BIOENERGETICS OF NESTLING RED-BACKED SHRIKES (*LANIUS COLLURIO*)

BARBARA DIEHL
AND
ANDRZEJ MYRCHA

Polish Academy of Sciences
Institute of Ecology
Dziekanów Leśny
Poland

This study was undertaken in connection with the productivity studies of grassland ecosystems. Only a few papers exist on bioenergetics of nestlings throughout the nestling period (Kendeigh 1939; Dawson and Evans 1957, 1960; Brenner 1964, 1968; Royama 1966; Korodi Gál 1969; Myrcha et al. 1972). In this paper, production and metabolic rate were estimated, and, using these data, assimilation and consumption were calculated.

The breeding season of the Red-backed Shrike (*Lanius collurio*) in central Poland occurs from mid-May to mid-July. The average clutch size is five eggs. The nestling period averages 15 days. The body weight at fledging is less than the average adult weight, 30 g. More detailed data on nestling development and biology of the species are presented by many authors (Schreurs 1936, 1941; Böni 1942; Durango 1956; Münster 1958; Havlin 1959; Korodi Gál 1969).

MATERIALS AND METHODS

A total of 13 broods containing 59 individuals was examined. They were collected from the Strzeleckie Meadows in the Kampinos Forest near Warsaw (52° 20′ N, 20° 50′ E), between 19 June and 5 July. The Red-backed Shrike is one of the dominant species there. Broods were removed from the nests in the meadow and carried in other nests to the laboratory. One nestling in each brood was always left within the nest to prevent the parents from abandoning the nest.

When the day of hatching was unknown, the age of nestlings was estimated by comparing their weights and feather development on consecutive days of life with previously established patterns (Diehl, unpubl. data).

Metabolic rate was calculated from metabolism tests lasting 1.5–2.0 hr in an open-flow respirometer (Diaferometer, Kipp and Zonen) in which oxygen consumption and carbon dioxide production were measured concurrently. The air flow rate was 0.86 liter/min. The tests were conducted before noon, at a constant air temperature of 25–26°C. This temperature was about 6°C above the average air temperature in Strzeleckie Meadows at that time. Nests containing broods were placed inside the respirometer chamber. The oldest nestlings were tested singly at 14–15 days of age, the age that they leave the nest. Usually, 15–30 min passed between removing the nestlings from the nests in the meadow and placing them in the respirometer chamber. At the beginning of the tests the nestlings did not beg, which proved that at least the young nestlings had been well fed by the parents. Since older nestlings show fear responses to humans, their lack of begging is not as readily explained. The youngest nestlings slept during nearly the entire experimental period. The oldest usually perched motionless but were awake and anxious.

For each day of nestling life two to three broods were examined. A total of 38 metabolism tests was made throughout the nestling period (15 days), including 31 tests on broods of five birds (average brood size in the Strzeleckie Meadows), 3 tests on four-bird broods, and 4 tests on single individuals. Small variation in the brood size in the Strzeleckie Meadows prevented consideration of variations in metabolic rate related to brood size; such variations are significant (Mertens 1969).

Immediately after the respiration tests, the temperature of nests containing nestlings, and cloacal body temperature of nestlings, were measured with a thermistor thermometer, type 4416, from the Thermophil Co. The measurements were taken to the nearest 0.1°C, at the same ambient temperature of 25–26°C. The temperature in the nest bowl was calculated as a mean of six measurements: two at the top edge, two at the side wall, one at the bottom, and one above the nest. The body temperature was taken by inserting the thermometer 0.5 cm into the cloaca. Finally, each nestling was weighed to the nearest 0.01 g and then returned to the nest from which it had been collected.

In order to obtain some additional information on the rate of homeothermy development, the cloacal body temperatures of five broods exposed to four or five different ambient temperatures, ranging from 11–34°C, were taken.

Metabolic rate is expressed in ml O_2/g/hr, in Kcal/bird/24 hr, and in Kcal/kg$^{3/4}$/24 hr. The expression of metabolic rate on a per day basis is an abstraction that is useful only for comparative purposes. The total heat production will be less than the value calculated from daytime measurements because of the nocturnal decrease of metabolic rate (Brenner 1964; Lewis and Dyer 1969; Hudson and Kimzey 1964; West and Hart 1966; Aschoff and Pohl 1970).

The instantaneous energy balance of an individual on successive days of development was calculated according to the equation: $A_i = P_i + R_i$, where A_i is instantaneous assimilation, P_i is instantaneous production, and R_i is instantaneous respiration (Petrusewicz 1967; Klekowski 1970). The instantaneous consumption C_i was calculated from the formula $C_i = A_i/0.70$, where 0.70 is the average assimilation coef-

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TABLE 1. Average body weight, metabolism, respiratory quotient and rectal body temperature in nestling Red-backed Shrikes at an ambient temperature of 25–26°C.

Age (days)	No. of broods	Brood size	Avg. body weight (g)	RQ	Metabolism ml O_2/g/hr	Metabolism cal/g/24 hr	Metabolism Kcal/ $kg^{3/4}$/24 hr	Rectal body temperature (°C)
1	2	5	3.2	0.70	1.88	203	81.25	28.6
2	3	5	5.1	0.72	2.75	304	103.33	30.8
3	3	5	7.6	0.71	2.92	355	112.50	33.8
4	2	5	10.3	0.75	3.38	398	132.26	35.8
5	2 + 1	5 + 4	12.7	0.75	4.13	437	154.17	37.3
6	2	5	15.4	0.75	4.27	484	173.26	38.4
7	3	5	18.6	0.72	2.58	306	116.33	39.2
8	3	5	20.9	0.72	2.75	318	120.91	39.9
9	1 + 1	5 + 4	22.7	0.70	3.12	337	131.90	40.1
10	3	5	24.3	0.72	3.19	348	137.40	40.6
11	2	5	25.5	0.71	3.11	355	143.65	40.1
12	2	5	26.3	0.70	3.01	341	138.00	40.8
13	2 + 1	5 + 4	24.9	0.70	3.22	348	139.84	40.6
14	3	1	24.5	0.71	3.79	380	151.22	40.6
15	1 + 1	5 +1	22.5	0.70	4.79	455	176.72	40.3

ficient for nestlings of this species (Diehl 1971). The energy content of the daily change in body weight was calculated as the difference between body energy content on consecutive days. The body energy content was calculated by multiplying the body weight by caloric value of 1 g of body weight of *L. collurio* on consecutive days (Diehl et al. 1972). Consumption was calculated in grams from the known caloric value of food, which averaged 1.6 Kcal/g fresh weight (Myrcha, unpubl. data; Diehl 1971).

The cumulative energy balance (A_c, R_c, P_c) and cumulative coefficient of production efficiency (Klekowski 1970) of an average brood of five nestlings, throughout the nestling period of 15 days, were calculated from the elements of the instantaneous energy balance of an individual on consecutive days according to the general formula $X_t = \sum_{i=1}^{t} X_i$.

RESULTS

BODY WEIGHT AND PRODUCTION

The body weight of nestling Red-backed Shrikes as a function of time followed a sigmoid curve. It ranged from 2.5 g at hatching to a maximum of 26.3 g at 12 days of age, and then decreased to 22.5 g at fledging (table 1). The relative growth rate was highest at 3 days when it approximated 50% of the value of the preceding day.

The instantaneous production rate (table 3) was 0.64 Kcal/nestling/24 hr at the age of 1 day, reached the maximum of 6.96 Kcal/nestling/24 hr at 10 days, and then declined.

NEST AND BODY TEMPERATURES

The nest and body temperatures increased with the growth of nestlings from a level near the ambient temperature of 25–26°C on the first days (fig. 1, table 1).

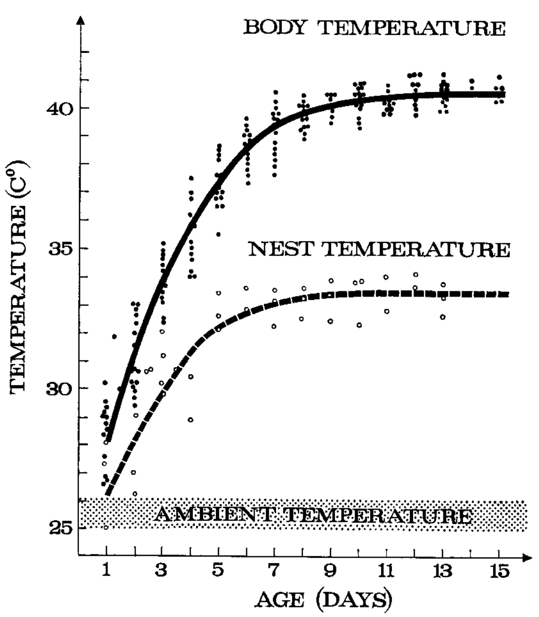

FIGURE 1. Cloacal body temperature in nestling Red-backed Shrikes and nest temperature at 25–26°C.

The nest temperature stabilized on day 6 at about 33°C, which was about 8°C above the ambient temperature. This difference indicates the insulative value of the nest, which is different for various species. Brenner (1964) found that the nest temperature of the Red-winged Blackbird (*Agelaius phoeniceus*) was 4.8°C above the ambient temperature of 25.3°C.

The body temperature stabilized on day 10 at about 40.5°C, which was about 8°C above the nest temperature. Brenner (1964) found

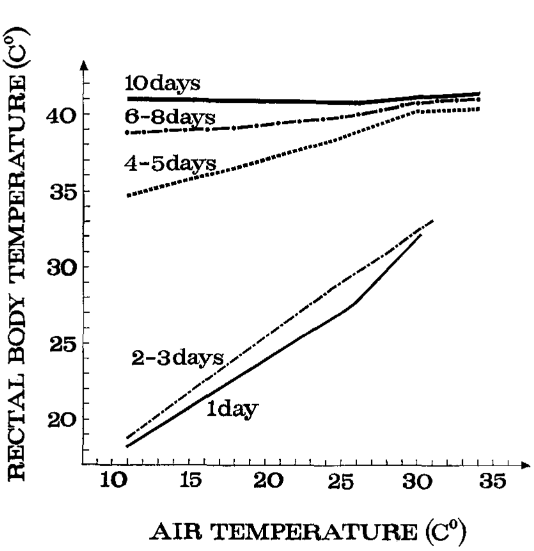

FIGURE 2. Relation of cloacal (rectal) body temperature to ambient temperature in nestling Red-backed Shrikes.

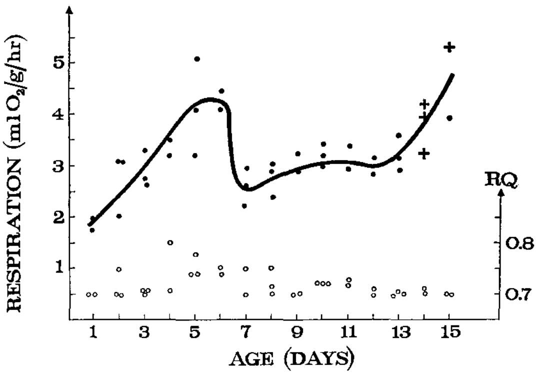

FIGURE 3. Respiration (dark circles and crosses) and respiratory quotient (open circles) in nestling Red-backed Shrikes. Each point represents a single measurement for a brood; each cross represents an individual tested singly. The solid line is drawn through the averages for each age.

the same difference between body and nest temperatures for the Red-winged Blackbird. Rectal body temperature of nestlings exposed to different ambient temperatures was independent of them also on day 10 (figure 2). The same result was reported by Böni (1942). The body temperature of 40.5°C is within the range reported for other small passerines (King and Farner 1961). Böni (1942) found similar body temperatures in nestling Red-backed Shrikes at an ambient temperature of 25°C, but starting from 13 days of age. Also the body temperatures during the first few days were lower than those in our test, and the rate of body temperature increase was more rapid than in our nestlings of the same age. These differences may be due to the differences in keeping nestlings: Böni kept them singly; we kept them in broods.

METABOLISM

Oxygen consumption per unit of body weight changed with age of the birds (table 1, fig. 3). It increased from 1.9 ml O_2/g/hr on the first day to about 4 ml O_2/g/hr on the 6th day. On the 7th day a sudden decrease by about 40% of the value on the preceding day was observed. It coincided with the rapid transition toward homeothermy reported by Böni (1942), so it may be due to a qualitative change of the body responses to ambient temperature. Then, a rapid increase in oxygen consumption took place during the last few days before fledging, up to 4.8 ml O_2/g/hr on the 15th day. The average value throughout the nestling period was about 3.26 ml O_2/g/hr. A similar value can be seen from the curve of oxygen consumption for nestling Red-winged Blackbirds at the ambient temperature of 25°C (Dyer 1968).

The respiratory quotient (RQ) was 0.70–0.72 throughout the nestling period, except on days 4–6 when it reached 0.75 (table 1, fig. 3). The RQ values reported for other species were higher (Kendeigh 1939; Dyer 1968; Myrcha et al. 1972).

The daily metabolic rate (table 2) calculated for the newly hatched nestlings was about 0.65 Kcal/bird/24 hr. On the 6th day it reached 7.5 Kcal/bird/24 hr, and on the 7th day suddenly decreased by 25% of the previous day's value. On the day of fledging it was about 10 Kcal/bird/24 hr, or 455 cal/g/24 hr. This value was higher than the standard metabolic rate theoretically predicted for adult birds of the same body weight from the Lasiewski and Dawson equation (1967), which is 8.27 Kcal/bird/24 hr, and exactly the same as that from the Aschoff and Pohl equation (1970) for daytime, which is 9.97 Kcal/bird/24 hr.

Metabolic level, i.e., following Kleiber's (1961) definition of daily heat production of an individual divided by the metabolic body size, was calculated from Kleiber's (1961) equation: $M = k\ W^{3/4}$, where M is the basal metabolic rate, W is body weight, and k is constant. It is expressed in Kcal/kg$^{3/4}$/24 hr.

Metabolic level in nestling Red-backed Shrikes (table 1) was comparatively low on the first day, about 81 Kcal/kg$^{3/4}$, but on the second day it exceeded 100 Kcal/kg$^{3/4}$/24 hr and then fluctuated between 116 and 177 Kcal/kg$^{3/4}$/24 hr. The latter value approximates that which can be calculated from the formula: $M = 140.9\ W^{0.704}$ reported by As-

TABLE 2. Production, metabolism, assimilation and production efficiency coefficient $K_{2i} = Pi/Ai \times 100$, in nestling Red-backed Shrikes.

Age (days)	Production/ P_i/Kcal/ nestling/ 24 hr	Respiration/ R_i/Kcal/ nestling/ 24 hr	Assimilation/Kcal/ nestling/ 24 hr	$P_i/A_i \times 100$
1	0.64	0.65	1.29	49.61
2	1.33	1.55	2.88	46.18
3	2.07	2.70	4.77	43.39
4	4.12	4.10	8.22	50.12
5	2.60	5.55	8.15	31.90
6	5.39	7.45	12.84	41.97
7	6.08	5.70	11.78	51.61
8	6.96	6.65	13.61	51.13
9	4.12	7.65	11.77	35.00
10	3.70	8.45	12.15	30.45
11	2.27	9.05	11.32	20.05
12	1.14	8.97	10.11	11.27
13	–2.02	8.67	6.65	–30.37
14	1.99	9.30	11.29	17.62
15	–1.52	10.25	8.73	–17.41

For numbers of nestlings see table 1.

TABLE 3. Consumption in nestling Red-backed Shrikes.

Age (days)	Consumption			
	Kcal/ nestling/ 24 hr	cal/g/ 24 hr	g/nestling/ 24 hr	% of body weight
1	1.84	575	1.15	35.9
2	4.11	806	2.57	50.4
3	6.81	896	4.26	56.0
4	11.74	1140	7.33	71.2
5	11.50	905	7.18	56.5
6	18.34	1191	11.46	74.4
7	16.83	905	10.53	56.6
8	19.44	930	12.14	58.1
9	16.81	740	10.49	46.2
10	17.36	714	10.84	44.6
11	16.17	634	10.10	39.6
12	14.44	549	9.02	34.3
13	9.50	381	5.93	23.8
14	16.13	658	10.07	41.1
15	12.47	554	7.78	34.6
Total	193.49	11,578	120.85	
Average	12.90	772	8.06	48.2

choff and Pohl (1970) for the daytime metabolic rate in adult passerine birds. Metabolic levels of nestling Tree Sparrows (*Passer montanus*) and House Sparrows (*Passer domesticus*) considerably exceeded 200 Kcal/kg$^{3/4}$/24 hr during the last part of the nestling period (Myrcha et al. 1972). It is assumed that these differences may reflect the differences in the physiological development rate of nestlings of various passerine species.

ENERGY BALANCE OF THE NESTLING PERIOD

Components of the instantaneous energy balance are presented in table 2 (production, metabolism and assimilation) and in table 3 (consumption). The highest assimilation rate occurred in the middle of the nestling period, i.e., between days 6 and 10. During the same period, the consumption was about 18 Kcal/bird/24 hr, or about 896 cal/g/24 hr, assuming the assimilation coefficient of 70%. The average consumption throughout the nestling period was about 13 Kcal/bird/24 hr, or about 770 cal/g/24 hr. This represents about 8 g of food per bird per day, or about 48% of average body weight. For smaller broods, containing two nestlings each, the food consumption found in feeding experiments averaged 56% of the average body weight (Diehl 1971). Korodi Gál (1969) found, using the "collar method," that food consumption in nestling Red-backed Shrikes averaged 6.65 g/bird/24 hr, or about 36% of average body weight. The middle of the nestling period, days 6–10, showed the greatest difference in results. Korodi Gál recorded the lowest food consumption during this period, about 35% of average body weight, whereas in this paper calculated consumption was the highest, and averaged 56% of the body weight. In this paper we assumed a constant average assimilation coefficient of 70%, which might partially explain this difference. The data for Tree Sparrows and House Sparrows (Myrcha et al. 1972) indicate that the assimilation coefficient changes with age of nestlings and reaches its highest value in the middle of the nestling period.

The instantaneous coefficient of production efficiency, $K_{2i} = Pi/Ai \times 100$, was very high during the first half of the nestling period, up to 50% (table 2), but it rapidly decreased after day 9. At the end of the nestling period the energy losses in metabolic processes exceeded the energy assimilated from food.

Cumulative energy balance for one nestling is presented in figure 4. Cumulative production of body weight increased most quickly at the age of 5–11 days. After 15 days, it reached 39 Kcal/bird. Cumulative assimilation increased quickly and rather steadily and reached 135 Kcal/bird after 15 days of development. The cumulative production efficiency coefficient, $K_{2c} = Pc/Ac \times 100$, was about 45% during the first half of the nestling period, then it gradually decreased to about 29% after 15 days. This indicates that tissue production

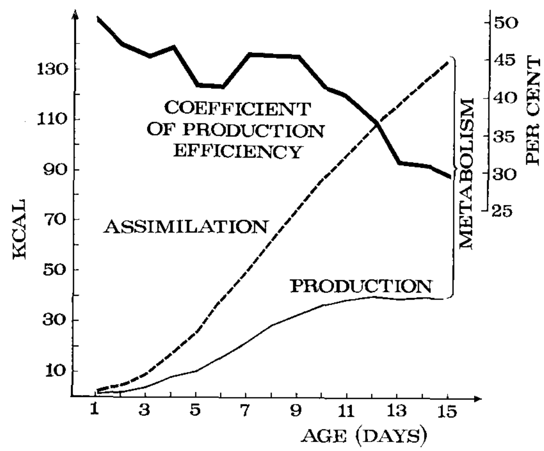

FIGURE 4. Cumulative production, assimilation and coefficient of production efficiency in nestling Red-backed Shrikes.

in nestlings is a very efficient process. To produce 1 Kcal of body tissue, 3.5 Kcal of energy must be assimilated. This index is slightly lower in nestling Tree and House Sparrows (Myrcha et al. 1972).

The cumulative energy balance of an average brood size of five nestlings throughout the nestling period, expressed in Kcal/5 nestlings/15 days, was: production, 194.3; metabolism, 483.4; assimilation, 677.7; assimilation coefficient, 70%; and consumption, 968.1. This consumption is equivalent to about 600 g of fresh food.

DISCUSSION

Extrapolation of the data presented here on experimental birds to those in the field would require additional studies. It was found that nestlings without effective thermoregulation are maintained at near normothermic adult temperatures in the nest by parental brooding (Baldwin and Kendeigh 1932; Irving and Krog 1956; Brenner 1964; Ricklefs and Hainsworth 1968). Nestling Red-backed Shrikes are brooded without interruption for the first few days after hatching (Münster 1958). This implies that their body temperatures during this period, and thus metabolic rates, are higher under natural conditions than in our tests. The increase in the metabolic rate at the end of the nestling period may be partially due to the behavioral responses of the nestlings, which show fear of humans at 11 days of age (Münster 1958).

According to Brenner (1964), heat production during the day is higher than at night; in nestling Red-winged Blackbirds it is 2.91 and 1.65 cc O_2/g/hr, respectively. Thus, the ratio between the day and night metabolic rate is 1.76. Assuming a similar ratio for nestling Red-backed Shrikes, our data on oxygen consumption have been recalculated for 15 hr of daytime and RQ = 0.74. In this case the average daily metabolic rate was 307 cal/g/24 hr; a value is comparable to the 282 cal/g/24 hr found by Brenner (1964).

Shilov (1968) distinguished two qualitatively different stages in nestling development. Based on our data, it is also possible to distinguish two stages in the nestling period of the Red-backed Shrike: the first from hatching to 7–8 days of age; the second from 7–8 days of age to fledging. In the first stage, nestlings have no effective thermoregulation. It is replaced by parental brooding allowing the nestlings to develop under presumably optimal temperature conditions. Thus, they can use most of their assimilated energy for rapid growth. During the second stage, nestlings have effective thermoregulation. Brooding is limited to very short periods of time, and a great amount of assimilated energy is used for heat production. The rate of growth decreases. Plumage development (sheaths of primaries split open at 7 days of age), increase in body size, and huddling of the nestlings prevent too rapid metabolic heat loss.

The nestlings had their highest energy requirements in the middle of the nestling period. Under unfavorable nutritive conditions, i.e., during cold and rainy weather, this period may limit brood size. The average daily metabolic rate for fledglings is about 50% greater than that for nestlings measured throughout the nestling period (Diehl 1971). Fledgling Red-backed Shrikes are fed exclusively by parents for some time after leaving the nest. If it can be assumed that the normal clutch size corresponds with the average number of young that the parents can raise (Lack 1954), bioenergetics during the fledgling period may limit clutch size. The importance of this period for other passerines has been stressed by Royama (1966) and Ricklefs (1968).

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