0.13 at the end of

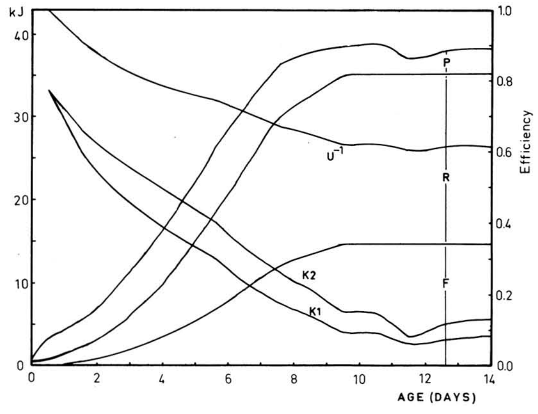

Fig. 12. The daily energy budget of an average willow warbler nestling. The symbols are as follows: P production, R respiration, F faeces, U^{-1} assimilation efficiency, K1 gross production efficiency, and K2 net production efficiency.

the nestling period. Besides the increase in the dry matter percentage, feathers are still being produced at the time of fledging (Gwinner 1969, Tiainen 1978). Later, the young begin their post-juvenal moult and fat deposition (Gwinner 1969). Thus, the daily production of juveniles does not cease during their stay at the birth grounds (cf. Tiainen 1983a, b). The assimilation efficiency U^{-1}_{d} decreases from the initial value of over 0.90 toa relatively constant 0.61 on the last third of the nestling period. This decrease in the assimilation efficiency is most probably due to early maturation of the alimentary canal, the relative mass of which decreases with maturation of other tissues (O'Connor 1977).

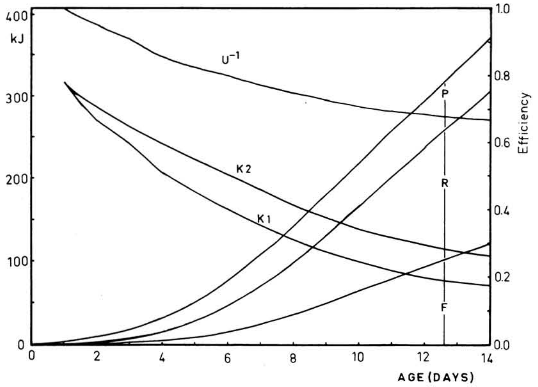

Fig. 13. The cumulative energy budget of an average willow warbler nestling. The symbols are like in Fig. 12.

In the earlier paper (Tiainen 1978), it was found that young in large broods grew faster, but remained lighter than young in small broods. This was interpreted by probable differences in parental behaviour. The present study offers an alternative, more plausible explanation, which, though based on few observations, was supported by information available in literature (see Sections 3.2 and 3.3.). At the time of developing endothermy, the nestlings' capacity for effective thermoregulation was somewhat poorer in small than in large broods. This may delay the time when the female gradually increases her share in feeding the young, and thus decrease the amount of food for the young. Moreover, after the capability for thermoregulation has developed, young in small broods must allocate more energy to thermoregulation than young in large broods, which tends to decrease their net production efficiency (*K2*). Young in small broods have, however, the advantage that their parents are more likely to be capable to satisfy the increasing energy requirements when they are growing, which is the requirement of higher fledging weights.

About 370 kJ is needed to grow one fledgling willow warbler (Fig. 13). Of this, 17 % is allocated to the production ($K1_{c}$), and 67 % to the assimilation (U^{-1}_{c}). Twenty-six per cent of the total assimilation (A_{c}) is allocated to the production ($K2_{c}$).

The willow warbler is the smallest species in which nestling bioenergetics have hitherto been studied. Only slight interspecific differences can be found in the allocation of energy to growth and maintenance or the proportion of waste energy among passerines with the exception of the house martin whose cumulative net production efficiency is clearly higher than that of other species (Table 2; the higher daily net production efficiency of the house martin and willow warbler in the beginning of life than of other species may be due to differences in the time span considered). Other differences in Table 2 may be due to methodological differences, or they may reflect differences in the ability to assimilate and convert to biomass the food provided by the parents, or, in the case of the redbacked shrike and sparrows, by researchers (Kendeigh et al. 1977, Dunn 1980). In any case, the hypothesis of Dunn (1980) that "nestling energy budgets are molded by natural selection, correlate to adult reproductive strategy, and can reflect adaptation to selective pressures on a species" are supported by the data on the house martin, willow warbler and starling, the three species whose nestlings were fed by the parents with natural food. Of these species, the different house martin nestlings have developed

Table 2. Bioenergetic efficiencies of nestlings of some passerines. Daily gross ($K1_d$) and net ($K2_d$) production efficiencies are indicated separately for the beginning of life after hatching (A) and for the end of the nestling period (B); the respective cumulative production ($K1_c$ and $K2_c$) and the assimilation (U^{-1}) efficiencies are given only for the end of the nestling period. The efficiencies for the end of the nestling period can be compared only roughly, because the young leave the nest at somewhat different stages of development.

	$K1_d$		$K2_d$		$K1_c$	$K2_c$	U^{-1}	Source
	A	B	A	B				
Delichon urbica	—	—	0.74	0-0.10	—	0.42-0.43[1]	—	Bryant & Gardiner 1979
Phylloscopus trochilus	0.77	0.08	0.77	0.13	0.17	0.26	0.67	This study
Lanius collurio	0.35	0-0.14	0.50	0-0.17	0.20	0.30	0.70	Diehl & Myrcha 1973
Sturnus vulgaris	—	—	—	0.11	0.14	0.22	0.64	Westerterp 1973
Passer domesticus	0.40	0-0.10	0.65	0-0.10	0.15-0.17	0.19-0.20	0.78-0.85	Myrcha et al. 1972
	0.30	0.10	0.50	0.16	0.15	0.23	0.67	Blem 1975
Passer montanus	0.40	0-0.10	0.65	0-0.10	0.16-0.18	0.21-0.24	0.75-0.76	Myrcha et al. 1972

[1] For brood sizes 2 and 5. For brood sizes 3 and 4 the respective efficiencies were 0.37 and 0.42 (all figures for the 21st day, fledging on 25th day).

the capacity to store fat for accommodating unpredictable fluctuations in the parental feeding capacities, while the other two have not. Thus the differences in energy budgets reflect differences in the nestling growth and brood size determination strategies (O'Connor 1978, 1980). The study of Bryant & Cardiner (1979) on the house martin also demonstrated some intraspecific variation in, at least, the net production efficiency as a consequence of the brood size (see the footnote to Table 2).

3.6. Ecological energetics of the Wood Warbler and Chiffchaff nestlings

The data gathered are not sufficient for construction of complete energy budgets of wood warbler and chiffchaff nestlings. Their live weights have been described in an earlier paper (Tiainen 1978). Figures 1, 3, and 4 suggest that the carcass composition of these species is similar to that of the willow warbler. The preliminary measurements of the oxygen consumption also suggest that there are no great differences in the metabolism of the three species. The carbon contents of the faeces of wood warbler nestlings averaged at 389.3 ± 28.8 ($\bar{x} \pm SD, N = 9$) which is significantly higher than that of willow warbler nestlings (t-test, $P < 0.001$). This results in the higher conversion factor of 43.73. The dry weight is proportionally the same as in the willow warbler faeces. Thus, if the defaecation rate of wood warbler nestlings is not lower than that of willow warblers, their assimilation efficiency is slightly lower. This, together with the fact that wood warbler nests are not lined with feathers like those of the willow warbler and chiffchaff, thus probably providing inferior insulation, may be of importance to the determination of the northern limit of its range (cf. Haftorn 1978). The northern limit of the distribution of the wood warbler in Finland is several hundred kilometres further south than that of its two related species.

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