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PRODUCTIVITY INVESTIGATION OF TWO TYPES OF MEADOWS IN THE VISTULA VALLEY

XII. ENERGY REQUIREMENT IN NESTLING AND FLEDGLING RED-BACKED SHRIKE (*LANIUS COLLURIO* L.)

(Ekol. Pol. 19:235–248). Daily food consumption of the Red-backed Shrike averaged 56% of the mean body weight for nestlings and 50% for fledglings Gross energy intake was 15.9 kcal/nestling/day, and 22.8 kcal/fledgling/day. Average daily metabolic rate was 8.4 kcal/nestling/day and 14.9 kcal/fledgling/day. Food consumption and metabolic rate were largely affected by the ambient temperature. Amount of food consumed by young birds until a month of age in the Red-backed Shrike population was 3.5 mg fresh weight of insects per day per m^2.

This paper is an attempt to estimate food consumption in the Red-backed Shrike (*Lanius collurio* L.) population in Strzeleckie Meadows, near Warsaw. A feeding experiment was made to determine food consumption for young birds under outdoors conditions. Using these data and the field data on the population size, the food consumption of young birds per day and per m^2 was calculated.

MATERIAL AND METHODS

Nestling Red-backed Shrikes were collected from Strzeleckie Meadows in 1968. 6 individuals at 3–29 days of age (Tab. I) were kept for 7–20 days in the period of 24 June–13 July.

Age of the nestlings was determined partly on the basis of known hatching day, partly due to the earlier fixed pattern of body weight and feather development in consecutive days of life.

The number and age of experimental birds

Tab.I

No. of individual	Age		
	nestlings (days)	fledglings	
		growing (days)	not growing (days)
1	3–9	—	–
2	3–9	–	–
3	9–15	16–19	20–28
4	10–16	17–21	22–29
5	11–15	16–21	22–28
6	10–14	15–18	19–27

All nestlings were placed in natural nests in groups of 2 individuals in each of them. The nest containing 2 youngest nestlings, which have not effective thermoregulation (Böni 1942, Diehl and Myrcha in press), was placed in an incubator at 37°C. It was kept outdoors at the time of feeding young, that is about every half hour for some minutes. Under natural conditions the youngest nestlings are brooded by a female (Münster 1958). It appeared that the environmental conditions in the incubator were not convenient for the nestlings, which were weakened and grew much slower then under natural conditions. One of them died at the seventh day of keeping, the second one was not kept any longer. Two nests containing the older nestlings, having the ability to regulate body temperature, were kept outdoors, under natural conditions of temperature and photoperiod. Average daily air temperature during the experiment ranged from 13.2 to 25.9°C (Fig. 1), with a mean of 18.9°C. It approximated air temperatures in Strzeleckie Meadows during the breeding period (June-July).

There was not difficulty with keeping the older nestlings. They left the nest at 15–17 days of age, thus like under natural conditions. The first few days after fledging they were kept in a large outdoor pen, then they lived free in the garden adjacent to a forest, thus under environmental conditions similar to that in which Shrikes can settle themselves. They were being supplied with

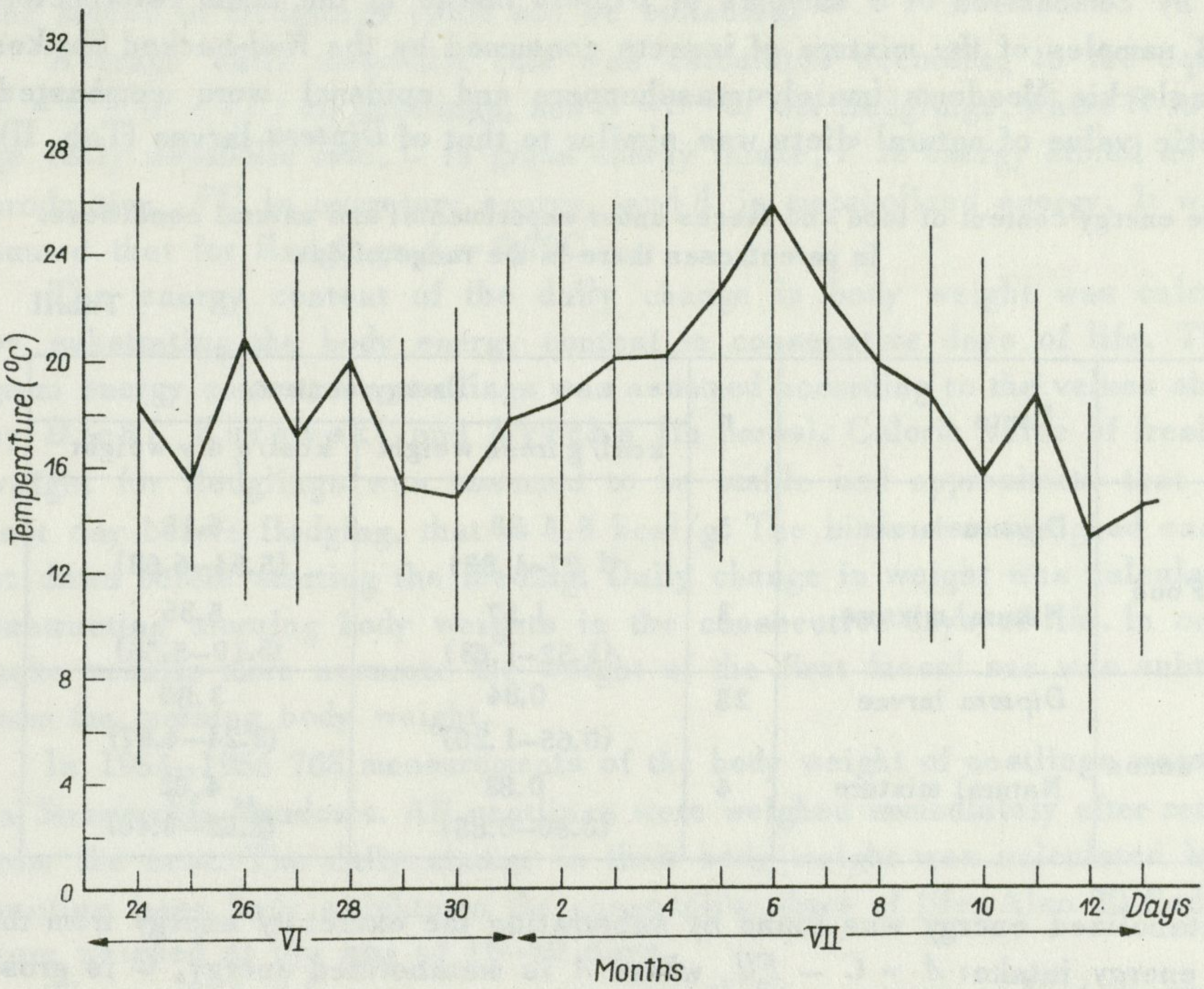

Fig. 1. Average daily air temperature during the feeding experiment. The vertical lines indicate the range of data

food until reaching full independence, thus until the age of 45 days. In nature fledglings are fed by their parents also for a month or so, during which they gradually come to feed themselves and to acquire independence.

The expermimental birds were not afraid of people. It was possible to catch them at any moment to take measurements. Measurements were taken until the fledglings were 29 days of age, ie., until self-feeding began.

Daily energy requirement was determined by measurement of food consumption. The birds were fed on *Diptera* larvae, for 15–16 hours every day – since dawn to twilight. In nature they are mainly fed on insects and spiders living in litter and on grasses. Feeding frequency and size of food items were influenced by the reponse of the young. They begged extremely violently when they were short of food and much less when they were well fed. The only exception represent the first 4 days of experiment when the feeding frequency of 4 older nestlings did not follow the frequency of begging. This resulted in lost in their body weight.

Food items were weighed every day. The caloric value of food was determined by combustion of 5 samples of *Diptera* larvae in the bomb calorimeter. Also 3 samples of the mixture of insects consumed by the Red-backed Shrikes in Strzeleckie Meadows (mainly grasshoppers and spiders) were combusted. Energetic value of natural diets was similar to that of *Diptera* larvae (Tab. II).

The energy content of food and faeces under experimental and natural conditions. In parentheses there is the range of data

Tab.II

	Diets	*n*	Energy content	
			kcal/g fresh weight	kcal/g dry weight
Food	*Diptera* larvae	5	1.58 (1.27–1.83)	6.15 (5.54–6.68)
	Natural mixture	3	1.57 (1.52–1.63)	5.35 (5.19–5.55)
Faeces	*Diptera* larvae	28	0.84 (0.65–1.20)	3.80 (3.24–4.87)
	Natural mixture	4	0.83 (0.80–0.88)	4.02 (3.82–4.40)

Metabolized energy was found by substrating the excretory energy from the gross energy intake: $A = C - FU$, where A is metabolized energy, C is gross energy intake, FU is excretory energy including the wastes from both the alimentary tract and kidneys. This difference represents existence and production energy.

Energy loss in the excreta was found by multiplying its energy content by the fresh weight of faeces voided during the day. The energy content of the excreta was determined by combustion of 28 samples of faeces voided during the whole day. Also 4 samples of faeces voided by the nestlings fed by their parents were combusted. Energetic values of faeces under experimental and natural conditions were similar (Tab. II).

Faecal sacs were weighed immediately after voiding. In order to obtain the more accurate results, the weight of the first faecal sac was subtracted from the total weight of faeces voided during the day and added to the weight of faeces voided the previous day. There is the possibility of an error here due to the fact that certain little amount of faeces was voided between two succesive feeding. In such a case it was not known to which of 2 nestlings in the nest it belonged. Normally the young defecated only immediately after being fed.

Average digestive efficiency was calculated as the percentage ratio of metabolized energy to gross energy intake. It was assumed that digestive efficiency for fledglings was similar to that for nestlings, that is 70%, because the faeces of fledglings could not be collected.

Average daily metabolic rate was calculated according to the equation: $R = C - (P + FU)$ for nestlings, and $R = A - P$ for fledglings, where R is average daily metabolic rate, C is gross energy intake, P is energy stored as tissue production, FU is excretory energy, and A is metabolized energy. It was assumed that for fledgings $A = 0.70C$.

The energy content of the daily change in body weight was calculated by substrating the body energy content in consecutive days of life. The per gram energy content for nestlings was assumed according to the values obtained by Diehl, Kurowski and Myrcha (in press). Caloric value of fresh body weight for fledglings was assumed to be stable and approximate that at the last day before fledging, that is 1.8 kcal/g. The birds were weighed each day at dawn before starting the feeding. Daily change in weight was calculated by subtracting morning body weights in the consecutive days of life. In order to make results more accurate the weight of the first faecal sac was subtracted from the morning body weight.

In 1964–1966 768 measurements of the body weight of nestlings were taken in Strzeleckie Meadows. All nestlings were weighed immediately after removing from the nest. The daily change in their body weight was calculated by subtracting mean body weights in the consecutive days of life. Also 20 fledglings were weighed at the age of 16–30 days.

The method of least squares was used to fit equations of food consumption and metabolic rate data, measured in calories per gram weight of bird per day (cal/g/day).

The data were grupped into 3 age classes: nestlings, growing fledglings, and fledglings that reached the mean body weight of adults (about 30 g). The weight fluctuation within the last group were less than 4% of their mean body weight.

RESULTS

Body weight

Mean body weight of the nestlings under natural conditions followed the typical sigmoid growth curve (Fig. 2). The body weight increased by 1.7 g/day. Under experimental conditions the growth rate was lower and averaged 1.5 g/day.

There was no difference in the rate of gain in weight of fledglings under natural and experimental conditions (Fig. 2).

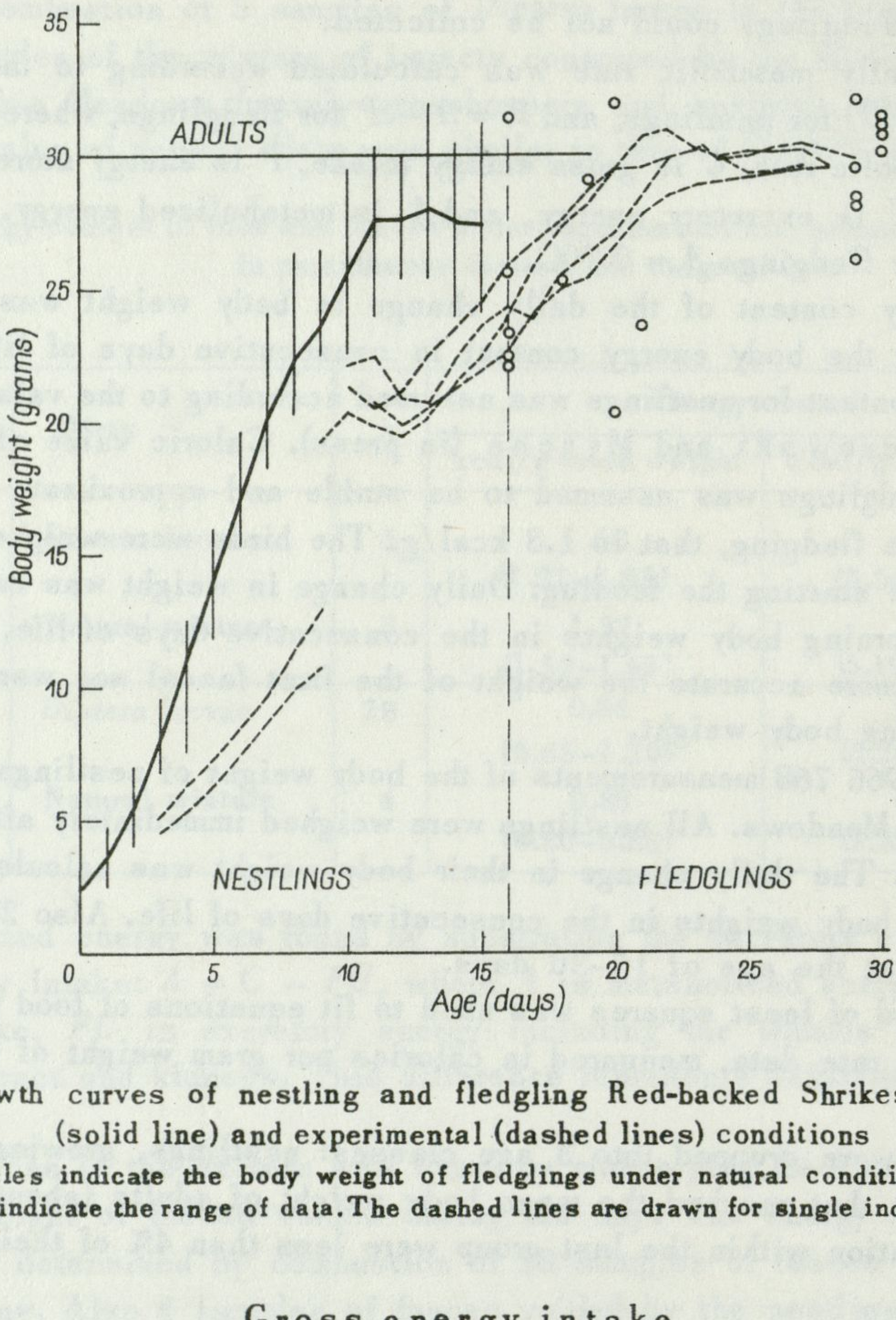

Fig. 2. Growth curves of nestling and fledgling Red-backed Shrikes under natural (solid line) and experimental (dashed lines) conditions

The open circles indicate the body weight of fledglings under natural conditions. The vertical lines indicate the range of data. The dashed lines are drawn for single individuals

Gross energy intake

Nestlings. The food consumption under experimental conditions in the nestling period averaged 9.5 g fresh weight/nestling/day or approximately 56% of the mean body weight (Tab. III). Average gross energy intake approximated 0.9 kcal/g fresh body weight/day.

These results exceed by about 20% those obtained by Korodi Gál (1969). He found, using the "collar method", that average daily food consumption during the nestling period under natural conditions represents about 36% of nestling body weight. It seems that the higher consumption under experimental conditions could be an outcome of greater heat loss resulting from small number of nestlings in the nest (Royama 1966, Mertens 1969). The mean brood size under natural conditions is 5 nestlings/brood. The absence of brooding under experimental conditions also could resulted in the increase of food requirement;

The average daily food consumption and metabolic rate in nestling and fledgling Red-backed Shrike under experimental conditions

Tab. III

Age classes		n	Average body weight /g/	Food consumption				Metabolism	
				g/bird/day	% of body weight	kcal/bird/day	cal/g fresh weight/day	kcal/bird/day	cal/g/day
Nestlings		38	16.5 (4.5–24.5)	9.5 (8.6–15.7)	56.0 (40–78)	15.0 (3.1–26.5)	910 (64–125)	8.4 (0.6–1.8)	510 (110–830)
Fledglings	growing	19	26.9 (22.7–28.5)	14.3 (10.6–17.9)	55.5 (42–74)	23.0 (17.0–28.6)	880 (670–1110)	14.4 (10.4–18.2)	550 (380–670)
	not growing	30	29.7 (28.8–30.9)	13.8 (8.3–17.7)	46.6 (27–59)	22.3 (13.2–28.3)	750 (530–1000)	15.1 (9.9–20.5)	510 (320–690)
	average	49	28.3 (22.7–30.9)	14.0 (8.3–17.9)	50.0 (27–74)	22.8 (13.2–28.6)	800 (430–1110)	14.9 (9.9–20.5)	530 (320–690)

under natural conditions nestlings are brooded until 10 days of age (Münster 1958). Part of the differences in results probably account for climat which is more severe in Poland than in Rumania. Using the oxygen consumption data (Diehl and Myrcha in press) it was calculated that average daily consumption for nestlings at 25–26°C approximated 48% of their body weight. This value exceeds only by 12% that obtained by Korodi Gál.

Fledglings. Daily food consumption for fledglings averaged 14 g fresh weight/bird/day, or 50% of mean body weight (Tab. III). There was a clear relationship between daily gross energy intake and average daily air temperature. The regression line for the fledgling that reached the mean body weight of adults (Fig. 3) was described by the equation: $C = 1284.6 - 28.5\ T$ ($r = 0.79$, $n = 30$), where C is gross energy intake in cal/g/day, T is mean daily air temperature in °C. The daily energy requirement in this group of birds, at an average daily air temperature in Strzeleckie Meadows during the breeding period of about 18°C, averaged 770 cal/g fresh body weight/day, or 22.9 kcal/fledgling/day. The energy content of natural food averaged 1.6 kcal/g fresh weight.

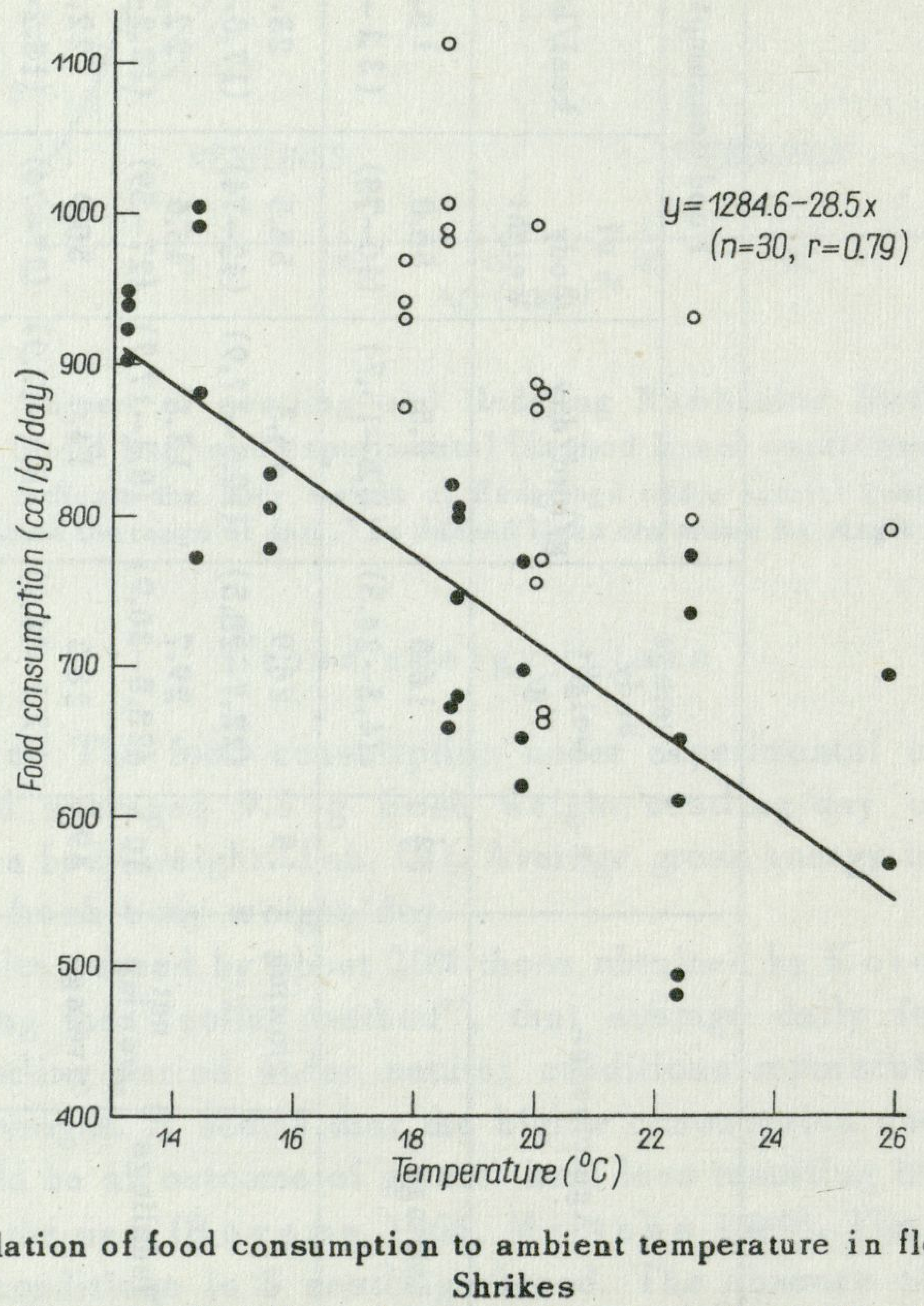

Fig. 3. The relation of food consumption to ambient temperature in fledgling Red-backed Shrikes
Solid circles indicate the fledglings that reached mean body weight of adults. Open circles indicate the growing fledglings. The regression line is drawn only for solid circles

Thus the young that have already reached the body weight of adults but are still being fed by their parents must consume 14.4 g of food, or 48% of body weight. This is the food requirement of free-living, thus normally active birds.

The younger fledglings, which were still growing, consumed more food per unite of body weight than the older ones, especially at the lower ambient temperature (Fig. 3), but the food consumption per individual was approximately the same for both age classes (Tab. III).

Metabolized energy

The average digestive efficiency for nestlings was 70%, with extremes of 60 and 80%.

There are few data on digestive efficiency of natural food for insectivorous birds. Gibb (1957) found that digestive efficiency of adult Coal Tits (*Parus ater* L.) on a diet of mixed insects consisting of caterpillars, weevils, *Hemiptera* and spiders was approximately 67%. This is the value similar to that obtained in this experiment for nestlings. Thus the digestive efficiency of 70% may be supposed to approximate to that under natural conditions.

Respiration

Nestlings and fledglings. Weight specific metabolic rate was 510 cal/g/day for nestlings and 530 cal/g/day for fledglings (Tab. III). Fluctuation in metabolic rate were affected by air temperature (Fig. 4). For nestlings

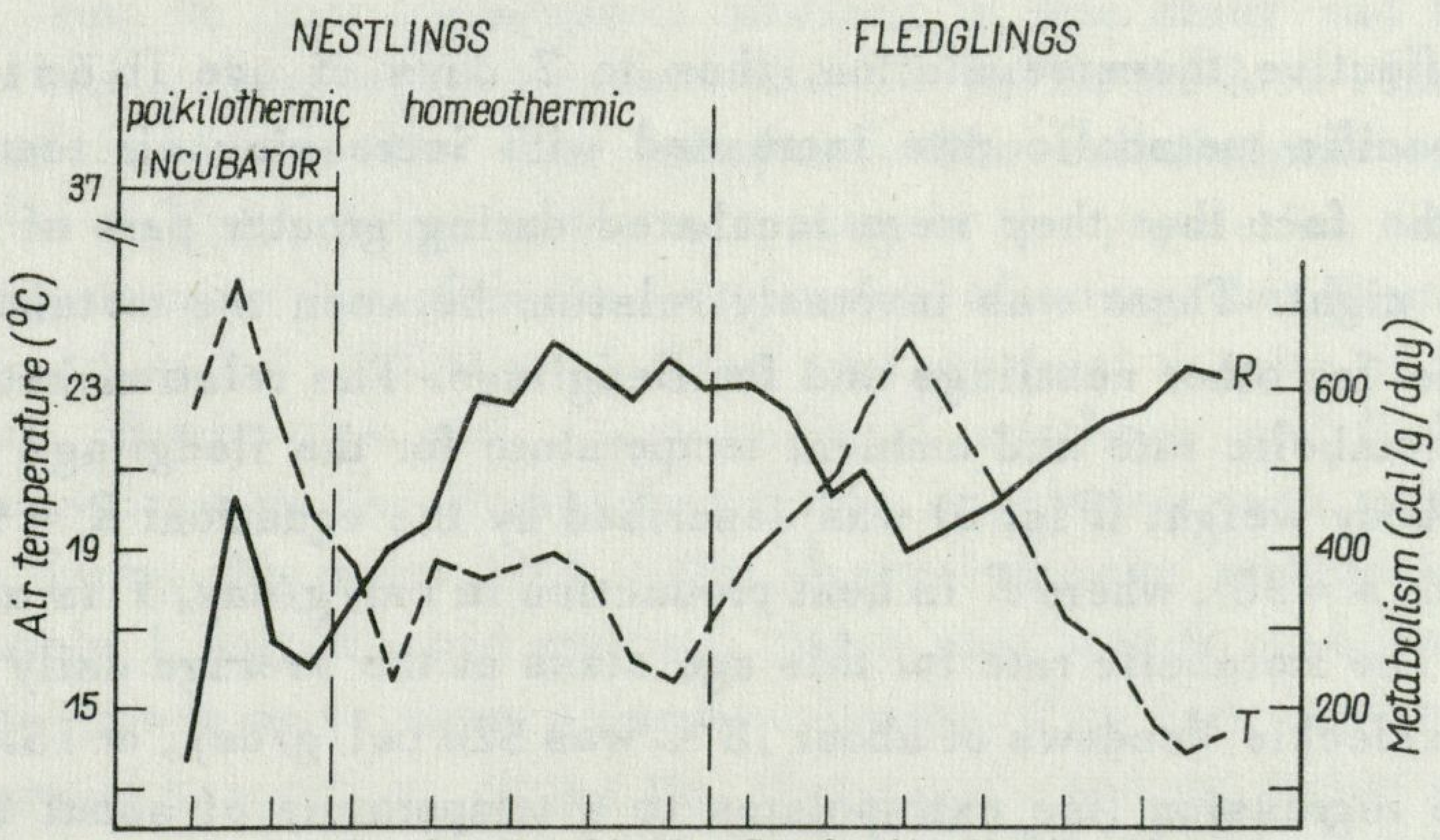

Fig. 4. The relation of metabolic rate (solid line) and ambient temperature (dashed line) in nestling and fledgling Red-backed Shrikes

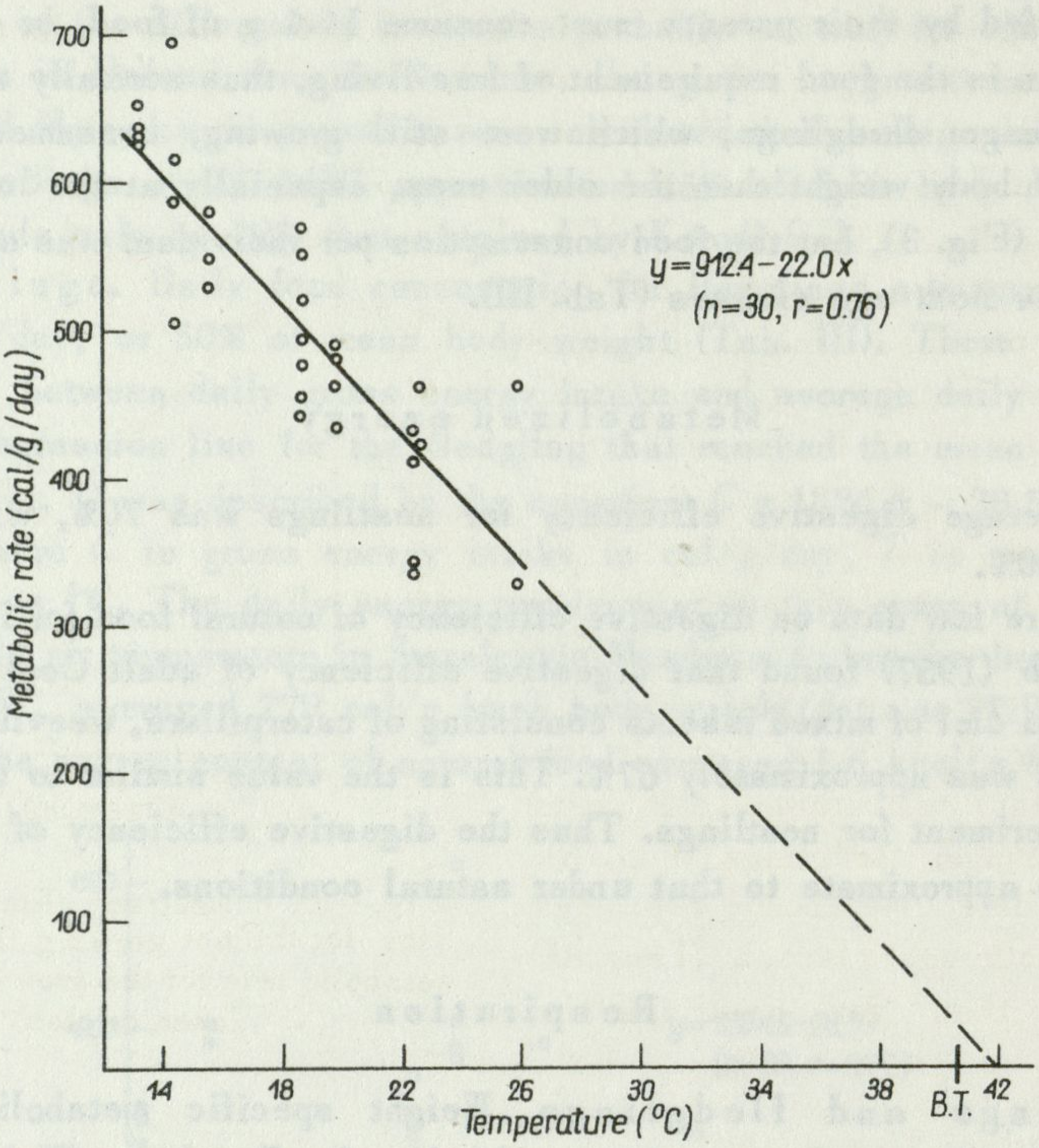

Fig. 5. The relation of metabolic rate to ambient temperature in the fledgling Red-backed Shrikes that reached mean body weight of adults

without effective thermoregulation, thus to 7 days of age (Böni 1942), the weight specific metabolic rate increased with increasing air temperature, in spite of the fact that they were incubated during greater part of the day and the whole night. There was inversely relation between the metabolic rate and temperature for other nestlings and for fledglings. The relation between weight specific metabolic rate and ambient temperature for the fledglings that reached the adult body weight (Fig. 5) was described by the equation: $R = 912.4 - 22.0\ T$ ($r = 0.76$, $n = 30$), where R is heat production in cal/g/day, T is air temperature in °C. The metabolic rate for this age class at the average daily air temperature in Strzeleckie Meadows of about 18°C was 520 cal/g/day, or 15.4 kcal/bird//day. The regression line extrapolates to a temperature of about 42°C at zero metabolism, thus above the usual level of body temperature, which is about 40.5°C (Diehl and Myrcha in press).

The limits of the zone of thermal neutrality for the Red-backed Shrike are not known. Theoretically predicted standard energy metabolism of a 30 g bird, calculated according to the equation presented by Lasiewski and Dawson (1967): $M = \log 129 + 0.724 \log W \pm 0.113$, where M is heat production in kcal, W is body weight in kg, and the ± value represents the standart error of estimate of $\log M$, would be 10.2 kcal/bird/day, or 340 cal/g/day. This is the value similar to that of free-living birds energy metabolism obtained in this paper for the oldest fledgling at about 26°C (Fig. 5). Thus it can be expected that this temperature is within the range of thermoneutral zone.

The weight specific metabolic rate of growing fledglings at the higher ambient temperatures approximated to that of older fledglings, but at the lower ambient temperatures it was higher for younger fledglings (Fig. 6).

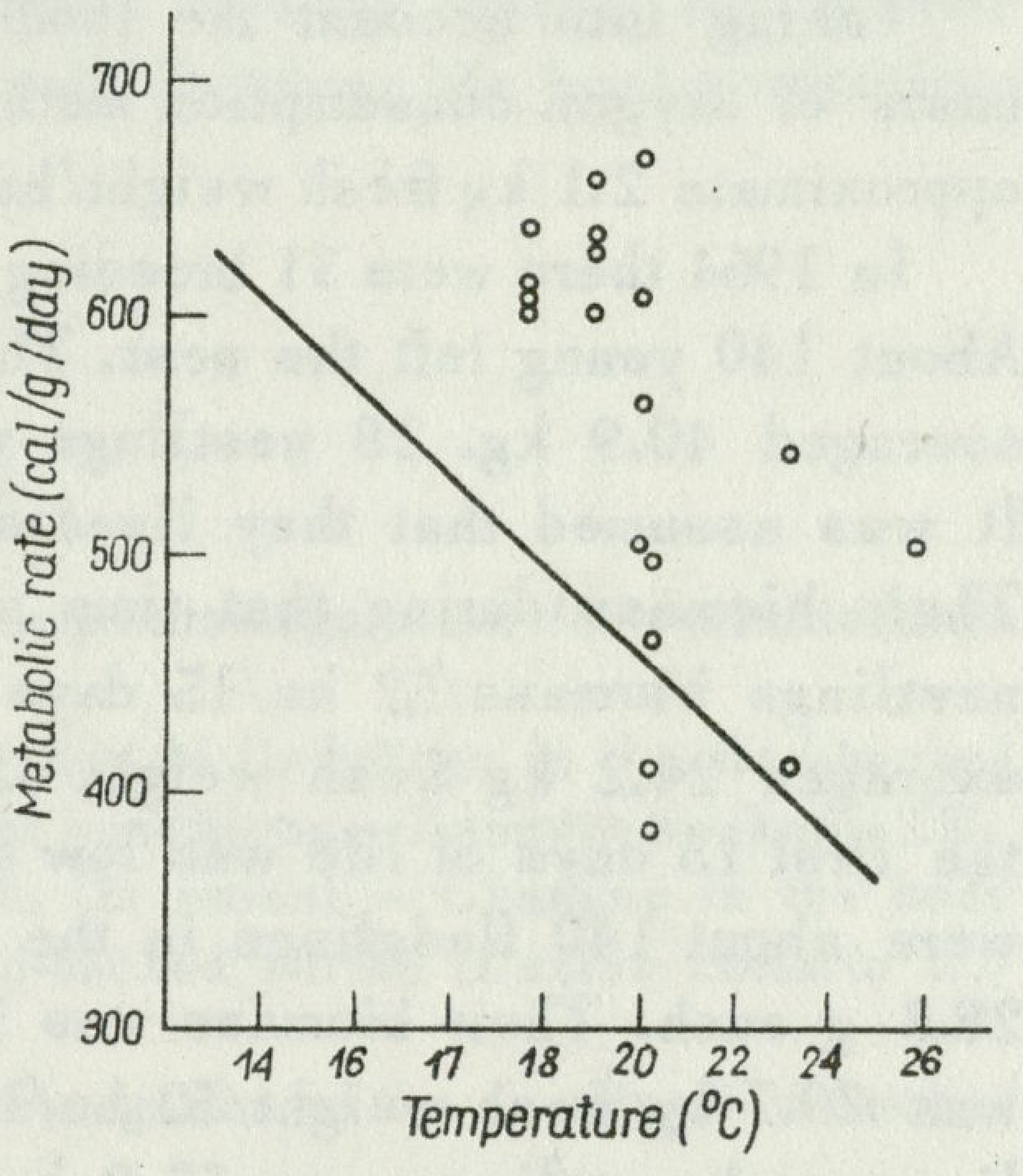

Fig. 6. A comparison of the regression line for the not growing fledglings and metabolic rate for the growing fledglings (open circles)

Average daily metabolic rate was similar for both age classes (Tab. III) and higher than for nestlings by about 50%.

Food requirement in the nestling and fledgling Red-backed Shrike population

Using the data on food consumption obtained in this study and those on the population size in Strzeleckie Meadows (Diehl 1971), the food consumption per day and m^2 of the meadow was calculated. The calculations were done not only for the really existing number of young in the population during one of the breeding seasons but also for that number of young that theoretically could existed within the population if there were maximal density of breeding pairs, maximal clutch size and no mortality of nestlings and fledglings.

Field observations on the Red-backed Shrike population were made in an area of 52 ha during the years 1964–1970. Maximal density of breeding pairs was approximately 1 pair/ha, and maximal clutch size was 6 eggs/clutch. On the basis of the growth curve under natural conditions (Fig. 2) it was calculated that the biomass of 6 nestlings during the 15 days of nestling period would be 1.7 kg. The food consumption for nestlings averaged 56% of body weight, thus, in our case, 1 kg fresh weight/ha/15 days. The biomass of 6 fledglings, weighing approximately 28.3 g each, during the next 15 days, that is when they are fed exclusively by parents, would be 2.5 kg. The food consumption for fledglings was about 50% of body weight, thus about 1.3 kg fresh weight/ha/15 days.

Total maximally possible food consumption for nestlings and fledglings until the age of a month would be 2.3 kg fresh weight of insects/ha/month, or 7.7 mg fresh weight/m²/day.

Taking into account the food consumption for nestlings calculated on the basis of oxygen consumption method (C = 48% of body weight), the value would approximate 2.1 kg fresh weight/ha/month, or 7.0 mg/m²/day.

In 1964 there were 31 breeding pairs, or about 0.6 pairs/ha in the study area. About 140 young left the nest. Their biomass during 15 days of nestling period averaged 40.9 kg. 28 nestlings were lost at different age due to predation. It was assumed that they lived approximately a half of their nestling period. Their biomass during that time averaged 2.3 kg. Thus there were 43.2 kg of nestlings biomass/52 ha/15 days within the population, and food consumption averaged 24.2 kg fresh weight/52 ha/15 days. The fledgling mortality during the first 15 days of life was low and was not included in calculations. So there were about 140 fledglings in the population during the next 15 days, weighing 28.3 g each. Their biomass was 59.4 kg/52 ha/15 days, and food consumption was 29.7 kg fresh weight/52 ha/15 days. The total food consumption for fledglings and nestlings was 53.9 kg fresh weight/52 ha/month, or 3.5 mg fresh weight/m²/day.

If the food consumption calculated on the basis of oxygen consumption method is considered, this value would average 50.4 kg fresh weight/52 ha//month, or 3.2 mg fresh weight/m²/day.

The food consumption of adult birds should be added in order to obtain more accurate data on food consumption in the population. Assuming that it is not less than that for the fledglings that reached the constant body weight, the obtained values of food consumption would increase by approximately 1.7 mg fresh weight/m²/day.

DISSCUSION

Average daily food consumption for fledglings, during the period when they are fed exclusively by parents was greater than that for nestlings under experimental conditions by about 50%. This difference is still greater if to compare the data for fledglings with those found by Korodi Gál (1969) for nestlings under natural conditions. If it can be assumed that the normal clutch size corresponds with the average number of young that the parents can raise (Lack 1954) the period of the first fortnight after fledging would be of basic importance for the clutch size of the Red-backed Shrike. Especially it seems that the first few days after fledging are the most critical period, because at the low ambient temperature both metabolic rate and daily energy requirement showed a significant increase at that time.

This increase is probably due to the fact that fledglings after leaving the nest had most feathers in growth; the length of primaries at the day of fledging approximated 3 cm, for fledglings with constant body weight – 5–6 cm, for adults – 7 cm. Also their body surface compared to body volume was greater than for older fledglings. These both factors could increase the heat production to maintaine constant body temperature.

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BADANIA PRODUKTYWNOŚCI DWÓCH TYPÓW ŁĄK W DOLINIE WISŁY

XII. ZAPOTRZEBOWANIE ENERGETYCZNE PISKLĄT I PODLOTÓW DZIERZBY GĄSIORKA (*LANIUS COLLURIO* L.)

Streszczenie

W okresie 24 VI–13 VII 1968 r. hodowano 6 osobników dzierzby gąsiorka w wieku 3–29 dni w naturalnie zmieniających się warunkach temperatury i oświetlenia. Cały materiał podzielono na 3 grupy wiekowe: pisklęta, podloty rosnące i podloty, które osiągnęły średni ciężar ciała osobników dorosłych.

U piskląt mierzono codziennie ilość zjadanego pokarmu, wydalanych fekaliów oraz przyrosty ciężaru ciała. Fekalia podlotów nie były ważone.

Na podstawie tych danych obliczono średnie dzienne zapotrzebowanie energetyczne oraz średnie dzienne tempo metabolizmu na osobnika i na jednostkę masy ciała.

Zmierzono również tempo wzrostu piskląt i podlotów w warunkach naturalnych na Łąkach Strzeleckich.

W oparciu o te dane oraz o znaną wielkość populacji na Łąkach Strzeleckich obliczono przybliżone zużycie pokarmu przez populację młodych gąsiorków w wieku do 1 miesiąca, z powierzchni 1 m^2 łąki w ciągu 1 dnia.

Konsumpcja pokarmu w warunkach eksperymentalnych wyniosła średnio 9,5 g/osobnik/dzień dla piskląt, 14,3 g/osobnik/dzień dla podlotów rosnących i 13,8 g/osobnik/ /dzień dla podlotów nierosnących. W procentach ciężaru ciała odpowiednie wartości wyniosły 56,0, 55,5, i 46,6%.

Dzienne zapotrzebowanie energetyczne wyniosło 15,0 kcal/osobnik/dzień dla piskląt, 23,0 kcal/osobnik/dzień dla podlotów rosnących i 22,3 kcal/osobnik/dzień dla podlotów nierosnących. Średnio zapotrzebowanie energetyczne podlotów było o ok. 50% wyższe od zapotrzebowania energetycznego piskląt.

Średnie dobowe tempo metabolizmu wyniosło 8,4 kcal/osobnik/dzień dla piskląt, 14.4 kcal/osobnik/dzień dla podlotów rosnących i 15.1 kcal/osobnik/dzień dla podlotów nierosnących.

Zarówno tempo metabolizmu jak i konsumpcja pokarmu były w dużym stopniu zależne od temperatury powietrza.

Ilość pokarmu zjadanego przez populację młodych gąsiorków na Łąkach Strzeleckich w jednym z wybranych sezonów lęgowych wyniosła ok. 3,5 mg świeżej masy owadów /m^2/dzień.

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