ACTA THERIOLOGICA  
Vol. 24: 1  3-24, 1977

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Energy Metabolism of the Roe Deer

January WEINER


Energy metabolism of the roe deer Capreolus capreolus (Linnaeus, 1758) was investigated by means of the respirometric method. The level of metabolism in roe deer is similar to that of other wild ruminants but higher than the mean interspecies metabolism of mammals. Fastig heat production (FHP) shows seasonal variations, being the highest during spring mating season, slightly lower in summer and the lowest in winter: 177.6, 79.4, and 81.3 kcal X kg$^{-0.75}$ X day$^{-1}$, respectively. In spring and summer the metabolism increases at lower temperatures: FHP (kcal X kg$^{-0.75}$ X day$^{-1}$) = 205.5 X 5.5 X 10$^{-4}$, where F = C. Resting metabolism of non-fasted animals (RNP) is higher than FHP by 75-309%, and this difference represents the specific dynamic action of food (SDA). Motoric activity causes a rise of metabolism by 9-29.4%, the cost of maintaining of upright position being equal to 1.1 kcal X kg$^{-0.75}$ X hr$^{-1}$. Resting metabolism of fawns up to 80 days of life is linearly correlated with their body weight (W kg): RHP$=73.35W$ (where RHP = kcal X animal$^{-1}$ X day$^{-1}$). RHP reaches the highest values in 7th day of life. In fawns 8 to 8 month old FHP amounts to 102.9 kcal X kg$^{-0.75}$ X day$^{-1}$, and RHP is higher by 2.7%. The mean respiratory quotient (R.Q.) was equal to 0.82; the lowest values were observed in fasting and resting animals, while the highest (0.86) in active non-fasting ones.

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I. INTRODUCTION

Population of roe deer, Capreolus capreolus (Linnaeus, 1758) play an important role in both energy flow and matter circulation in almost all European forest ecosystems (Bobek et al., 1974; Grodzinski, 1975). Moreover, roe deer belongs to game and is a species of direct economical value, being at the same time potentially responsible for damages in forest economy.

Studies of the role of roe deer in forest ecosystems and optimization of hunting economy must be based on the knowledge of energy and food requirements of these animals (Grodzinski, 1975). Hitherto roe deer were rarely the subject of ecological-physiological studies.

1 Praca została zrealizowana w ramach problemu wczesnego 09.17 koordynowanego przez Instytut Ekologii PAN.
III. RESULTS

1. Fasting Metabolism (FHP) of Adult Animals

In summer (June—August) 1973 and 1974 19 series of measurements of fasting metabolism were carried out in 5 adult individuals of roe deer (2 ♂♂ and 3 ♀♀). The measurements were made at ambient temperature ranging from 3 to 26°C. Body weight of examined animals was between 18 and 24 kg, amounting on the average to 21.5 kg.

FHP measured in temperatures between 17 and 26°C was almost constant and amounted on the average to 990.5 kcal×animal⁻¹×day⁻¹ (99.4 kcal×kg⁻⁰.⁷⁵×day⁻¹, Table 1). FHP measured in temperatures between 3 and 17°C showed a strong negative correlation with ambient temperature (r = -0.90; p<0.001). The relationship between FHP and ambient temperature in the range of 3 to 17°C can be expressed in the form of rectilinear regression:

\[ FHP = 181.5 - 5.32t \]

where: FHP — kcal×kg⁻⁰.⁷⁵×day⁻¹, t — ambient temperature °C (Fig. 2).

The coefficient of regression shows a strong significance (p<0.001) with the confidence interval of ±1.36; the regression explains 81% of variability of FHP.

The results of measurements of FHP in summer season did not reveal significant differences associated with sex, nor any relationship between metabolic rate and body weight.

In two winter seasons (December—February) 14 measurements of

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### Table 1

<table>
<thead>
<tr>
<th>Season</th>
<th>kcal×animal⁻¹×day⁻¹</th>
<th>kcal×kg⁻¹×day⁻¹</th>
<th>kcal×kg⁻⁰.⁷⁵×day⁻¹</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SUMMER (temp. 10°—20°C), N=10</td>
<td>990.5 ± 140.6</td>
<td>46.1 ± 5.5</td>
<td>99.4 ± 11.6</td>
</tr>
<tr>
<td>WINTER (temp. 9°—22°C), N=14</td>
<td>858.6 ± 35.9</td>
<td>46.2 ± 4.1</td>
<td>91.3 ± 5.4</td>
</tr>
<tr>
<td>MOLTING SEASON (temp. 16°C), N=4</td>
<td>1233.0 ± 130.7</td>
<td>69.8 ± 12.1</td>
<td>142 ± 14.5</td>
</tr>
<tr>
<td>(temp. 20°C), N=4</td>
<td>1018.6 ± 192.1</td>
<td>57.0 ± 8.5</td>
<td>117.0 ± 13.2</td>
</tr>
</tbody>
</table>

RHP

SUMMER, N=3

928.0 ± 32.9 | 55.1 ± 5.0 | 129.8 ± 22.9 |

WINTER, N=8

1072.7 ± 183.1 | 49.6 ± 5.9 | 113.8 ± 18.1 |

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![Fig. 1. Respirometric chamber for measuring metabolism of adult roe deer.](image)

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(1) fasting heat production, FHP (=fasting metabolic rate, SMR). A post-absorptive state in the examined animals is an essential condition for this measurement. This was achieved by fasting of roe deer during 48 hr, which leads to a decrease of R.Q. below 0.8. According to Blaxter (1963) total emptying of the intestinal tract requires so long time that it causes physiological disturbances, hence fasting for 2 days is generally regarded as sufficient. A similar procedure in the studies of wild ruminants was employed by Silver et al. (1969, 1971), Wesley et al. (1970, 1972), and by others.
Winter FHP of roe deer showed a strong relationship between metabolism and body weight (Fig. 3). The regression describing the relationship between metabolism and body weight calculated by double logarithmic transformation appears in the following formula:

\[ FHP = 193.6 \times W^{2.51} \]

where: \( FHP \) — kcal\times animal\(^{-1}\)\times day\(^{-1} \), W — body weight, kg.

The regression coefficient (0.51) is significantly different from the exponent 0.75 (p<0.001). The mean winter fasting metabolism of adult roe deer after computing for kg\(^{-0.51}\) amounted on the average to 180.0 ± 21.5 kcal\times kg\(^{-0.51}\)\times day\(^{-1} \) (± 95% confidence interval).

Four animals were used for 8 determinations of FHP during spring molting (May). The mean body weight of the examined animals was 18.5 kg (16.5 to 22.0 kg). The measurements were made at two ambient temperatures: 10 and 20°C. At 20°C FHP amounted on the average to 1019.0 kcal\times animal\(^{-1}\)\times day\(^{-1} \) (117.0 kcal\times kg\(^{-0.75}\)\times day\(^{-1} \), Table 1). At 10°C metabolism was higher reaching 142.1 kcal\times kg\(^{-0.51}\)\times day\(^{-1} \). The difference in metabolism at these two temperatures (25.1 kcal\times kg\(^{-0.51}\)\times day\(^{-1} \)) is statistically highly significant (0.001<p<0.001).

FHP in the molting period is higher than in summer both at 20°C (0.02<p<0.05) and at 10°C (0.05<p<0.1).

2. Resting Metabolism (RHP) of Adult Roe Deer

Resting metabolism was measured in non-fasted animals. On the basis of weighing animals during FHP and RHP determinations in short intervals of time it was found that the difference in body weight, corresponding to the content of intestine, amounted on the average to 1.7 kg. When computing metabolic rate for body weight unit the weight of fasted animals was used.

In the winter period (December—February) 8 measurements of RHP were made in three individuals (2 ♂♂ and 1 ♀♀). The mean body weight was 21.5 kg. The runs were completed for ambient temperatures between 10 and 24°C. In the whole range no effect of temperature on metabolic rate was observed, thus the measurements in all temperatures were analyzed jointly. Resting metabolism of non-fasted roe deer ranged from 838.3 to 1357.2 kcal\times animal\(^{-1}\)\times day\(^{-1} \), amounting on the average to 1072.7 kcal\times animal\(^{-1}\)\times day\(^{-1} \) (i.e. 113.8 kcal\times kg\(^{-0.75}\)\times day\(^{-1} \), Table 1).

RHP of adult roe deer measured in summer (August) was higher than in winter (Table 1) reaching the average value of 129.8 kcal\times kg\(^{-0.51}\)\times day\(^{-1} \). The difference, equal to 16.0 kcal\times kg\(^{-0.75}\)\times day\(^{-1} \) is, however, statistically not significant (0.1<p<0.5). In both seasons the RHP values of adult roe deer did not show any relationship with body weight.

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FHP were made in 4 adult roe deer (1 ♂, 3 ♀♀) with the mean body weight of 19.0 kg (range of variability 15.5—22.5 kg). In the range of temperatures between 9 and 22°C no relationship was found between metabolic rate and ambient temperature.

Fig. 2. Relationship between fasting metabolism (FHP) of roe deer and ambient temperature.

Continuous line — FHP; broken line — 95% confidence interval. FHP = 181.5—5.324, for t<17°C.

Fig. 3. Relationship between FHP of adult roe deer and their body weight in winter (doubly logarithmic scale). FHP = 193.6 W^{2.51}.

The mean rate of fasting metabolism in winter (N=14) was slightly lower than in summer: 91.3 kcal\times kg\(^{-0.75}\)\times day\(^{-1} \) (Table 1), but the difference (8.1 kcal\times kg\(^{-0.75}\)\times day\(^{-1} \)) was statistically not significant (0.1<
more than 9%. The lowest level of metabolism in standing position was higher than during rest by approximately 22%, and the cost of this activity amounted on the average to 1.1 kcal/kg^{0.75} hr^{-1} (N=11, SE=± 0.12). Slow movements in standing position caused a rise of metabolism rate by more than 45%, and fast movements of turning around the cage — by more than 100%. The highest activity, anxiety, etc., resulted in the increase of metabolism by 130—210% (Fig. 4).

5. Metabolism of Fawns below 80th Day of Life

In four fawns born in captivity (two single litters and one twin litter) resting metabolism (RHP) was measured during first 80 days of life. On the whole 31 measurements of RHP were made, and out of this number 22 fell for the first month of life. All runs were at ambient temperature of 22 to 24°C.

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3. Metabolism during Pregnancy and Lactation

In March 1973 a single measurement of fasting metabolism was determined in a pregnant female (body weight 23.5 kg). FHP in this period amounted to 103.9 kcal/kg^{0.75} day^{-1} (Table 2), hence it was slightly higher than winter metabolism (the difference is 12.6 kcal/kg^{0.75} day^{-1}). In a later period of pregnancy metabolic determinations were not carried out in order not to disturb the doe.

In June and July 1973 RHP was determined in the same female during intense lactation (11th and 30th day). The doe nursed two fawns. On 11th day of lactation her body weight was 24 kg and metabolism reached

<table>
<thead>
<tr>
<th>Period of measurement</th>
<th>Item</th>
<th>Body weight</th>
<th>kcal\times\text{animal}^{0.75}\times\text{day}^{-1}</th>
<th>kcal\times\text{kg}^{-1}\times\text{day}^{-1}</th>
<th>kcal\times\text{kg}^{0.75}\times\text{day}^{-1}</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pregnancy 8. month</td>
<td>FHP</td>
<td>23.5</td>
<td>1112.6</td>
<td>47.3</td>
<td>103.9</td>
</tr>
<tr>
<td></td>
<td>Difference in relation to winter FHP</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lactation 11. day</td>
<td>RHP</td>
<td>24.0</td>
<td>2447.2</td>
<td>102.0</td>
<td>226.6</td>
</tr>
<tr>
<td></td>
<td>Difference in relation to summer RHP</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lactation 30. day</td>
<td>RHP</td>
<td>22.5</td>
<td>2565.3</td>
<td>69.6</td>
<td>152.2</td>
</tr>
<tr>
<td></td>
<td>Difference in relation to summer RHP</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

226.6 kcal/kg^{0.75} day^{-1} (Table 2). However, during the experiment the doe preserved upright position. On 30th day of lactation body weight of the female decreased to 22.5 kg, and resting metabolism was then equal to 152.2 kcal/kg^{0.75} day^{-1}. The results of the two measurements conspicuously exceed the mean RHP in summer (p<0.001, Table 2).

4. Energy Costs of Locomotor Activity

In standard measurements of FHP and RHP only the periods of total rest (lying position) were taken into account, as corresponding to the lowest oxygen consumption. During most of the runs roe deer developed periodically some motoric activity which increased their metabolism by 9 to 210% (Fig. 4).

Small slow movements in lying position increased metabolism by not
The course of changes of resting metabolism jointly with actual changes of body weight were continuously followed in two fawns (a' and b') during the first month of life (Fig. 6). In this period RHP ranged from 54.5 to 91.1 kcal×kg⁻¹×day⁻¹, with the maximum occurring in both animals on 7th day. On 80th day RHP amounted on the average to 80.1 kcal×kg⁻¹×day⁻¹, and body weight was then equal to 9.3 kg. During the whole 80-day period the resting metabolism rate showed a strong relationship with body weight. The correlation coefficient for this relationship reached $r = 0.95$ ($p < 0.001$), and rectilinear regression drawn through point 0 of the coordination plot is expressed by the following equation:

$$RHP = 73.53 \times W$$

where $RHP$ is given in kcal $\times$ animal⁻¹ $\times$ day⁻¹, $W$ — body weight, kg. This regression explains over 90% variability of RHP with the confidence interval of $95% = b \pm 10.5$ (Fig. 7). The same relationship is shown after double logarithmic transformation:

$$RHP = 79.4 \times W^{0.9313}$$

($r = 0.96$, $p < 0.001$). The exponential is significantly different from 0 ($p < 0.001$) and from the exponential of 0.75 ($0.001 < p < 0.01$), but not from the exponential equal to 1 ($0.1 < p < 0.5$), Fig. 8.

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The increase of body weight of fawns from 3 to 80 days of life is shown in Fig. 5. Changes in body weight of fawns in this period are expressed by a second order regression equation:

$$W = 1.5098 + 0.1506 \times X - 0.000676 \times X^2$$

where: $W$ — body weight, kg; $X$ — age, in days after birth ($p < 0.001$).

Fig. 5. Growth curve of fawns during first 80 days of life:

$$W = 1.5098 + 0.1506 \times X - 0.000676 \times X^2$$

Fig. 6. Changes in resting metabolism (A) and body weight (B) in two fawns during first month of life.
In all series of respirometric measurements the respiratory quotient (R.Q.) ranged from 0.71 to 0.95; on the average it was equal to 0.82. R.Q. of fasted and non-active animals was the lowest reaching in adult animals the mean value of 0.79 (Table 4). Locomotor activity caused increase of R.Q. to the mean value of 0.84, the difference being statistically signifi-

cant (p<0.001). The value of respiratory quotient was higher in RHP than in FHP measurements, amounting to 0.84 in adult animals, and 0.82 in half-year-old fawns. At the same conditions of measurements no significant differences were observed in R.Q. of adult roe deer and fawns (Table 5).

### IV. DISCUSSION

Hitherto metabolism has been measured only in a few species of wild ruminants, including four species of deer: white-tailed deer (Odocoileus virginianus) (Silver et al., 1969, 1971; Thompson et al., 1973; Holter et al., 1975), mule deer (Odocoileus hemionus) (Nor旦 et al., 1970), red deer (Cervus elaphus) (Brockway & Maloiy, 1967; Ma-

### Table 3

Metabolism of fawns in the age of 6 to 9 months (mean ± 95% confidence interval).

<table>
<thead>
<tr>
<th>Item</th>
<th>kcal×animal⁻¹×day⁻¹</th>
<th>kcal×kg⁻¹×day⁻¹</th>
<th>kcal×kg⁻¹×day⁻¹×10⁻³</th>
</tr>
</thead>
<tbody>
<tr>
<td>FHP, N=14</td>
<td>788.2 ± 54.3</td>
<td>57.1 ± 4.7</td>
<td>109.0 ± 8.5</td>
</tr>
<tr>
<td>RHP, N=5</td>
<td>883.9 ± 145.1</td>
<td>71.2 ± 9.2</td>
<td>133.7 ± 18.1</td>
</tr>
</tbody>
</table>

### Table 4

Values of the respiratory quotient (R.Q.) obtained for roe deer and fawns during different experimental conditions. The right side of the Table shows significant differences between R.Q. values (+ = statistically significant difference at the level of 1%, − = non-significant difference).

<table>
<thead>
<tr>
<th>Measurement</th>
<th>N</th>
<th>R.Q. ± SD</th>
<th>Significance of differences, P&lt;0.01</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 FHP, ad., resting</td>
<td>21</td>
<td>0.70 ± 0.052</td>
<td>+ +</td>
</tr>
<tr>
<td>2 FHP, ad., active</td>
<td>5</td>
<td>0.84 ± 0.043</td>
<td>−</td>
</tr>
<tr>
<td>3 RHP, ad., resting</td>
<td>14</td>
<td>0.80 ± 0.045</td>
<td>+ −</td>
</tr>
<tr>
<td>4 RHP, ad., active</td>
<td>11</td>
<td>0.86 ± 0.040</td>
<td>−</td>
</tr>
<tr>
<td>5 FHP, ad., total</td>
<td>26</td>
<td>0.80 ± 0.032</td>
<td>−</td>
</tr>
<tr>
<td>6 RHP, ad., total</td>
<td>25</td>
<td>0.84 ± 0.030</td>
<td>−</td>
</tr>
<tr>
<td>7 FHP, subad.</td>
<td>10</td>
<td>0.82 ± 0.051</td>
<td>+</td>
</tr>
<tr>
<td>8 RHP, subad.</td>
<td>5</td>
<td>0.82 ± 0.041</td>
<td>+</td>
</tr>
<tr>
<td>9 FHP, all animals</td>
<td>42</td>
<td>0.80 ± 0.048</td>
<td>+</td>
</tr>
<tr>
<td>10 RHP, all animals</td>
<td>39</td>
<td>0.84 ± 0.039</td>
<td>+</td>
</tr>
<tr>
<td>11 RHP+FHP, resting</td>
<td>35</td>
<td>0.81 ± 0.049</td>
<td>+</td>
</tr>
<tr>
<td>12 FHP+FHP, active</td>
<td>16</td>
<td>0.83 ± 0.040</td>
<td>+</td>
</tr>
</tbody>
</table>

During winter (January — beginning of March) measurements of FHP and RHP were made in fawns 6 to 9 months old. Body weights of examined individuals were equal to 13.5 kg on the average, ranging from 11.5 to 15.0 kg. These rather large variations of weight were not clearly associated with age.

Altogether 14 measurements of winter FHP were completed in 6 fawns at ambient temperature between 8 and 23°C. In this range no relationship was found between metabolism and temperature. The mean body weight of individuals in this series of measurements was 14.0 kg (13.0—15.0 kg). FHP reached on the average 788.2 kcal×animal⁻¹×day⁻¹ (109.9 kcal×kg⁻¹×day⁻¹×10⁻³, Table 3), hence it was higher by more than 20% from the mean winter FHP in adult animals (p<0.001).

Resting metabolism (RHP) was measured in three non-fasted fawns (jointly 5 runs). Body weight of examined animals ranged from 11.5 to 13.0 kg (mean 12.8 kg). The mean RHP was 133.7 kcal×kg⁻¹×day⁻¹ (Table 3), hence it exceeded fasting metabolism by almost 22% (0.001<p<0.01). In the investigated range of temperatures no relationship between RHP and temperature was observed.

![Fig. 8. Relationship between resting metabolism (RHP) of fawns and their body weight presented as the allometric function: RHP=79.4 W0.8313.](image-url)
The results of measurements of minimum FHP in roe deer in various seasons indicate the occurrence of distinct seasonal rhythmicity. The lowest value of FHP was found in winter and the highest during molting season (change of the coat) (Fig. 9). Seasonal rhythmicity of metabolism appears to be characteristic for deer. Silver et al. (1969, 1971) observed in summer over 80% increase of metabolism in white-tailed deer. McEwan & Whitehead (1970) discovered analogous variations (but of a smaller amplitude) in caribou (Rangifer tarandus), and Nordan et al. (1970) in young mule deer. Segal (1962) reported similar phenomena in Siberian reindeer (Table 5). In distinction to the above-mentioned results Brockway & Malooy (1967) and Malooy et al. (1968) did not observe seasonal changes of metabolism in red deer (Cervus elaphus). Increase of metabolism in summer may be due to changes in the insulating properties of the coat (Silver, 1969). Deteriorated insulating properties of the fur are probably responsible for increased metabolism of roe deer during change of the coat. On the other hand, Hoffman & Robinson (1966) demonstrated that the annual cycle of the hormonal system (pituitary, thyroid gland) directly affects metabolism of deer (Silver et al., 1969; Ozoga & Verme, 1970).

2. Costs of Thermoregulation

In roe deer the increased heat production negatively correlated to ambient temperature was observed only in summer during measurements of fasting metabolism (FHP). In the remaining seasons and in different species of wild ungulates (Table 5), and in two races of reindeer (Rangifer tarandus) (Segal, 1962; McEwan, 1970). Metabolism was measured also in two species of African antelopes: eland (Taurotragus oryx) and wildebeest (Connochaetes taurinus) (Rogerson, 1968), and in American pronghorn antelope (Antilocapra americana) (Wesley et al., 1970, 1973). Comparison of the results obtained by these authors with our studies on roe deer will permit to describe a few general features of metabolism of wild ruminants.

### Table 5

<table>
<thead>
<tr>
<th>Species</th>
<th>Season</th>
<th>Body wt. kg</th>
<th>FHP, kcal x kg⁻¹ x day⁻¹</th>
<th>Reference</th>
</tr>
</thead>
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<tr>
<td>Cervidae</td>
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</tr>
<tr>
<td>Odocoileus virginianus</td>
<td>winter</td>
<td>65</td>
<td>97.1</td>
<td>Silver et al., 1969</td>
</tr>
<tr>
<td>3 Cervus elaphus</td>
<td>summer</td>
<td>59</td>
<td>143.6</td>
<td>Silver et al., 1969</td>
</tr>
<tr>
<td>4 Rangifer tarandus</td>
<td>winter</td>
<td>100</td>
<td>95-111</td>
<td>Segal, 1962</td>
</tr>
<tr>
<td>5</td>
<td>summer</td>
<td>100</td>
<td>158-190</td>
<td>Segal, 1962</td>
</tr>
<tr>
<td>6</td>
<td>winter</td>
<td>54</td>
<td>91.0</td>
<td>McEwan, 1962</td>
</tr>
<tr>
<td>7</td>
<td>winter</td>
<td>19</td>
<td>91.3</td>
<td>this paper</td>
</tr>
<tr>
<td>Capreolus capreolus</td>
<td>summer</td>
<td>21.5</td>
<td>99.4</td>
<td>this paper</td>
</tr>
<tr>
<td>Bovidae</td>
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<td></td>
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<tr>
<td>Taurotragus oryx</td>
<td></td>
<td>230 (7)</td>
<td>112.2</td>
<td>Rogerson, 1968</td>
</tr>
<tr>
<td>Connochaetes taurinus</td>
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<td>90 (7)</td>
<td>104.3</td>
<td>Rogerson, 1968</td>
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<tr>
<td>Antilocapra americana</td>
<td></td>
<td>22</td>
<td>48.8</td>
<td>Wesley et al., 1973</td>
</tr>
</tbody>
</table>

1. Basal Metabolic Rate

The measurement of the proper basal metabolism (BMR) is practically impossible in wild ruminants, since standard conditions essential for such studies cannot be obtained. However, the lowest values of fasting metabolism (FHP) measured during rest and in the thermoneutral zone may represent a good approximation of BMR.

In roe deer the minimum value of FHP always exceeds the mean interspecies value given by Kleiber (1961). The lowest fasting metabolism in roe deer, occurring in winter, amounts to 91.3 kcal x kg⁻¹ x day⁻¹ and is very close to the values obtained by various authors for several species of wild ungulates (Table 5). In all examined species of wild ruminants fasting metabolism is conspicuously higher from the interspecies mean; this may be caused partly by an error of measurements since the results do not correspond exactly to basal metabolism. On the other hand, it cannot be excluded that increased metabolism is a characteristic feature of wild ungulates (McEwan, 1970).
experimental conditions ambient temperature had no significant effect on metabolism. The lower limit of the thermoneutral zone for roe deer falls for approximately 17°C in summer. Below this temperature metabolism increases linearly with decrease of temperature, and the slope of regression (equation 1) amounts to -5.32 kcal X kg^-0.25 X deg^-1. The literature is lacking any data for direct comparison of this value with other deer species. However, by utilizing the published measurements of FHP in summer in white-tailed deer (Silv e r et al., 1971) it was possible to calculate the analogous regression for that species. In the range of temperatures from -14°C to +17°C the relationship between FHP and ambient temperature shows in Odocoileus virginianus the slope of approximately -5.1 kcal X kg^-0.25 X day^-1 X deg^-1, hence it is rather close to that found for roe deer. During winter measurements of metabolism of roe deer no additional heat production was observed since the animals were well acclimated to the employed temperatures and were not below 0°C. W e s l e y et al. (1974) investigated on a rather limited material the relationship of FHP and ambient temperature in the pronghorn antelope and described the regression slope as equal to 1.7 kcal X kg^-0.25 X day^-1 X deg^-1. This last value refers to the animals adapted to very severe climatic conditions and is based on measurements during the whole year, including winter. It can be supposed that improvement of insulating properties of coat and seasonal adaptation causes also in the roe deer shifting the thermoneutral zone to lower temperatures and appeasement in the slope of regression of metabolism and temperature. This phenomenon could blur the effect of ambient temperature on metabolism in winter measurements. The results of determinations of winter metabolism in white-tailed deer are very broad range of temperatures indicate that below 0°C metabolism increases by ca 2 kcal X kg^-0.25 X day^-1 X deg^-1 (Silv e r et al., 1969, 1971). Increase of metabolism due to calorigenic effect of food and costs of activity compensate totally the costs of thermoregulation. This effect may explain the lack of relationship between metabolism rate and temperature during measurements of RHP. Analogous relationships between metabolism rate and temperature were observed in white-tailed deer by H o l t e r et al. (1975).

2. Resting Metabolism (RHP) and Calorigenic Effect of Food (SDA)

In all measurements of RHP, both in summer and winter, resting metabolism of non-fasted animals (RHP) exceeded by 25—30% analogous values of fasting metabolism (FHP). This difference represents calorigenic effect of food, in a broad meaning of this term, i.e. both specific dynamic action (SDA), and metabolism of the flora of rumen (B l a x t e r, 1962; M a y n a r d & L o o s l i, 1962). The difference between RHP and FHP was slightly higher in summer than in winter, and this may be related to increased consumption and change in the chemical composition of food. This increase in heat production in non-fasting roe deer is similar to analogous measurements in other deer. M c E w a n (1970) estimated the difference between FHP and RHP in reindeer as almost 20%, whereas S i l v e r et al. (unpubl. results) found 18% difference in summer and 11% difference in winter in white-tailed deer. After measuring metabolism in pronghorn antelope W e s l e y et al. (1973) observed over 50% difference (20% of consumed energy) between FHP and RHP. These latter results significantly deviate from other values reported in ruminant deer and may be explained by a different diet composition in antelopes.

4. Energetic Costs of Locomotor Activity

Preserving the upright position was the most distinct level of spontaneous activity of roe deer. Energetic costs of such activity amounted to 1.1 kcal X kg^-0.25 X hr^-1 (22% FHP) — the value comparable with other data obtained for ruminants. The costs of standing approach in the sheep 9 to 11% of resting metabolism, according to different authors (B l a x t e r, 1962; B r o c k w a y, 1965; C r a m p t o n & H a r r i s, 1969), in cattle 18—20% (V e r c o e, 1973), in white-tailed deer approximately 20% of resting metabolism (Silv e r et al., unpubl.). In pronghorn antelope this cost was estimated as ca 1.9 kcal X kg^-1 X hr^-1, or over 37% (W e s l e y et al., 1973). The remaining levels of spontaneous activity developed by roe deer in the metabolic chamber cannot be defined in a way enabling direct comparisons with other available data. T a y l o r et al. (1970) estimated the energetic costs of movement at different speed in various animal species by employing the universal function:

\[ M'_{run} = 8.5 \times W^{0.65} + \frac{6.0}{V} \times W^{0.75} \]  

where: \( M'_{run} \) — costs of running the distance of 1 km, \( W \) — body weight in g, \( V \) — speed of movements, \( km/hr^{-1} \). After comparison of increase of metabolism during moderate activity of roe deer in the respiratory chamber (45—100% FHP) with the values of equation (6) solved for roe deer it can be stated that such increase corresponds to the movement of ca 1—2 km/hr^-1, while intense activity in the chamber (increase of metabolism by 130—210%) — to the speed of 2—4 km/hr^-1.

Energetic costs of work in tamed reindeer were determined by H a m m e l (1962). Costs of standing of a 100 kg weighing animal amounted on the average to 132.8 kcal X kg^-0.75 X day^-1, hence exceeded...
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by approximately 30% resting metabolism determined in this species by other authors (McEwan, 1970; Segal, 1962; Table 5). Pulling of a load by these animals required almost a fourfold increase of metabolism in comparison with that measured at standing position.

5. Metabolism during Pregnancy and Lactation

In a herd of roe deer reared in a large pen in Kraków Zoological Garden three successful pregnancies were observed during the period of investigations. However, only in one case the female was sufficiently tamed for carrying respiratory measurements. In order to reduce excitement of the doe a single measurement in early pregnancy and two runs during lactation were accomplished.

A single measurement of metabolism of a pregnant doe was carried out in the initial period of pregnancy. A small increase of metabolism observed in comparison with winter FHP in other adult roe deer cannot be unequivocally interpreted as additional costs of pregnancy. Analogous measurements in ruminant farm animals (cattle, sheep) indicate that during the initial period of pregnancy, where the growth of embryo is small, changes in the metabolism of a pregnant female are barely perceptible (Black et al., 1965; Saunders, 1965; Hafez & Dyer, 1968; Salmon-Le Leguineur, 1968).

Measurements of metabolism during lactation showed its considerable increase in comparison with non-lactating females (Table 2). The doe examined on 11th day of lactation was very annoyed by separation of fawns and during the whole run kept standing position. After making a suitable allowance for locomotor activity and caloric effect of food (lactating doe was of course not fasted) it was possible to estimate the increase of heat production as approximately 85 kcal\(\times\)animal\(^{-1}\)day\(^{-1}\). This strong overloading of the energy budget in the early period of lactation caused also a conspicuous decrease of body weight (by approximately 1.5 kg). On 30th day of lactation the difference between resting metabolism of the lactating doe and analogous level of metabolism in other roe deer in the same season was only 285 kcal\(\times\)animal\(^{-1}\)day\(^{-1}\). A gradual decrease of lactation is associated with lowered share of milk in the total diet of fawns, which rather early begin to utilize green feed.

6. Metabolism of Fawns

The metabolic rate of fawns during growth was strongly correlated in a linear way with body weight. Attempts of fitting this correlation with a rectilinear or doubly logarithmic equations gave almost identical results (equations (4) and (5)). A very similar result was obtained by
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Blüzma (1967) reported that in four-month old fawns of roe deer the thermoregulation-dependent increase of fasting metabolism amounts to 1.7—2.57°× deg⁻¹, and of RHP — to ca 0.2—0.8°× deg⁻¹ (in ambient temperatures below 12°C). However, these data are rather fragmentary and poorly documented (the author did not give absolute values) hence they cannot be used for direct comparisons.

7. Changes in R.Q.

The oscillations of respiratory quotient within the range of 0.71—0.95 observed in all series of respirometric measurements suggest that various substrates are catabolized during investigations of various metabolic states. The lowest R.Q. values (mean 0.79—0.81), indicating a significant proportion of lipid metabolism, occurred in animals resting and fasting. An increase of R.Q. to the mean values of 0.83—0.84 (Table 4) in well-fed animals results from metabolism of carbohydrates, which constitute the principal component of the roe deer diet. Still further increase of the respiratory quotient in active animals (up to 0.84 in fasted and to 0.86 in well-fed, Table 4) is caused probably by augmented utilization of carbohydrates (glucose) — the phenomenon characteristic for muscular work.

The evaluation of energy budgets of roe deer, taking into account various factors affecting energy requirements in natural conditions, is difficult. However, the results of respirometric measurements in the laboratory may constitute a good basis for construction of energy budgets (Gessaman, 1973; Moen, 1973). Analysis of such budgets by means of simulation in digital computers (Weiner, 1975; Weiner, in press) indicates that in roe deer particularly important is the knowledge of the fasting metabolism rate (FHP) and resting metabolism rate (RHP).

Acknowledgements: The author is grateful to Dr. W. Grodziński for stimulating discussions during the experiments and to Mr. S. Rojkowski for invaluable technical assistance.

REFERENCES

METABOLIZM ENERGETYCZNY SARNY

Streszczenie
Zbadano metabolizm energetyczny sarn używając respirometru Systemu otwartego i specjalnej komory (Riz. 1). Poziom metabolizmu sarn jest podobny jak i u innych dzikich przeważnie, chociaż wyższy niż średni międzygatunkowy dla sżków. Metabolizm gladowy (FHP) wykazuje właściwości sezonowe; jest najwyższy w okresie wiosennym; zmiany stderr, nieco niższy jest, a najniższy zima: 117,6, 99,4, 91,4, 113,4 kcal×kg⁻¹×doba⁻¹ (Tabela 1). W okresie wiosenno i lata metabolizm wzrasta ze spadkiem temperatury: FHP (kcal×kg⁻¹×doba⁻¹) = 181,5×5,23 (t, gdy t = -40°C) (Riz. 2). W okresie zimy metabolizm jest skorelowany z ciężarem ciała: FHP (kcal×xwzrost⁻¹×doba⁻¹) = 193,6 W/A³ (Riz. 3). Metabolizm spoczynkowy zwiększa się w ciągu dnia dla wszystkich osób; dla wczesnych godzinodzię, około 11,1 kcal×kg⁻¹×godz⁻¹ (Riz. 4). Wzrost metabolizmu w początkowym okresie ciężar nieznaczny, jednak w okresie intensywnej laktacji (11 i 30 dni) metabolizm wzrasta z do wartości 225,6 i 152,2 kcal×kg⁻¹×doba⁻¹ (Tabela 3). Metabolizm spoczynkowy kwadrat do 80 dni życia jest skorelowany liniowo z ciężarem ciała (W, w kg): RHP = 73,33×W (widge RHP w kcal×xwzrost⁻¹×doba⁻¹), Fig. 7 i 8. RHP osiąga najwyższe wartości w 7 dniu życia (Riz. 6). W ciągu 6-9-miesięcznych FHP osiąga 109,9 kcal×kg⁻¹×doba⁻¹, zaś RHP jest wyższy o około 22% (Riz. 4). Współczynnik oddechowy (RQ) we wszystkich pomiarach wynosił średnio 0,82, przy czym wartości najsłodsze (0,78) przybierał u zwierząt głodzonych w sporządu, a najniższe u zwierząt śrzednich i nieurodzenych, a najniższe u zwierząt śrzednich i nieurodzenych, i niedatarcjalnych; jest wyższy od średniej międzygatunkowej i zmienia się w cyklu rocznym (Tabela 6, Fig. 9).