

Nocturnal hypometabolism as an overwintering strategy of red deer (*Cervus elaphus*)

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Arnold, Walter, Thomas Ruf, Susanne Reimoser, Frieda Tataruch, Kurt Ondersheka, and Franz Schober. Nocturnal hypometabolism as an overwintering strategy of red deer (*Cervus elaphus*). *Am J Physiol Regul Integr Comp Physiol* 286: R174–R181, 2004. First published September 11, 2003; 10.1152/ajpregu.00593.2002.—Herbivores of temperate and arctic zones are confronted during winter with harsh climatic conditions and nutritional shortness. It is still not fully understood how large ungulates cope with this twofold challenge. We found that red deer, similar to many other northern ungulates, show large seasonal fluctuations of metabolic rate, as indicated by heart rate, with a 60% reduction at the winter nadir compared with the summer peak. A previously unknown mechanism of energy conservation, i.e., nocturnal hypometabolism associated with peripheral cooling, contributed significantly to lower energy expenditure during winter. Predominantly during late winter night and early morning hours, subcutaneous temperature could decrease substantially. Importantly, during these episodes of peripheral cooling, heart rate was not maintained at a constant level, as to be expected from classical models of thermoregulation in the thermoneutral zone, but continuously decreased with subcutaneous temperature, both during locomotor activity and at rest. This indicates that the circadian minimum of basal metabolic rate and of the set-point of body temperature regulation varied and dropped to particularly low levels during late winter. Our results suggest, together with accumulating evidence from other species, that reducing endogenous heat production is not restricted to hibernators and daily heterotherms but is a common and well-regulated physiological response of endothermic organisms to energetically challenging situations. Whether the temperature of all tissues is affected, or the body shell only, may simply be a result of the duration and degree of hypometabolism and its interaction with body size-dependent heat loss.

hypometabolism; hypothermia; winter adaptation; body temperature regulation

MANY UNGULATES ARE CAPABLE of withstanding long and cold winters with low food availability. Large body size, excellent fur insulation, and countercurrent heat exchange mechanisms contribute to minimize energy requirements under cold load. However, reduced heat loss alone can hardly explain the substantially lowered metabolic rate (MR) of northern ungulates and the apparently ubiquitous decrease of voluntary food intake during winter (4, 13, 18, 28, 35, 37, 42, 44, 59, 63, 72). The search for mechanism to explain reduced energy expenditure during winter has so far produced equivocal results. Studies on white-tailed deer [*Odocoileus virginianus* (66)], moose [*Alces alces* (56, 57)], roe deer [*Capreolus capreolus* (69)], and wapiti [*Cervus elaphus nelsoni* (49)] reported that animals had reduced MRs during winter. However, other studies failed to find any differences between summer and

winter basal metabolic rate (BMR) and concluded that seasonal variations in MR were merely consequences of different activity levels and failures to measure animals within their thermoneutral zone (TNZ) or in a postabsorptive state (34, 39, 42, 46, 50, 72). Indeed, MR can increase substantially because of food ingestion, particularly under a protein-rich diet [so-called heat increment of food (9)]. For instance, elevated MR has been found in wapiti for several days after a meal (30). On the other hand, controlling for the confounding effect of heat increment of food when measuring MR is difficult. Fasting ruminants for longer periods of time is detrimental to rumen symbionts and can thus be hazardous for the animal before a truly postabsorptive state is reached. Furthermore, physiological measurements under artificial experimental or feeding regimes are likely to prevent natural responses of wild animals (19, 41).

To circumvent these problems, we chose a multivariate telemetry approach with unconstrained red deer held under close to natural conditions. We aimed to determine whether hypometabolism is a mechanism employed by red deer to cope with winter conditions. As an indicator for field MR, we monitored heart rate. Numerous studies have demonstrated that heart rate is highly correlated with metabolic activity, and there is increasing consensus that heart rate therefore represents a reliable index of energy turnover (6, 8, 10, 30, 40, 58, 71). To understand the mechanism of winter acclimatization in red deer, we monitored heart rate simultaneously with subcutaneous body temperature (T_s) and animal movements to evaluate the independent effects of thermoregulation and locomotor activity on MR. In addition, we analyzed seasonal changes of nutrients in the typical diet of red deer from chemical analyses of the rumen content of free-living animals to assess the role of varying heat increment of food for annual changes of heart rate.

MATERIALS AND METHODS

Study area and animals. The study was conducted from 1994 to 1998 in a 35-hectare enclosure located in foothills near Veľčice, Slovak Republic (48°18'N 18°09'E, 280 m above sea level). This area consisted of 41% agricultural fields, 35% forest cover, mainly black locust (*Robinia pseudoacacia*) and blackthorn (*Prunus spinosa*), and 24% meadows. Between 12 and 16 red deer inhabited the enclosure during the study period. From October to April, the natural forage was supplemented with hay ad libitum, 25 kg sugar beet, and 7 kg mixed grain/day.

Long-term physiological and behavioral measurements were performed with nine adult red deer (age 2–10 yr, body mass 90 to 240 kg) selected randomly from the herd in the enclosure. After the end of the experiment, all study animals were culled by the owner, the Institute

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of Animal Production, Nitra, Slovak Republic, except for one male, which was found dead in the enclosure in the third year of the study. Because the head was cut off, we assume that this specimen fell victim to poachers. Among the four experimental males, the oldest individual was clearly dominant. The five experimental females produced 16 calves during the study period. However, we had no clear evidence for a lack of reproduction in the remaining four opportunities (i.e., female-years), and thus did not discriminate between nonparous and parous females.

Treatment of animals in this study was in accordance with the Slovak Republic Animal Welfare Act No. 115 (1995, §§ 24, 28, 31, Protocol No. 672/96–500) and followed the guiding principles for research involving animals and human beings (1).

Weather data. Air and ground temperature, humidity, wind speed, and direction were recorded every 6 min throughout the study period in a weather station located in the study area and stored in a data logger (model DL2; Delta-T devices).

Telemetric measurements. We used a self-constructed telemetry system consisting of two units, a radiotransmitter implant and a repeater system located in a collar. Transmitters (55 g, 75 × 35 × 10 mm) contained an electronic package, battery, and a temperature sensor and were encapsulated in a physiologically inert medical-grade silicone rubber. The two electrode plates (surgical steel, 8 mm diameter) detecting the QRS complex of the electrocardiogram (ECG) were connected to the transmitter with coiled silicone rubber-insulated wire of multistranded stainless steel, fitted in silicone rubber tubing to form an elastic and extremely flexible lead.

Heart rate and T_s were coded by modulating the pulse-interval of a transmitter and distinguished by different pulse duration. The 100-kHz short-distance (ca. 50 cm) signals from the implant were received by a repeater in the collar. Heart rate pulses were further modulated in length according to a sensor in the collar determining head position (up or down), information that was used for classifying behavior (see below). Repeaters operated within 142–143 MHz and transmitted over up to 10 km. Theoretical life span of the system was 5 yr. However, because of technical and medical problems, transmitters had to be replaced during the study in eight cases and because of lost repeater collars in six cases. On average, individual transmitters operated for a median of 207 days (range 49–803 days).

Signals from repeaters were received by a directional antenna mounted on a 10-meter-high pole that covered the whole enclosure. A separate receiver was used for each transmitter, and signals were recorded continuously with computers located in a trailer. Average heart rate, T_s , and information about locomotor activity were stored for all minutes with at least 50 s of reliable telemetric recordings.

Resolution of heart rate measurement was ± 2 beats/min. Because we did not expect heart rates to reach values as low as actually found, the lower limit of the measurement range was preset to 24–34 beats/min, depending on the individual repeater system. For any heart rate below this threshold, the collar sent a signal with a constant pulse interval according to the preset threshold. The rationale for this design was to obtain a constant pulse frequency if an animal had died. Data sets with average minute heart rates equal to the lower resolution limit of a repeater system were eliminated from the database before analyses. However, at heart rates close to the threshold, the stored minute average could include both pulse intervals indicating true heart rates and pulse intervals indicating the preset threshold. Therefore, the lowest minute averages of heart rates in the analyzed data actually overestimate the true heart rate.

Temperature dependency of the pulse-interval was calibrated in all transmitters before implantation in the range of 35–41°C. Resolution of T_s measurement was $< 0.1^\circ\text{C}$. Power functions fitted best to calibrated values, and individual fits were used to convert recorded pulse intervals into temperatures. Recalibration of five transmitters after ca. 3–9 mo of operation revealed that temperature measurements tended slightly to drift downward with time. We estimated the magnitude of this error by comparing the mean T_s measured during a

particular day of the year with the mean determined for the same day in subsequent years. Comparison of 389 such pairs of values available showed that temperature measurement drifted per year on average by $-0.14 \pm 0.741^\circ\text{C}$ (SD), an error that we considered negligible for the purpose of this study.

Locomotor activity was discriminated from resting solely from telemetry data. Minutes were classified as “at rest,” “moving,” or “feeding” according to the predominant behavior of an animal with an algorithm using information about head position, signal-strength variation caused by movements of the transmission antenna attached to the collar, and heart rate. Minutes with locomotor activity during which the collar sensor indicated that the head of the animal was at least 40 s down were considered as feeding. For validating this algorithm, we simultaneously video-recorded five animals for a total of 300 h. Comparison of both data sets showed that the error in discriminating minutes of locomotor activity from those spent mainly at rest was 5.9%. Further discrimination of minutes of locomotor activity into those predominated by moving or feeding was less reliable and resulted in 27.5% of false classification.

Anesthesia and surgery. Red deer were immobilized by intramuscular injection of a mixture of 35 $\mu\text{g}/\text{kg}$ ethorphine-0.14 mg/kg acepromazine-0.36 mg/kg xylazine or 1.2 mg/kg tiletamine-1.2 mg/kg zolazepam-2.3 mg/kg xylazine with dart projectors (33) and transported by vehicle to a field surgical facility disposed in the enclosure. Anesthesia was maintained with ketamine administered intravenously. To reverse anesthesia after surgery, we injected 84 $\mu\text{g}/\text{kg}$ diprenorphine-0.23 mg/kg yohimbine or 0.45 mg/kg yohimbine-36 $\mu\text{g}/\text{kg}$ sarmazenol intravenously. After recovery, deer were released in the enclosure.

Surgery was conducted on a portable operating table by a veterinarian, one anesthetist, and two assistants. A 10-cm ventral midline neck incision was made through the skin ending 2 cm cranial of the manubrium sterni. Subcutaneous tissue was separated by blunt dissection to form a pouch on the left neck side, between the ventral midline of the neck and jugular groove. We made two further 2- to 4-cm incisions through the skin along the ventral midline ~20 and 38 cm caudal of the pouch for the ECG electrodes. Electrodes were subcutaneously pulled from the transmitter pouch through a subcutaneous tunnel prepared with a sterile gynecological catheter (4 mm in diameter). Transmitter and electrodes were fixed to the subcutis, and the skin incisions were closed with sutures of absorbable material. As a precaution against infection, we injected Duplocillin in each of the three incisions and 6 $\mu\text{g}/\text{kg}$ buprenorphin hydrochloride intramuscularly for analgesic reasons.

For further details about surgical procedures, veterinary care, and the telemetry system, see Refs. 23 and 62.

Nutritional analyses. Annual changes in the composition of the natural diet were determined from samples of the rumen content of free-living red deer culled during 1972–1998 in various parts of Austria and Switzerland throughout all seasons (average altitude of culling sites 1,072 m above sea level, range 458–2,000 m). Rumen content samples from 291 males and 333 females were analyzed for crude protein, crude fat, crude ash, crude fiber, and nitrogen free extract (NFE) by Weender analysis (67). From these results, seasonal changes of the gross energy content of ingested dry organic matter were calculated with rounded values of 23 kJ/g for protein, 40 kJ/g for fat, and 17 kJ/g for carbohydrates (51).

Data analyses. For calculating daily means of heart rate, T_s , or the proportion of time of locomotor activity, only days with reliable recordings of these variables for at least 40 min during each 2-h interval of a day were used. T_s was slightly elevated after a surgery for a median of 16 (range 7–70) days. Such days as well as the first 3 days after an immobilization of an animal for collar replacement were discarded from statistical analysis to avoid a bias resulting from handling and surgery. Data remaining for analysis included 106, 103, 94, and 11 days from four males and 607, 484, 330, 68, and 29 days from five females. For each parameter measured, mean values were

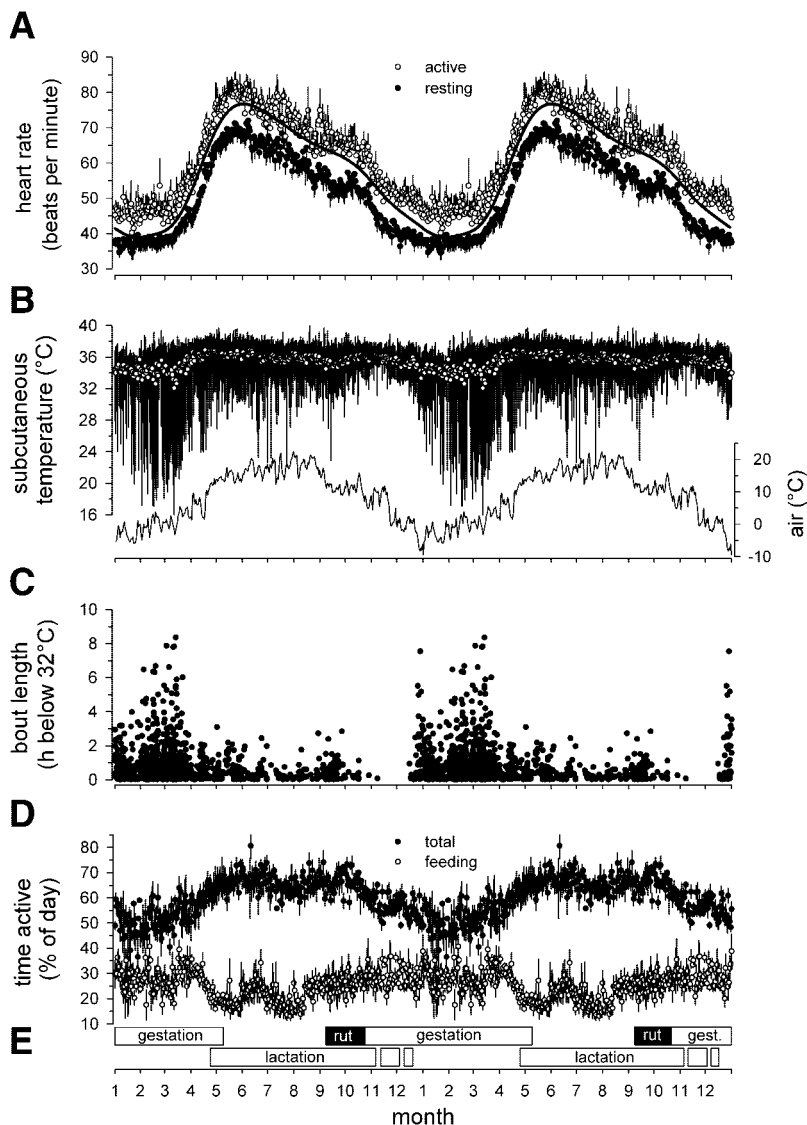


Fig. 1. Seasonal changes in physiological and behavioral parameters. Data are double plotted to ease visualization of the annual pattern. A: daily mean heart rate during locomotor activity (+SE) and at rest (-SE). Solid line: spline fit to total averages. Note that the fitted line during winter is closer to mean heart rate at rest and during summer closer to mean heart rate during minutes spent active because of seasonally varying locomotor activity (D). B: top, daily subcutaneous temperature (range and mean); bottom, daily mean air temperature. C: duration of bouts with subcutaneous temperatures <32°C (only bouts with <10 min of missing data). D: top, mean ± SE total proportion of time of locomotor activity per day; bottom, proportion of time spent feeding per day (mean ± SE). E: approximate timing of reproductive phases in red deer; variability in cessation of lactation indicated by broken bar.

calculated for each individual and each day of the year from all minute values available for this day from one or more years. Plots and analyses of seasonal changes (Fig. 1 and Table 1) are based on these daily means. Measures of variation therefore reflect differences between individuals.

Statistical analyses were performed using S-Plus 2000. We generally used linear mixed modeling (package nlme3) for repeated-measurement analyses (53). Differences in mean heart rates between individuals were adjusted by entering a factor “individual” as random effect. Inspection of residuals showed that the slight accumulation of minute averages of heart rates at the lower resolution threshold of a

repeater system (see above) did not cause problems for the statistical models applied.

RESULTS

Annual changes in heart rate and locomotor activity. Measured average heart rate of the deer peaked in early June and decreased to a nadir of only 40% of the yearly maximum during late winter. Locomotor activity elevated heart rate throughout all seasons by an average of $20 \pm 10.9\%$ (SD; Fig. 1A). However, locomotor activity varied considerably through-

Table 1. Determinants of daily mean heart rate (repeated-measurements multiple-regression analysis of data shown in Fig. 1)

Fixed Effects	Coefficient	SE	Standardized Coefficient	DF	t Value	P Value
Air temperature	-0.36	0.024	-0.462	1301	-14.80	<0.0001
Locomotor activity except feeding	0.19	0.017	0.422	1301	11.46	<0.0001
Feeding	0.14	0.022	0.224	1301	6.46	<0.0001
Subcutaneous temperature	1.15	0.124	0.220	1301	9.32	<0.0001
Sex	-0.13	1.920	-0.010	7	-0.07	0.9475

DF, degrees of freedom. t-Value is the t-statistic for testing the deviation of the partial regression coefficient from 0.

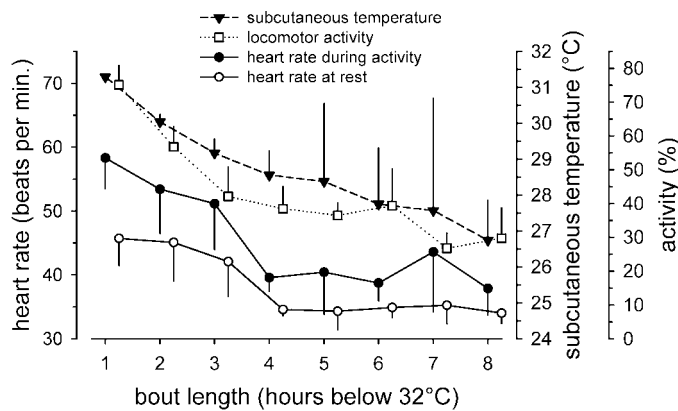


Fig. 2. Changes of heart rate during locomotor activity and at rest (means \pm SE), subcutaneous temperature (means \pm SE), and proportion of locomotor activity (means \pm SE) during bouts of different duration with subcutaneous temperature $<32^{\circ}\text{C}$. Means were calculated using a single value per individual, representing the mean of all minute values of a bout. SEs therefore represent variation between individuals. Note that mean heart rate levels off at a bout length >4 h because of the fact that a constant signal interval corresponding to the lower resolution limit of a repeater system was sent when heart rate fell off scale (see MATERIALS AND METHODS for details).

out the year. Deer were moving or feeding for 20 to 88% of the day, depending on the season. Total locomotor activity, including foraging behavior, increased during April and May, remained high during June to October [$66 \pm 7.5\%$ (SD)], and declined continuously after the end of rut to the low winter level of on average $51 \pm 10.0\%$ (SD) during January and February (Fig. 1D). In contrast, the proportion of time spent feeding per day increased during fall, was even higher during winter than during summer, and declined sharply with the onset of plant growth in April (Fig. 1D).

Nocturnal hypometabolism and peripheral cooling. Daily mean and maximal T_s showed small but distinct variation over the year. In contrast, minimal daily T_s varied considerably, with the lowest values of $16\text{--}17^{\circ}\text{C}$ during February and March and the highest values of 35°C during November after molt into the winter fur was completed (Fig. 1B, top). Longer bouts with T_s below 32°C typically began after midnight (median start time 0156, see Fig. 3 for an example), lasted up to 502 min, and hence coincided in most cases with the period of the day with the lowest air temperatures. The longer T_s remained below 32°C , the lower was the average heart rate during a bout, both during locomotor activity and at rest (Fig. 2). The proportion of time of locomotor activity during a bout declined similarly with increasing bout length, as did average T_s [Fig. 2, bivariate repeated-measurement regression statistics with independent variable length of bout with $T_s < 32^{\circ}\text{C}$ ($n = 862$): mean heart rate (log-transformed to compensate for skewness to the right), $t = -8.7$, $P < 0.0001$; mean T_s , $t = -21.1$, $P < 0.0001$; proportion of bout spent with locomotor activity, $t = -7.3$, $P < 0.0001$]. Furthermore, mean heart rate and locomotor activity during a bout decreased as average T_s reached lower values ($t = 6.0$, $P < 0.0001$ and $t = 2.1$, $P = 0.039$, respectively). Particularly long bouts with $T_s < 32^{\circ}\text{C}$ occurred predominantly from mid-December to April (Fig. 1C). From November 15 to April 15, mean T_s per minute during such bouts was $28.7 \pm 3.2^{\circ}\text{C}$ (SD), on average 6.5°C lower than during periods of time with $T_s > 32^{\circ}\text{C}$ [$35.2 \pm 1.2^{\circ}\text{C}$ (SD)]. The associated reduction of heart rate per minute was on

average 17% but more pronounced for minutes of locomotor activity than for minutes at rest (Table 2 and Fig. 3). Interestingly, the annual minima of T_s did not coincide with those of air temperature. Lowest T_s occurred weeks after daily mean air temperatures had reached their annual minimum (Fig. 1B). During the summer months, T_s also dropped below 32°C but less frequently and only for shorter periods of time (Fig. 1, B and C).

Annual changes of the heat increment of food. The heat increment of food is predominantly determined by the content of protein and metabolizable energy of the ingested material (9). Gross energy and hence the correlated content of metabolizable energy of the natural diet of red deer was lowest in January [19.8 ± 0.04 (SE) kJ/g] when the dry organic matter of food plants contained on average only $17.4 \pm 0.46\%$ (SE) crude protein and $3.4 \pm 0.16\%$ (SE) crude fat but $31.8 \pm 0.48\%$ (SE) crude fiber and $47.4 \pm 0.41\%$ (SE) NFE (Fig. 4). Energy content was maximal at the peak of the growth period in July [21.4 ± 0.06 (SE) kJ/g], when food plants were rich in crude protein [$30.9 \pm 0.58\%$ (SE) of dry organic matter] and crude fat [$6.91 \pm 0.20\%$ (SE)], but low in crude fiber [$21.5 \pm 0.59\%$ (SE)] and NFE [$40.6 \pm 0.48\%$ (SE); Fig. 4]. The substantial seasonal fluctuations of both the content of protein and energy in natural food plants of red deer suggest that the heat increment of food is considerably lower during winter. Unfortunately, the volume and nutrient composition of the food ingested by the deer used for telemetric recordings could not be measured. Thus a straightforward quantification of the importance of the heat increment of food for annual changes of heart rate was not possible.

Determinants of MR. To eliminate the unknown but presumably strong influence of heat increment of food on daily mean heart rate, we removed in a first step all large-scale seasonal variation from the heart rate data before evaluating the influence of other factors on the energy budget. This was done by fitting a spline function to total mean daily heart rates (Fig. 1A) and calculating the difference of individually measured daily means to the value predicted from this function for each day of the year. Regression analyses of the remaining residual day-to-day variation of heart rates revealed a significant influence of T_s . Within the range of daily mean T_s measured, the corresponding average heart rate during a day sank by 1.15 beats/min for each degree centigrade decrease in daily mean T_s (Table 1). Ambient temperature also influenced heart rate significantly. This influence was negative in the range of average daily mean air temperatures that occurred throughout the study ($-12.6\text{--}24.3^{\circ}\text{C}$). Feeding and other types of locomotor activity further contributed significantly to energy expenditure, and both sexes appeared to react similarly (Table 1).

Table 2. Effect of reduced T_s on average heart rate per minute during the time period November 15 to April 15

Minutes	$T_s > 32^{\circ}\text{C}$			$T_s < 32^{\circ}\text{C}$			Difference, %
	Mean	SD	n	Mean	SD	n	
With locomotor activity	51.8	11.9	133,691	42.9	11.6	7,080	-17.2
At rest	40.2	7.1	144,667	35.1	4.9	11,985	-12.7
Total	46.0	11.4	290,789	38.1	9.1	19,531	-17.0

T_s , subcutaneous temperature.

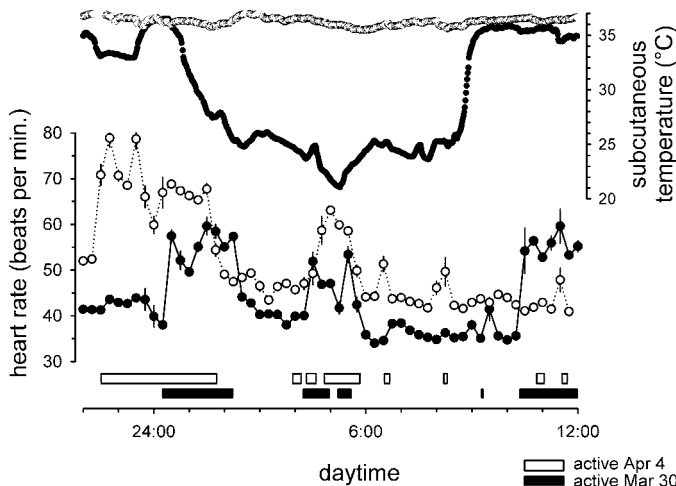


Fig. 3. Subcutaneous body temperature (*top*), simultaneously measured heart rate (15-min means \pm SE, *middle*), and periods of locomotor activity (*bottom*) of the dominant male during two late winter nights. ●, Representative night with peripheral cooling; ○, a night 5 days later without peripheral cooling.

DISCUSSION

Annual changes of MRs and underlying causes. Heart rates of red deer of both sexes varied considerably over the year, similar to seasonal changes in other northern deer (42, 43), and as previously reported for farmed red deer (55). These changes in heart rate reflect changes in field MRs because a close relation exists between heart rate and oxygen consumption (6, 8, 10, 30, 40, 58, 71). This relation is typically linear in resting animals but curvilinear while exercising and is known to vary between individuals (6, 7, 10, 40, 58). However, this was not a problem for our study because our statistical analysis corrected for individual differences. Furthermore, our focus was not to quantify the magnitude of energy expenditure but to understand the origin of relative changes throughout the year.

The annual changes of nutrients and content of energy found in the natural forage of red deer suggested that a substantial component of the annual variation of MR was caused by changes in the heat increment of food. Indeed, the approximately twofold difference between the annual maximum and minimum of daily mean heart rate corresponded well with the also twofold higher protein content of natural deer forage at the summer peak compared with the winter low (cf. Fig. 1A and Fig. 2). However, the lack of quantitative information about seasonal variation of the heat increment of food in the deer studied telemetrically prevented us from directly including this variable in our multiple-regression analysis. We solved this problem by removing all large-scale seasonal variation of heart rate before assessing the short-term influence of thermoregulation and locomotor activity on the remaining residual variation of energy expenditure. Calculation of residual heart rate as the difference of individual values to the population mean was in our view justified because we could safely assume that most seasonal variation of heart rate was caused by extrinsic factors like food composition, food availability, or ambient temperature, which affected all individuals similarly. Our approach is conservative because some of the removed variation was certainly because of seasonally changing energy requirements for thermoregulation and locomotor activity. For instance, the deer

reduced their daily locomotor activity during January and February by about a quarter compared with the summer level. Most of the locomotor activity during winter was foraging, which is certainly less energy demanding than activities like running or fighting. Furthermore, long bouts with pronounced decreases of T_s occurred predominantly during winter, and air temperatures were of course lower (Fig. 1). Nevertheless, the analysis of residual, nonseasonal variation of daily mean heart rates still revealed a highly significant and independent positive relation with daily mean T_s and the total proportion of time spent active per day. Thus the deer decreased energy expenditure during winter not only by reducing locomotor activity, as already reported for northern ungulates [e.g., red deer (21, 22), Svalbard reindeer (14)], but also by reducing the energetic cost of endogenous heat production. This view is further corroborated by the analysis of bouts with $T_s < 32^\circ\text{C}$, which underlines that the decline of T_s resulted from hypometabolism and thus decreased endogenous heat production. The alternative explanation that reduced locomotor activity caused less heat production, lower heart rate, and eventually the fall of T_s can be

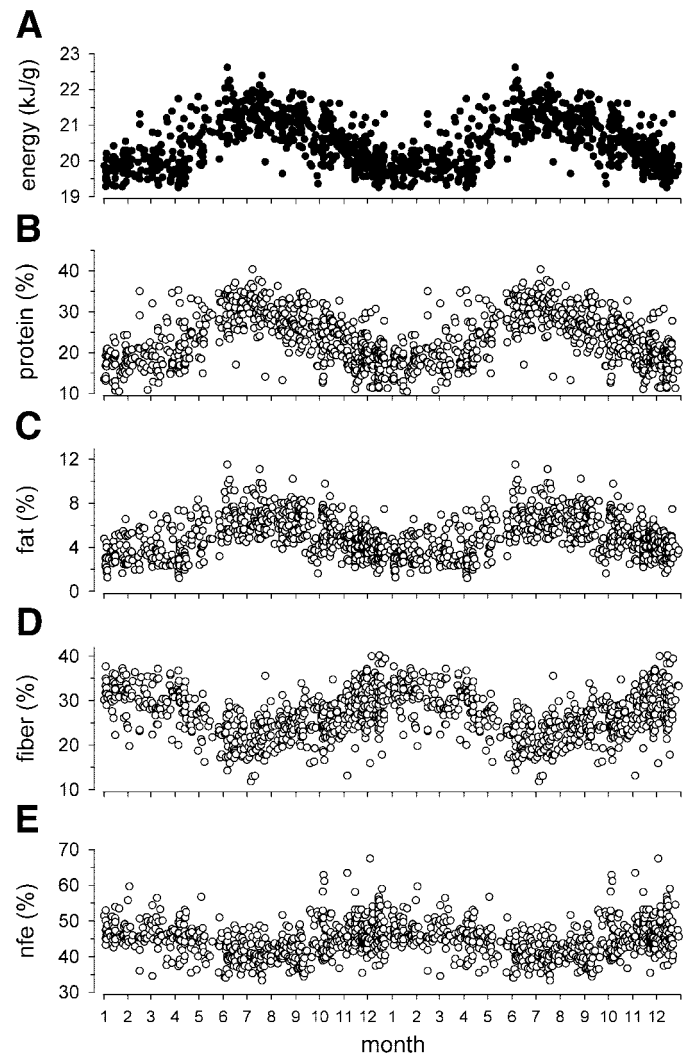


Fig. 4. Double plots of seasonal changes of chemical composition (% dry organic matter) and gross energy content (kJ/g dry organic matter) of the diet of free-living red deer as determined by rumen content analyses. NFE, nitrogen free extract.

excluded, because the decrease of heart rate was similar both during periods of locomotor activity and during periods at rest (Fig. 2). Notably, the reduction of heart rate during bouts with $T_s < 32^\circ\text{C}$ was even highest during phases of locomotor activity (Table 2), suggesting that the deer moved more slowly when the periphery of the body was cold. The fact that bouts of peripheral cooling were most frequent and longest during late winter could have been related to the progressive depletion of body fat stores. If “numb legs” impair maneuverability and therefore increase the risk of predation for a typical flight animal that cannot retreat into safe shelters, one would indeed expect that low temperatures in the periphery of the body are restricted to periods when a reduction of energy expenditure becomes inevitable for survival.

The amount of energy actually saved by nocturnal hypometabolism can only roughly be estimated from our data because during longer bouts with $T_s < 32^\circ\text{C}$ (e.g., >4 h, Fig. 2) T_s sank to levels where the corresponding heart rate was below the resolution limit of our repeater system. Thus the reduction of energy expenditure achieved by reduced endogenous heat production is certainly larger, as indicated by the recorded decrease of heart rate (Table 2). Furthermore, T_s was measured in the ventrolateral neck region close to the body core. Temperatures in more distal parts of the body are much lower (32). Therefore, a reduced T_s probably reflected the shutting off of larger parts of the body from intense circulation. In this case, reduced blood flow to the heart may have attenuated heart minute volume and metabolism much more strongly than indicated by lowered heart rate alone (54, 73).

Peripheral cooling: More than physical thermoregulation. The capability of sustained peripheral cooling is generally assumed to be a major winter adaptation of northern nonhibernating endotherms (2, 31). Thermophysicologists recognized already decades ago that increased insulation by a winter fur or behavioral reactions alone are insufficient to explain the enormous ability of warm-blooded organisms of temperate and arctic zones to sustainably withstand even extremely low ambient temperatures. However, the classical view of a TNZ with vasoconstriction increasing as ambient temperature decreases to keep heat loss and hence MR minimal and constant down to the threshold for the onset of cold-induced thermogenesis seems to be incompatible with our results. Heart rate of our red deer did not remain constant but continuously slowed down as T_s decreased, at least above the lower limit of the measurement range of heart rate (Fig. 2). This result suggests that a decrease in peripheral tissue temperatures was accompanied not only by attenuated heat loss but by a significantly reduced metabolic heat production. However, TNZ is only well defined for a given set point (T_{set}) of body temperature regulation. Any change in T_{set} will lead to a corresponding change in the lower and upper threshold of thermoregulatory responses. It is well known that T_{set} , BMR, and body core temperature (T_c) can fluctuate on a circadian and circannual basis (3, 27, 36, 74). Therefore, it is most likely that prolonged peripheral cooling in red deer associated with a reduction of heart rate is the result of an expansion of the amplitude of the circadian T_{set} rhythm. A similar decrease of T_{set} occurs during entrance into hibernation and has led to the suggestion that hibernation is an extension of thermoregulatory adjustments that normally occur during slow-wave sleep (16, 17). The gradual decrease of T_{set} during entrance into hibernation per-

mits the shutoff of heat production and maximal reduction of MR, leading to the continuous decline of T_c toward the low values close to ambient temperature (47).

Temporary hypometabolism: A ubiquitous survival strategy of endotherms? The apparent lack of a classical TNZ is not a specific characteristic of wintering red deer. MR decreasing continuously with ambient temperature has also been observed in other large north-temperate ruminants (44, 48). However, the responsible mechanism remained unresolved because T_c apparently did not change and temperatures in the body shell were not measured (48). The results of our study demonstrate for the first time for a large ungulate that peripheral cooling indicates a reduction of metabolic heat production and hence energy expenditure. Failures to find a reduction of T_c could be because of the fact that longer periods of hypometabolism as actually occurring are necessary for detectable changes of T_c to develop in the large bodies of animals like bison or deer, even when endogenous heat production is a magnitude lower (e.g., see Ref. 45).

Reduction of metabolic heat production is apparently a ubiquitous reaction of endotherms to cope with energetically challenging situations. For instance, barnacle geese decrease their abdominal temperature to reduce total fat consumption during migration and to ease restoration of fat reserves after the migratory flight (11). Penguins tolerate during diving a decrease of T_c (measured in the abdomen) to save energy and to extend their aerobic dive limit (5, 11, 25). A decrease of BMR is also a common response to water deprivation (61), food restriction and starvation (12, 15, 64, 65), or low ambient temperatures (41). However, such reactions apparently do not indicate impaired thermoregulation but seem to be well-regulated adaptive extensions of adjustments normally occurring during sleep and circadian rhythmicity (24, 52, 64). Together, data from other species and the results of our study suggest that, among terrestrial species, abandoning the defense of high body temperature levels to decrease energy expenditure is not restricted to hibernators and daily heterotherms but may be a common physiological response to periods of food shortage and harsh climatic conditions.

The temporal pattern and amplitude of T_s in red deer during bouts of peripheral cooling resembled the course of T_c in mammals and birds undergoing daily torpor (Fig. 3 and Refs. 29, 38, and 60). Major differences were that the deer were not totally quiescent during these bouts and that T_c must be expected to show only minor if any measurable reduction as a result of nocturnal hypometabolism. However, the principal relationships between physiological and behavioral variables were identical to daily torpor, since average heart rate, T_s , and percentage of time of locomotor activity decreased with increasing duration of bouts with $T_s < 32^\circ\text{C}$ (Fig. 2). It has been argued that phenomena like daily torpor, estivation, and hibernation are all based on identical physiological mechanisms reducing MR (20, 26, 68, 70). The results of our study suggest that any hypometabolism associated with a decrease of endogenous heat production should be viewed similarly. If this is the case, classifying species into nonhibernators, hibernators, estivators, and species employing daily torpor has little conceptual value because the differences that lead to this classification may simply be a result of the duration and extent of hypometabolism and its interaction with body size. The question that should direct further research is why endothermic species

differ so much in their ability to tolerate low tissue temperature and which features and adaptations determine this capability and its expression.

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