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Winter energetics of the Capercaillie — a methodological approach

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The parameters of ecological energetics were measured using three groups of Capercaillie *Tetrao urogallus*: caged, enclosured and free-living birds. This comparison makes it possible to evaluate the usability of caged birds for studies on ecological energetics. Determining daily energy budget (DEB) in free-living birds bases on the quantity of excrements left in the snow burrow, estimation of the digestibility coefficients of food stuffs and time budgets of individual birds. Studies on free-living birds revealed the strong influence of diet on energetics. Gross energy intake (GEI) in males was around twice that of enclosured birds, while digestion coefficient was clearly lower. DEB of free-living birds was very close the DEB in the enclosure. Using body weight correction the difference was only 5 %. DEB values of males expressed as multiples of basal metabolic rate were in cages 1.4, in the enclosure 1.8 and in the field 1.8. This paper describes the techniques used in Russian studies on winter energetics of grouse, and it gives some examples of the application of the method. This example also confirms the usefulness of birds in captivity for studies on ecological energetics.

1. Introduction

Pine needles *Pinus silvestris* is the principal winter food resource for the Capercaillie *Tetrao urogallus* throughout most of its vast range (see e.g. Cramp & Simmons 1980). In Lapland needles prevail in the diet from November to May (Semenov-Tjan-Sanskij 1960, Seiskari 1962, Pulliainen 1970). Needles contain a lot of less-digestible resins and celluloselike substances. By selecting feeding trees with low content of resinous substances in the needles (Lindén 1984a) Capercaillie may decrease the input of harmful substances, thus increasing the "pure" energy extraction (see Lindén 1988). However, utilization of an energetically costly food resource throughout winter would hardly be possible without some advanced adaptations.

To understand the complicated processes of Capercaillie digestion, we have to know much more about the physiology and energetics of free-living birds. In this study we concentrate on the ecological energetics, and we have measured the gross energy intake GEI, daily energy budget

DEB and metabolizable energy coefficient MEC (*in sensu* Kendeigh et al. 1977) using three groups of experimental birds: caged birds, birds living in the enclosure (wings clipped) and free-living birds. Using this kind of approach it is possible to determine the additional energy for free-living in the Capercaillie, even if the number of birds used in the experiments was relatively small. This approach gives the possibility to evaluate the usability of caged birds for studies on ecological energetics. We also try to give a detailed description of the methods in grouse energetics used in Russia (e.g. Andreev 1973, 1980, 1982, 1988, Potapov & Andreev 1973, 1985). A large part of the data presented here has been published earlier in Russian (Andreev & Lindén 1986).

2. Material and methods

Experiments and field studies have been carried out in 1984 between January 20 and February 9 at the Meltaus Game Research Station (66°55′N, 25°20′E). The station is equipped with a laboratory and an aviarium with special cages for bioenergetic measurements. Experimental birds used in this study (10 birds, wings clipped) were reared in captivity (see Lindén 1984b). Some additional data were also collected during the same period in the vicinity of the Värriö Subarctic Research Station (67°44′N, 29°37′E).

Average temperature in January in Meltaus is close to −12°C (Heino & Hellsten 1983). During the study period mean daily temperatures varied between −6.5° and −27° with absolute minimums at night and early morning down to −30°. Cloudless weather prevailed on frosty days. As temperature increased up to about −15° snowfalls and winds came up. Thickness of snow cover was increasing from 0.8 m in mid-January to 1.1 m in February.

The method of determining DEB in free-living birds is based on the quantity of excrements (woody droppings and liquid caecal faeces) left into the snow burrows during the night-time, estimation of the digestibility coefficient of food items, and building up time budgets of individual birds (Potapov & Andreev 1973, Andreev 1980). We conducted a series of experiments complementing each other. The following estimations most important to the goals of this study were made:

a) DEB_1 in caged birds (see also Lindén 1984b)
b) DEB_2 in semi-free birds, living in the enclosure
c) DEB_3 in free-living birds in the vicinity of Meltaus and Värriö.

2.1. Experiments with caged birds

The auxiliary cage experiments were aimed to ascertain preferencies of some food items and to determine digestibility of the diet. The cages (2×2 m) were equipped with wire floors having adjustments for collecting food remains and excrements. Food stuffs (oats, poultry feed, pine needles) and snow were given *ad libitum*. The caged birds were weighed at the start and end of each 2-day-experiment to determine the change in body mass. The coefficient of conventional digestibility (DC') was determined:

$$DC' = (M_f - M_d)/M_f, \qquad (1)$$

where M_f is the total mass of food consumed, and M_d is the total mass of woody droppings. Each diet fraction was weighed separately before and after cage experiments, and the proportions of different fractions were determined on the basis of dry mass. Knowing the proportions and the energy contents of different food items, the mean energy content of the mixture was calculated. The dry mass and calorific content of woody droppings and liquid caecal excrements were analyzed separately. The daily energy budget for caged birds (DEB_1) may be calculated in the following way:

$$DEB_1 = M_f q_f - M_d q_d - M_c q_c + dw_b q_b, \qquad (2)$$

where M_c is the total dry weight of caecal excrements; q_f, q_d and q_c are calorific values of food stuffs, droppings and caecal excrements, respectively, dw_b is the daily change in body mass (g/day) and q_b is the energy equivalent for the change in body mass (7.5 kJ/g; Andreev, own data). The cage experiments were carried out in 8 days with three males and one female.

2.2. Experiments with birds in the enclosure

In these experiments the same males were used as in cage experiments. In the enclosure (about one hectare) cocks tend to show a similar daily activity pattern as free-living cocks (except the disability to fly). They eat mostly oats and poultry feed; they forage also pine needles, but not at all in such quantities as free-living birds. At night birds burrow themself into the snow, construction of burrows being similar as in free-living birds. The exact moments of the start and end of the roosting period were registered, and rough time budgets were built during the experimental period.

After coming out of the burrow in the morning males leave certain amount of droppings as well as frozen caecal faeces in the burrow bottom. Dry mass and number of droppings is strictly proportional to the time spent in the burrow, while the mass of caecal wastes is proportional to the total daily amount of the food consumed (Andreev 1973, own observations). Both fractions of excrements were collected separately and dried in the vacuum oven at 80–90°C. After drying and weighing, the total quantity of droppings and the mean mass of a single dropping were determined. In few cases cocks were disturbed at midnight to confirm the idea of the digestion being a continuous and steady process when sleeping. Thus, it is possible to calculate the rate at which woody droppings are passed at night.

The total food mass utilized throughout the night (M_{fn}) can be calculated:

$$M_{fn} = M_{dn}/(1DC'), \qquad (3)$$

where M_{dn} is the dry mass of droppings in the snow burrow, and DC' is determined in cage experiments. Here we also assume that the diet composition of enclosured birds is similar to that of caged birds.

The mean level of night metabolism in the snow burrow in the enclosure (NM_2) was calculated as follows:

$$NM_2 = M_{fn}q_f/T_n - M_{dn}q_d/T_n - M_cq_c/24, \qquad (4)$$

where T_n is the duration (in hours) of night roosting. Metabolisable energy coefficient (MEC) may be calculated:

$$MEC = NM/M_fq_f. \qquad (5)$$

NM level in Eq. 4 represents the lower limit expected for DEB:

$$DEB_{2(min)} = 24NM_2. \qquad (6)$$

To estimate DEB more accurately one should keep in mind that the day-time activity requires at least 1.6–1.8 times higher metabolic rate compared with NM (see e.g. Moss 1973, and data on free-living birds in this paper). There are at least three factors causing the increase: 1) locomotory activity, 2) higher body temperature, 3) higher thermoregulatory costs due to lower temperatures. Thus Eq. 7 might give a more realistic estimate:

$$DEB_{2(average)} = NMT_n + 1.7NMT_d, \qquad (7)$$

where T_d is the duration of daylength.

2.3. Measurements with free-living birds

A third series of experiments with similar approaches was conducted in the field for the determination of M_f, NM and DEB. Since the main aim of the study was to find out the extra energy demands for free-living, the two previous sets of experiments (in cages and in enclosure, subscripts 1 and 2, respectively) act mainly as a basis for control and comparison.

Permanent ski routes were established to localities used by Capercaillie cocks. Routes were checked every day or every other day. All the birds (mostly cocks) encountered were registered and their roosting places described. The two fractions of excrements were collected and dried separately. The pattern of daily activity was reconstructed based on direct observations. Data on the quantity of droppings in day-time burrows were used to find out daily resting periods. Observations on enclosured cocks were also taken into account when determining the timing and partitioning of daily activity.

The dry mass and number of woody droppings were observed. Andreev (1980), based on an extensive material, used the difference between dry mass of food stored in the crop before roosting (M_{fn}) and mass of excrements left in the burrow (M_{dn}, M_c) for determination of NM in free-living birds (see Eq. 4). However, in this study this method

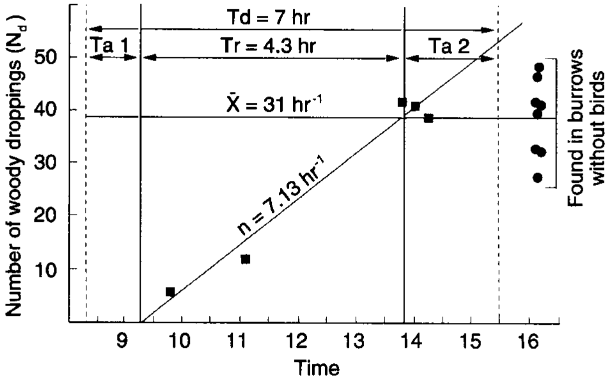

Fig. 1. Dependence of number of woody droppings (N_d) on the time spent in the snow burrow. The squares show the birds, when it was possible to determine exactly the time spent in the burrow. Td = day-lenght, Tr = roosting period and Ta = activity period.

was not acceptable due to very few observations. Instead, values of M_{fn} were calculated in the same manner as with the enclosured birds, i.e. by means of DC' coefficient (see Eq. 3).

To estimate digestion coefficiency (DC') of the natural diet (diet in the wild) we used the fact that pine needles were not totally destroyed after they had passed through intestines. Normally only the external part of a needle is crushed, while the inner part keeps unruined, being, however, at the same time chemically digested. This is readily seen on droppings collected from burrows. Thus digestibility of needles may be determined using difference between weights of needles' pieces of equal lenght before and after needles passage through intestines:

$$DC' = (m_1 - m_2)/m_1,$$

where m_1 = dry mass of 1 mm of the needle before digestion, and m_2 = the same after digestion. To confirm this idea we calculated two regression equations for dependence of dry mass of needles' parts on their lenght: fresh needles, $m_1 = 0.251L^{1.13}$ ($r = 0.94$, df = 26;); for digested pieces, $m_2 = 0.137L^{1.13}$ ($r = 0.80$, df = 27), where $m_{1,2}$ = mass in mg, L = lenght in mm. Thus DC' = 0.454.

On the basis of this result we may calculate NM_3 using Eqs 3 and 4. To transform NM_3 into DEB_3 alternative procedures may be used. Assuming body mass of free-living birds to be constant, i.e. mass changes are negligible (during the short experimental period), one should predict that the intensity of dropping production coincides in general with simultaneous changes in the metabolic rate. Consequently, daily number of droppings (N_d) must be proportional to the DEB_3, providing the mean mass of one dropping (p_o) to be constant, which was confirmed in the field.

In opposite to caecal faeces (M_c), collecting of daily droppings is not an easy task. Only in a few cases it may be done successfully. After leaving the burrow in the early morning Capercaillie usually flies some distance away, and no footprints can be found. However, in some cases birds did not fly, but a cock came out of snow and walked among small pines throughout the whole day. After moving a few hundred meters the bird burrowed into snow cover again. Then two night portions of droppings together with their daily quantity could be collected. In such a case, there is a possibility to estimate the rate of day-time excretion of droppings. In this study we analyze three such occasions. In addition, disturbing day-time resting birds in different hours, it is possible to estimate the rate of dropping excretion in day-time burrows (see Fig. 1). Observations support the idea, that the process of dropping accumulation in daily burrows is practically linear as well as in night-time. All considerations above enable us to propose the following equations for the determination of DEB_3 and its components (subscribe a for activity, n for night-time and r for rest):

$$M_d = m_{dn}T_n + m_{da}T_a + m_{dr}T_r, \qquad (8)$$

where m_{dn}, m_{da} and m_{dr} are rates of dropping excretion in night-time burrows, during daily activity period and in day-time burrows, respectively.

$$M_f = M_d/(1\text{-}DC') = 1.83M_d \text{ or} \tag{9a}$$

$$m_{fn} = 1.83m_{dn} \tag{9b}$$

$$DEB_3 = M_f q_f - M_d q_d - M_c q_c. \tag{10}$$

The second way to determine DEB_3 rises from Eqs 4 and 8:

$$DEB_3 = NM(T_n + T_a K_a + T_r K_r), \tag{11}$$

where $K_a = m_{da}/m_{dn}$; $K_r = m_{dr}/m_{dn}$.

Energy contents of food items and excreta were determined by burning them in an adiabatic bomb calorimeter (Gallenkamp). Throughout the period of field observations air temperature was registered. In some selected days we measured light intensity, using luxmeter couple directed to zenith. This parameter was correlated to the moments of start and end of cocks' activity in the enclosure. In average these moments coincide with the light intensity level of 5 lux. This is approximately the same what was stated by Semenov-Tjan-Sanskij (1960) in the Lapland state reserve (USSR). To compare data on free-living birds' activity collected in different geographical points (i.e. Meltaus and Värriö), we calculated local meridional corrections for standard time: in Meltaus it equals minus 36 min, in Värriö minus 54 min.

3. Results

3.1. Energy contents

The energy content of the experimental diet was calculated with respect to percentage of its components, being equal to 20.0 kJ/g (Table 1). The energy contents of oats, poultry feed pellets and pine needles were 20.4, 18.7 and 25.2 kJ/g dry matter, respectively. Energy content of excrements in cages was higher than that of the diet 22.3 kJ/g. It should be noticed here that the excrements were analyzed as a mixture of two types of faeces. In the second set of experiments, it was assumed that in the enclosure cocks consume the same diet as in cages. Energy content of the two fractions of excrements is found to be markedly different. Droppings contain 19.1 kJ/g — a little bit lower value compared with the diet; caecal fraction again is enriched with energy containing 26.2 kJ/g. This might be explained by specific features of the process of digestion of grouse: ether-extracted fraction or resins together with other digestible fractions of the crude browse diet are accumulated in the caeca being postponed for later transformation and partial absorbtion (e.g. Andreev 1980, Klaus et al. 1989). Results of this stratification are quite clear if a bird uses pure natural diet. With needle diet the energy content of the caecal ("liquid") fraction comes up to 31.1 kJ/g, since this substance includes up to 35% of ether extracted fraction. Energy content of the needles is high compared with the artificial diet, 25.1 kJ/g, but opposite to the latter, available or digestible part of needle diet is low. This is easily seen from relatively high energy content of droppings, 23.8 kJ/g.

Table 1. Average energy contents (kJ/g) of diets and excrements in different experimental groups: in cages, in enclosure and in field. Diets in cages consist of following proportions: oats 26 %, pellets 59 % and needles 15 %. It is assumed that the diet composition in enclosure is similar to that in cages.

Experimental group	Diet	Excrements "droppings"	Excrements "caecal"
Cages	20.0 ± 0.30	22.3 ± 0.33	
Enclosure	20.0 ± 0.30	19.1 ± 0.29	26.2 ± 0.39
Field	25.1 ± 0.38	23.8 ± 0.36	31.1 ± 0.47

3.2. Cage experiments

Results of cage experiments (Table 2) clearly show that cocks in aviary preferred artificial diets. They consumed 75–85% of oats and poultry feed and 15–25% of pine needles. However, it should be noticed that experimental birds were reared in captivity being always given artificial diet enriched with nitrogen.

Total food consumption was in males 156–182 g/day and, in one female 45–57 g/day. Estimations for digestibility coefficients gave similar results: DC' = 0.68; DC = 0.64.

Production of droppings in males was 53.5 g/day in average. In smaller females dropping production was 15.0 g/day. Mean dry mass of one male dropping is 0.66 g, and the rate of dropping production is 3.38 excrements/h. Mean dry mass of caecal excrements was 7.25 g/day (males). In females no caecal faeces were found. They are probably not wasted every day if the diet is an artificial one.

In the cage experiments certain decrease of body mass was observed. In males it was about 12 g/day and in female 10 g/day, which equals to about 0.3–0.5 % of the total body mass. This weight loss is generally considered acceptable in experiments of ecological energetics (see Kendeigh et al. 1977).

3.3. Enclosure experiments

On average, cocks spent about 16.3 hours per day in snow burrows in the enclosure (Table 3). Thus, they were exposed to ambient temperatures 7.7 hours (average −16°C), being active or having only short rest periods.

Five cocks which dwelled in the 1 ha enclosure were displaying every morning. After awakening they bordered individual territories, being aggressive to their neighbouring cocks and man. Usually displaying took 1.5–2 hours. Then cocks spent 40–60 min feeding, and after feeding they rested 3.5–4.5 hrs. After daily resting and before burrowing for sleep cocks fed again for about 1 hour.

Table 2. Mean food consumption and digestibility parameters in cage experiments. Altogether 9 experiments were made with 3 males, and 3 experiments with one female. Mean ± SD.

Parameter		Males	Female
Initial body weight, g		4290 ± 353	1940 ± 99
Average weight loss, g/day		11.5	10.0
Consumption, g dry matter/day		166.7 ± 6.7	50.3 ± 5.8
Pellets:oats:needles (%)		59 : 26 : 15	74 : 1 : 25
Excrements, g dry matter/day	M_d	53.5 ± 5.9	15.0 ± 5.4
	M_c	7.3 ± 2.3	–
Digestibility coefficients	DC'	0.68	–
	DC	0.64	0.66

Experiments were carried out between 25 January and 1 February 1984 at ambient temperatures between −15 and −22°C. Each experiment lasted 48 hrs (for experimental design and parameters, see text and Lindén 1984b).

The quantity of woody droppings in burrows (N_d) correlated with the time spent in the burrow (Fig. 1). The mean rate of excretion at night-time equals to 3.25 excrements/hr (Table 3). A single dropping (p_o) in the enclosure weighed slightly more than in cages (0.72 g vs. 0.66 g). The mass of the caecal dropping was high in the enclosure (M_c = 12.4 g), being also clearly variable (CV = 31 %).

Mean rate of dropping production throughout the night (m_{dn}) is $p_o n_n = 0.72 \times 3.25 = 2.34$ g/hr (see Table 3 for parameter values). Assuming the conventional coefficient of digestibility (DC') to be 0.68, we may calculate $m_{fn} = 7.27$ g/hr (Eq. 3). Applying Eq. 4 (parameters from Table 3) we may calculate the mean level of night metabolism (NM) in the snow burrow to be 87.5 kJ/hr.

The lower limit for DEB_2 is 24 NM = 2110 kJ/day (male, 4250 g, −3°C, in thermoneutral zone, see Marjakangas et al. 1983). Since this result refers to roosting birds it doesn't include any moving activity or thermoregulation. Use of Eq. 7 gives more reliable values for DEB_2. Assuming daylength (T_d) to be 7.7 hours, length of night roosting (T_n) to be 16.3 hours and the daytime activity coefficient (K_a) to be 1.7, we may estimate DEB_2 = 2578 kJ/day.

3.4. Field experiments

We describe the activity patterns of cocks and females on the basis of observations in the enclosure, field observations in the daytime, and on the basis of dropping accumulation in burrows. Assuming that cocks are active during the daylight (light intensity more than 5 lux), the total period

Table 3. Quantity of droppings in the burrows (n = 27) of the enclosured cocks. Mean ± SD.

M_{dn}, g dry matter per night	38.2 ± 6.1
P_o, g dry matter	0.72 ± 0.10
M_c, g dry matter	12.4 ± 3.8
T_n, hrs	16.3 ± 0.2

The following secondary parameters can be derived: N_d (droppings per night) = 53.1; n_n (droppings per hour at night- time) = 3.25.

of activity is 7 hours, and the night-roosting period 17 hours. The cocks prefer to spend most of the day in the snow, in so-called "daytime burrows". They are easily distinquished from night burrows by soft walls without ice, absence of caecal faeces and small amount of droppings (26–38 droppings, mean 31 droppings, n = 10). Disturbing cocks from the burrows at different hours of the daily-rest we found the rate of the dropping accumulation (n) to be about 7.13 droppings/hr in the enclosure (r = 0.98, df = 3, see Fig. 1). Thus the total period spent in the burrow should be expected to be 31/7.13 = 4.3 hrs. As seen in Fig. 1 the total period of feeding activity is 2.7 hrs consisting of two parts: morning foraging period (about 1 hour) and evening period (1.7 hours). Foraging periods are separated by the daily resting period. There are not enough observations on females' activity to make a reliable pattern of their time budget. It is noteworthy that females' daytime burrows were never found at Meltaus. At the same time when males were frightened out of snow, females were seen feeding in pine crowns.

Especially at windy or cloudy weather some cocks prefer walking on the snow to feeding in the pine crown. Tracing such cocks gives some additional data on time and energy budgets. In this case feeding activity consists of several shorter periods. Counts of daily dropping numbers along the walking routes of the cock show the rate of dropping production to be on the average 10.8 droppings/hr. This is 1.6 times higher rate compared with the same parameter estimated from daily burrows (Fig. 1).

Mean dry mass of a dropping is 1.29 g for males and 0.60 g for females (Table 4). Estimation for the rate of dropping production gives 4.78 (males) and 4.83 droppings/hr (females). Thus the mean rate of excretion (m_{dn}) is 6.2 g/hr (males) and 2.9 g/hr (females). Dry mass of caecal faeces is 42.7 g (mean value, males), being about three times higher compared with enclosure conditions and less variable (CV = 7.5 %). The difference in the dry mass of caecal faeces (M_c) between free-living and enclosured birds might be explained by higher proportion of resin components in the diet. Lower variability of M_c in free-living birds strengthens our opinion that caecal digestion functions near certain physiological limit.

Using the quantities of excrements, estimations of digestibility and time budgets, it is possible to determine DEB for free-living birds (using Eqs 8–11, data from Table 4, and using a similar approach as with enclosured birds in Chapter 3.3.). The parameters of ecological energetics for free-living birds are presented in Table 5, as well as the same parameters for caged and enclosured birds, for comparison.

4. Discussion

Being carried out by standard methods the cage experiments are more accurate and comparable with each other (see e.g. Gavrilov 1980, Lindén 1984b). Energy consumption values in cages in this study are markedly higher than in the previous studies. If only metabolizable energies are compared (no dw_b correction, dw_b = daily change in body mass), difference is high and significant, 550 kJ/day. The immediate cause for the difference is obviously due to the different amounts of food consumed: 110 g/day in previous experi-

Table 4. Intensity of excretion in the free-living Capercaillie males and females. Mean ± SD.

Parameter	Walking on snow M (day)	Resting on snow M (day)	Sleeping on snow M (night)	F (night)
Number of measurements	3	10	10	5
Average temperature, °C	–21	–20	–17	–21
Estimated duration of the event, hrs	5.8	4.6	17.2	17.0
Amount of droppings	64 ± 20	31 ± 5	82 ± 10	82 ± 6
Average rate of excretion/hr	10.8	6.7	4.8	4.8
Dry weight of a single dropping, g	1.30±0.05	1.30±0.05	1.29±0.16	0.60±0.03
Dry weight of caecal droppings, g	...	–	42.7±3.2	18.2±3.0

ments and 170 g/day in the present study. If corrections for dw_b and ambient temperatures are introduced the difference is still 350 kJ/day.

However, the high values obtained in our cage experiments do not seem to be accidental. They might be explained by the obvious fact that cocks in our experiments consumed also pine needles (15%), which leads to higher energy content and lower digestibility of the diet. According to Lindén (1984b, 1988) the digestibility decreases when the proportion of needles in the diet increases. He also found that gross energy intake, just as though automatically, increases with increasing proportion of needles in the diet.

In the enclosure conditions food consumption of males was higher than in cages. The difference between DEB values was nearly 600 kJ/day. In the enclosure DEB_3 was 2862 kJ/day (Table 5). Formally this difference enables us to state that "free living" in the enclosure requires 25% more energy compared with cages. Such a difference might partly be explained by higher activity of cocks, which intensively display, sing and walk in the enclosure, while in cages they usually stay silent and motionless. Furthermore, and perhaps more importantly, the proportion of needles in the diet of enclosured cocks was apparently higher than that of caged birds. This was confirmed by the higher mass of a single dropping, larger amount of caecal faeces (Table 5) and higher proportion of lipid fraction in the caecal faeces.

Otherwise, enclosured cocks spent most of the day in snow burrows at temperatures close to thermoneutrality (e.g. Marjakangas et al. 1983), while caged cocks were exposed to temperatures much lower than the critical temperature.

Analysis of energetics of free-living birds reveals the strong influence of the diet on energetics. The gross energy intake (GEI) in free-living birds was around twice as high as that of enclosured birds, while the digestive coefficient decreased. However, DEB in the field was very close to that of DEB in the enclosure (5% difference using body weight corrections) (Table 5).

It is worth noticing that night metabolism (NM) includes basal metabolism (BM) along with additional energy cost for thermoregulation, which comes from a necessity to warm up frozen food in the crop, to melt snow eaten for water requirements, and to increase temperature inside the burrow. All these costs are mainly paid at the beginning of night. According to Rintamäki et al. (1984), a Capercaillie male weighing 4250 g produces 18.7 W at thermoneutrality; thermal conductivity coefficient (c) is 0.378 W/°C; $t_{lc} = -3°$. Though these data were obtained on fastening birds, the energetical parameters are noticeably higher than might be calculated from generalized allometric equations (e.g. 10.8 W, Aschoff & Pohl 1970). In addition, Andreev & Lindén (1986) estimated 1.3 W to be produced for warming up the crop content and 1.25 W more for heating the burrow. Thus the expected rate of NM must be equal to 18.7 + 1.3 + 1.25 = 21.25 W. This is quite close to what was obtained by a "direct" measurement (22.7 W). Difference of 1.5 W (approximately 7 %) may be referred to the more intensive functional activity of intestines.

Data on energetics of free-living birds from this study are in good agreement with those obtained in the region of Leningrad (Andreev 1973). In a previous investigation (Potapov & Andreev 1973) food comsumption was determined from the crop (m_{fn}) on the basis of its dry mass and the duration of night roosting (T_n). It was found that m_{fn} varies from 11.0 to 12.1 g/hr providing T_n = 12–14 hrs. It caused some variability in NM values which varied from 17.2 to 21.9 W. DC' estimated from cited studies lays between 0.44 and 0.48, being close the values of the present study using, however, quite different approaches.

Comparative data (Table 5) clearly shows that free-living birds consume 50% more food than birds in the enclosure. This food passes

Table 5. Comparison of DEB components (averages only).

Parameter	Cage		Enclosure	Field	
	male	fem.	male	male	fem.
Wb, g	4250	1730	4250	4000?	1800?
Mf, g/day	166.7	50.3	226.0	328.7	143.5
Md, g/day	53.5	15.0	72.0	180.8	78.9
Mc, g/day	7.3	–	12.4	42.7	18.2
DC	0.64	0.7?	0.63	0.32	0.32
GEI, kJ/day	3337	1001	4565	8270	3610
DEB, kJ/day	2270	921	2862	2633	1164
DEB/BM	1.4	1.0	1.8	1.8	1.3

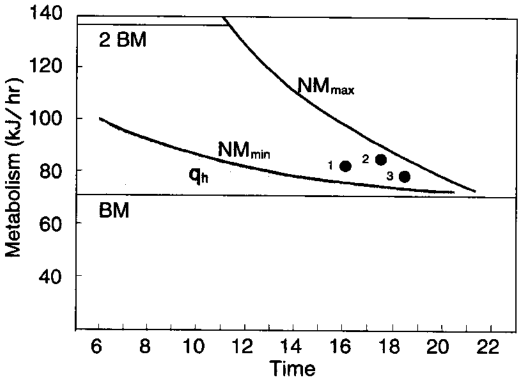

Fig. 2. Upper (NM_{max} = the upper limit of available energy for the night-time)) and lower (NM_{min}) limits for night metabolism. q_h denotes the additional energy needed for heating frozen food stuffs. BM is taken from Rintamäki et al. 1984. Tn = length of night roosting. Dots: 1 = according to Andreev 1973, 2 = birds in the enclosure, this study, and 3 = free-living birds, this study.

through intestines with higher speed. However, artificial diet is much more easily digested than natural one. As was already shown, the lower rate of night metabolism is explained by some fundamental physiological requirements of an individual; BM and thermoregulation. Theoretically the limit might be lower, when the body temperature (t_b) is also lower. However, practically no tetraonid bird decreases t_b under the normal limits 39.0–40.5°C (Andreev 1980, Marjakangas et al. 1983). The upper expected level of night metabolism (NM) is also apparently restricted by the volume capacity of the crop and energy resources stored in the contents of the gizzard and the intestine.

An "average" cock weighing 4250 g would forage needles before night roosting up to 340 g (143 g dry matter; Semenov-Tjan-Sanskij 1960, Andreev & Lindén 1986). This amount of food corresponds to 3600 kJ of gross energy, or 1080 kJ of available energy. Up to this amount should be added approximately 41 g or 287 kJ food stuffs, which fill the digestive tract (according to the data from Semenov-Tjan-Sanskij 1960). Thus the maximal energy reserve of the cock is close to 1367 kJ/T_n. The longer the night the lower is the upper limit of available energy (Fig. 2). At T_n = 20 hrs both limits — upper and lower — come together. It might indicate the fact that staying longer in the burrow is not possible without loss of body mass. The usual duration of night roosting in midwinter in Finnish Lapland is 16.5–18 hrs, which fit well with these calculations.

All the data described above clearly shows that especially Capercaillie cock under winter conditions in Lapland lives very close to a certain physiological limit. The limit becomes reality if the metabolisable energy coefficient (MEC) does not exceed 0.3. Longer nights, lower temperatures or less digestible food would force birds to compensate energy losses by consuming their energy reserves (see Hissa et al. 1990). Enclosured birds which are supported by nutritious artificial diets are apparently free of such exertions.

Contrary to wild birds, cocks in the enclosure are not restricted energetically. That's why they may allow themselves to more intensive and more diverse behavioural activity despite short days and low temperatures.

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Selostus: **Metson talvienergetiikasta eri mittaustapojen valossa**

Yksinkertaisinta on tutkia verrattain harvalukuisen ja isokokoisen metson energetiikkaa tarhaolosuhteissa, jolloin energetiikkaa kuvaavat tunnuskuvut ovat luotettavasti mitattavissa ja yksiselitteisiä. Luonnonoloissa tehdyt energeettiset mittaukset ovat huomattavasti vaikeampia. Esittelemme tässä Venäjällä käytetyn menetelmän, jolla voidaan arvioida vapaudessa elävän metson energiankulutusta. Menetelmä perustuu lumikiepin yölliseen ulostemäärään, aineenvaihduntatehokkuuden mittaamiseen sekä yksittäisten lintujen aikabudjettien laadintaan. Verrattaessa päivittäisiä energiabudjetteja (DEB) kolmella koeryhmällä (häkkikokeet, linnut tarhassa siivet leikattuina ja vapaana elävät linnut) havaitut erot olivat yllättävän pienet. Mikäli DEB ilmaistaan perusaineenvaihdunnan (BM) kerrannaisina, niin tulokset metsokukoilla olivat seuraavat: 1.4 BM (häkki), 1.8 BM (tarha) ja 1.8 BM (vapaat linnut). Laskelmamme osoittivat myöskin, että Lapin olosuhteissa, noin 20 asteen pakkasessa, metsojen kiepissä viettämä noin 20 tunnin jakso on maksimaalisen pitkä siinä mielessä, että pidempi jakso johtaisi ruumiinpainon pudotukseen. Työ osoittaa, että tarhakokeet antavat oivallista tietoutta energetiikasta ja että luonnossa elämisen aiheuttama "lisäpanos" on verrattain vähäinen.

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