

# Winter time-budget and energetics of free-ranging black grouse *Tetrao tetrix* enduring human disturbance



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**THOMAS LEU**

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Leiter der Arbeit:

Prof. Dr. Raphaël Arlettaz,  
Conservation Biology,  
Zoologisches Institut der Universität Bern

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## **Abstract**

The aim of this study was to quantify the impact of direct human disturbance on activity pattern, feeding behaviour and energetic balance of Black grouse in winter. In order to estimate physiological costs in nature I first measured bird's oxygen consumption (respirometric metabolism) at different ambient temperature levels in captivity. Energy expenditures increased curvilinearly with decreasing temperatures (from +20°C to -20°C). Second, energy expenditures in the wild could be reconstructed, on the basis of that curve, by considering temperatures actually faced by birds resting either outside or inside snow burrows. Results showed that on days with low mean air temperature (under -10°C), free-ranging Black grouse can save a considerable amount of energy (up to 15%) by resting in snow burrows during their two daily classical passive periods. Third, feeding activity on days when birds stayed undisturbed was compared with feeding activity on days when birds were experimentally disturbed (flushed). The prediction that, on days when birds were flushed, the animals would show a higher feeding activity, due to extra energetic costs induced by disturbance, could not be verified statistically although there was a trend to increase feeding activity over the days following the onset of experiment. Although this points to a possible additive effect of disturbance, a larger sample size is required to test further for this pattern.

# **1 Introduction**

## **1.1 General introduction**

The black grouse (*Tetrao tetrix*) is distributed from Scotland in the west over central and northern Eurasia to the Amur region in the east, with some isolated populations in central and southeastern Europe and central Asia (Potapov 1985). It has the widest range among tetranoids. The bulk of its range falls within the limits of the boreal coniferous forest zone (taiga). The black grouse is mainly a lowland bird, but in central Europe and southern Siberia it also occupies mountain regions up to 3000 m (Hjorth 1970). The black grouse has to cope principally with cool temperatures, although temperature may fluctuate much in its environment. The principal adaptations to cold are plumage insulation, as well as specific behavioural and nutritional adjustments (Calder and King 1974), for instance the regular roosting in snow burrows (Porket 1969; Marjakangas 1980). This species is in decline over most of its European range. Declining factors are believed to be habitat loss and fragmentation, predation on adults and chicks (including hunting), winter sport and other leisure activities (Lindström et al. 1995; Ingold et al. 1992; Ellison et al. 1988; Kauhala et al. 2000).

This diploma work is part of a comprehensive research programme on the conservation biology of the species in the Swiss Alps, which was launched in 2002. The aim of this programme is to quantify the main threats affecting black grouse in the alpine chain, so as to draw sound conservation and management policies.

## **1.2 Roosting in snow burrows; an adaptation to severe winter conditions**

The observations by Pauli (1974) on black grouse in the Swiss Alps showed that even on the shortest day with 8.5 h of daylight, the birds adopt a general bimodal activity pattern throughout the winter (Aschoff 1966; West 1968; Pulliainen 1981) by resting in closed burrows both at night and around noon, and by being active in between. In southern Finland where the period of daylight falls below 8.5 h by mid February, the birds show a unimodal pattern. Thus filling the crop once a day in the morning apparently suffices to satisfy birds' food requirements (Marjakangas 1986). One reason for the bimodal activity pattern in the Alps (Pauli 1974) may lie in the milder climate, so that the bird can afford to dig and to warm up two cavities each day. From December to January birds' diurnal activity in the Alps lasts on average 5.5 h, and therefore snow roosting 18.5 h. As the days lengthen the activity

periods become longer and the roosting periods shorter (Pauli 1974; Bossert 1980). The diurnal activity is shortest in mid winter : from December to January the active period in the morning lasts about 3.25 h, the one in the afternoon 2.25 h. Under severe winter conditions (a lot of snow, deep temperatures) the grouse reduce their activity phases down to about one hour, which corresponds to the time needed to pick up enough food. The rest of the time (up to 85 %) is spent in snow burrows (Pauli 1980). The four major factors that influence burrowing are snow depth, presence of crust layers within the snow cover, penetrability of these crusts, and thickness of soft snow on top of the crust (Marjakangas, 1986). Black grouse roost either in open burrows, on trees, or on snow surface when snow depth without hard crusts is about 10-26 cm, and exclusively in snow burrows when snow cover is about 27 cm or more (Marjakangas 1986). According to Semenov-Tjan-Sanskij (1960), Glutz von Blotzheim et al. (1973) and Pauli (1974), black grouse need a snow cover of at least 30 cm in depth to be able to construct closed burrows. Marjakangas (1986) observed that 23-25 cm of snow cover is quite enough, but then the birds tend to burrow down to the ground. For regular roosting in closed burrows about 27 cm of readily penetrable snow is required. Roosting of the black grouse in snow burrows appears to be an adaptation to save energy and avoid predation. A varied temperature gradient in the air space around the bird (Marjakangas et al. 1986), the compaction of the snow, as well as the different thermal conductivities of snow and air complicate the estimation of the energetic significance of burrowing (Franssila 1949). Korhonen (1980) nevertheless estimated from snow cavity temperatures and calorimetric data that willow grouse (*Bonasa bonasia*) would save almost half of body heat loss through burrowing compared with resting on snow surface. Energetic questions can only be answered if respirometric metabolism (oxygen consumption) at different ambient temperatures is known.

### **1.3 Respirometric metabolism**

Rintamäki et al. (1983) measured oxygen consumption of captive black grouse in a metabolic chamber (25 x 28 x 30 cm) with the inner walls painted black. The experiments were performed by elevating the temperature stepwise (six to nine different temperature levels for each bird) from -26.5°C to 34.0°C. During all measurements, (performed between 8:00 A.M. and 7:00 P.M.), the birds were sitting quiet in the chamber. Oxygen consumption was calculated by measuring the oxygen concentration in the air before and after the chamber. Therefore compressed air was let into the chamber at a flow rate of 120 l/h. For the

calculation of the metabolic rate, the energy equivalent of 1 ml of O<sub>2</sub> was assumed to be 19.68 J.

#### **1.4 Flushing distance from closed burrows**

According to Marjakangas (1986) flushing distance from snow burrows depends on several factors. One of this factor is the noise made on approaching the cavity, where the flushing distance is clearly proportional to the noise produced. Also, the flushing distance for a sleeping black grouse is presumably shorter than for one that is awake, and increases in the morning in the sense that the closer the time for spontaneous departure comes, the less the bird has to lose in terms of energy investment. Another factor is the time already spent in the iglu. Within the first couple of hours after the onset of roosting, the flushing distance decreases rapidly. Within a short occupancy the bird has invested relatively little energy in warming up the cavity, and it would hence be more beneficial to flee from a potential predator before it comes too near, and dig and warm up a new cavity elsewhere, than to run the risk of being caught. After a longer time of occupation a lot of energy has been spent in achieving the final cavity temperature, and then it would be more profitable to take a greater risk and keep the warm cavity for as long as possible. It is presumed that because of their smaller size (Calder & King 1974) and smaller volume to surface ratio, the females would benefit from keeping their warm cavities for as long as possible. Therefore the flushing distance for females should be shorter than for males (Marjakangas, 1986). The flushing distance for grouse roosting in flocks is also longer than for solitary birds, because of the higher alertness of individuals in a group (Bertram 1978).

#### **1.7 Aims and hypothesis**

Black grouse habitats in the Alps are more and more influenced by human activities. Outdoor sports like skiing, snowboarding and mountaineering ski, produce in winter a lot of direct disturbance on birds. The impact of those human factors on birds' energetic and fitness remains poorly understood. This diploma study is an attempt to quantify the effects of human-generated disturbance on free-living black grouse. The main aim is to describe daily time budgets of males in winter and to energetically quantify them, with respect to disturbed vs. undisturbed circumstances.

With regard to birds' time budgets we tested if the daily feeding activity of experimentally flushed black grouse was higher compared to non disturbed birds, predicting an extra

energetic cost in flushed birds (that have to roost outside iglus for longer periods of time), therefore potentially provoking a more intense feeding activity. We were also interested whether there was an additive effect of disturbance in birds, when they are disturbed on several days in succession. Finally we looked at the energetic significance of burrowing to see how efficient this strategy can be under different weather conditions.

## **2 Material and Methods**

### **2.1 Captive birds used for oxygen consumption measurements**

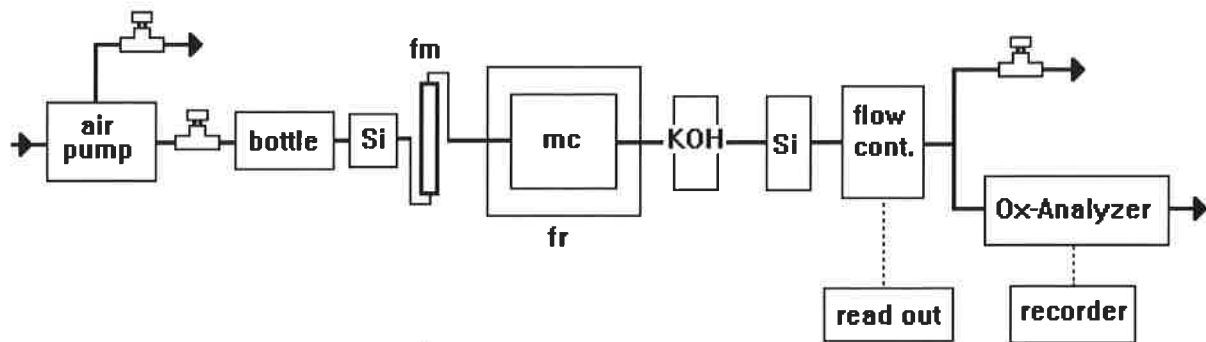
For laboratory experiments 3 males and 1 female kept at aviaries at Bern University were used. Before and between the experiments, individual birds were housed separately in outdoor cages. At Lausanne, where the grouse were measured, the birds were kept in a semi-outdoor enclosure divided in two parts, thus enabling one to keep two birds simultaneously. Because these cages were not large, the birds did not stay longer than three weeks in succession there. At the beginning and at the end of an experiment the animals were weighted to gather data on body mass during measurements. The experiments were carried out between the third week of March and the second week of May. To maintain winter metabolism as far as possible, birds were fed a special winter food (Protector SA, CH- 1522 Lucens). Handling the birds was not easy because they were permanently anxious. Whenever possible they tried to escape, requiring firm and quick manipulation. They were transported from Bern to Lausanne and back in soft carton boxes. During manipulation birds were losing lots of feathers, a mechanism called shock moult; it was therefore important to catch them only when really necessary.

### **2.2 Oxygen consumption - experimental methodology**

According to the method outlined in Arlettaz and Giorgi (Arlettaz et al. 2000, Giorgi et al. 2001), three males and one female were used to measure oxygen consumption at different ambient temperatures. Energy expenditures per time unit (kJ/h) were calculated. Each bird was measured at seven different temperature levels. A given bird was never used more than on 2 successive days.

Oxygen consumption of birds ( $\text{VO}_2$ ) was measured at  $-20$ ,  $-10$ ,  $-5$ ,  $0$ ,  $5$ ,  $10$ ,  $20^\circ\text{C}$  using an open-air flow respirometer (picture 1). Animals were placed in a metabolic chamber ( $40 \times 40$

x 40 cm), made out of 1cm thick Plexiglas, which was then placed in a thermo-regulated fridge. From  $-5^{\circ}\text{C}$  to  $20^{\circ}\text{C}$  air was pumped in the system at a flow rate of 124 l/h. Before entering the metabolic chamber the air was dried over silica gel; air flow was monitored with a flow meter. At temperatures of  $-10$  and  $-20^{\circ}\text{C}$ , flow rate had to be increased to 149 l/h due to higher oxygen consumption of the birds. The flow rate had to be kept as low as possible to minimize the pressure in the system and to maintain oxygen concentration in the chamber above 20%. After the metabolic chamber the air passed through a bottle of silica gel and KOH in order to fix the expired  $\text{H}_2\text{O}$  and  $\text{CO}_2$ . The flow rate was controlled and measured continuously by a calibrated mass flow controller (model 5850 E, Brooks Instruments) that was connected to a control and read out equipment (model 5878, Brooks Instruments). Finally oxygen concentration was measured using an oxygen analyser (Gas purity analyser Xentra 4100, Servomex) and recorded on paper by a potentiometric recorder (recorder 320, Scientific Instruments, Basel, CH).



Picture 1. System set up for measuring oxygen consumption of black grouse. Si = silica gel; fm = flow meter; mc = metabolic chamber; fr = fridge.

Before and after experiment the system had to be stabilized for at least one hour to get an exact baseline of oxygen concentration. Bird measurement lasted 4-5 h (only 4 h when two measurements were taken daily). In the metabolic chamber birds stayed in complete darkness and were monitored continuously with an IR-camera. Oxygen consumption was calculated according to Depocas & Hart (1957):  $\text{VO}_2 = V_2 \times (F_1\text{O}_2 - F_2\text{O}_2) / (1 - F_1\text{O}_2)$ , where  $V_2$  is the flow rate measured after an animal is removed from the chamber,  $F_1\text{O}_2$  is the concentration of oxygen at the beginning of experiment, and  $F_2\text{O}_2$  is the oxygen concentration in the chamber after the animal was removed. The mean oxygen consumption per time unit and body mass was calculated and transformed into energy expenditure ( $19,8 \text{ kJ l}^{-1}\text{O}_2$ ; Lindström & Kvist 1995, Svensson et al. 1998)).



## **2.3 Activity pattern, behaviour and ambient temperatures in free-ranging birds**

### **2.3.1 Study areas and birds**

We worked at 2 study plots: Verbier (Valais, 46°2'N / 7°21'E) and Les Diablerets (Vaud, 46°18'N / 7°12'E). Among the numerous study sites within the framework of our black grouse programme, only these two sites offered appropriate facilities (in particular winter accessibility and electrical power supply for laptop and radioreceivers). In both areas potential human impact on birds is high. However, in Verbier our monitored birds inhabited habitats just below ski infrastructures (ski lifts and tracks). Birds were therefore only little disturbed by traditional winter tourism activities, although there were regular fresh ski traces crossing the area. They were made by free-riding skiers and ski-lift employees who left the ski resort in that way. In Les Diablerets the habitat of the first monitored male was sporadically included in the intensive ski zone. One ski track crossed the area, but about 80% of the habitat was not directly influenced. As in Verbier, there were from time to time free-riding skiers who traversed the area. The second radiotagged bird in Les Diablerets commuted regularly, during his activity periods, between two separate habitats, both inaccessible to skiers.

### **2.3.2 Activity pattern**

Field work took place from 20.1.03 to 27.3.03. (Verbier: 20.1.-28.2.; Les Diablerets: 3.3.-27.3.). All birds used for the field experiments were equipped with transmitters containing an activity sensor. Pulse rate was fast when birds were active ("active signals"), and slow when birds were resting ("passive signals"). Considered over 24 h this produced a variable daily "activity pattern" and provided information about activity and behaviour. Data on activity patterns of birds in disturbed and undisturbed situation were constantly recorded by stationary receiving equipment. For each monitored bird we ran experiments consisting, at the beginning, of two days of initial recording in the absence of disturbance (control I) followed, after a gap of 3 days, by 4 successive days of disturbance (flushing by the observers). Just after an experiment, we recorded again two days with no disturbance (control II; see Fig. 1).

day:		-5	-4	-3	-2	-1	0	1	2	3	4	5
situation:		undist.	undist.				dist.	dist.	dist.	dist.	undist.	undist.
		control I					flushing experiments				control II	

Fig. 1. Design of field experiments. Dist. = with disturbance; undist. = no disturbance.

In the **disturbed situation** birds were intentionally flushed by an observer once a day, over 4 successive days, in order to record corresponding activity patterns. Depending on snow conditions we flushed the birds from snow burrow or from a tree. It was important to flush the birds at a time when they were in an inactive state to better be able to quantify energy expenditures elicited by the disturbance. All flushings were undertaken between 13 and 15h30, except the very first three flushings which took place early in the morning between 7 and 7h30. In order to flush birds we had to locate exactly the site of the snow burrow. In Verbier visual observation around 9 AM enabled us to locate the iglu, as this is the time when birds burrow after their morning activity. In Les Diablerets, locating of snow burrow was achieved relying on radio signals only. Note that flushing the birds was not without risk because the danger of avalanche rises in the afternoon. In Verbier, where the black grouse area is very steep, we had avalanches and snow-slides at three different places.

The **undisturbed situation** corresponds to the periods before (day -5 and -4) or after (day +4 and +5) the flushing events; it represents control I and control II. Data on activity patterns were constantly recorded by stationary receiving equipment and regularly downloaded onto a portable computer. The receiver (Telonics TR-5) was programmed to record signals of only one bird at a time and to record all active but none of the passive signals. Connected to an omnidirectional antenna, the receiver was placed on a fixed vantage point, overlooking bird's habitat. Together with the external battery pack (Fiamm-GS, 12 V) the receiver was placed in a hermetically closed box, and burrowed in the snow in order to avoid low night temperatures. This also enabled us to hide the equipment to passing-by people. A telemetry data output (Telonics TR-5) is shown in Table 1. One horizontal line corresponds to one **data record**.

Table. 1. Telemetry data output. Presented are 4 successive data records.

year	month	day	time [h:min:s:ms]	pulse period [ms]	pulse width [ms]	relative signal strength
03	01	21	11:38:15.520	749	13	156
03	01	21	11:38:15.935	817	12	254
03	01	21	11:38:16.269	890	25	160
03	01	21	11:38:17.159	749	12	127

Each **data record** describes one recorded “active signal”. All data records from one day provide us with a picture of birds’ activity during 24 h, and therefore a so called daily **activity pattern**. Such activity pattern consists of some thousands of data records per day. The whole amount of data records per bird and day depends on the quality of the obtained signals (relative signal strength, Table 1), which in turn depend on the location of the bird, some events being sometimes not recorded. For a comparison of activity patterns between days and birds, we performed a graphical standardisation, based on 10 min time intervals, i.e. 144 (24\*6) intervals in total for a bird and day. The sum of data records were counted for each of these 144 intervals in order to draw an absolute **activity curve** with 144 **data points** (Fig. 1). These absolute data points were then transformed into relative data points considering the whole data set available (Fig. 2)

**Activity curves** (Fig. 2) were further transformed into binary curves (example in Fig. 3). Because we were interested in the intensity of the **feeding activity**, we defined criteria to decide when a bird was feeding and when not. Therefore we considered all activities that could produce active signals. From field experience it was clear that feeding and flying produce distinct active signals, whereas walking, burrowing and quitting snow burrows produce only sparsely active signals. It is also assumed that grooming produces clear active signals because of intense head movements although this behaviour could never be observed in the field. Therefore only three behaviours deliver “active signals”: feeding, flying, and cleaning. Flying can be excluded because birds generally fly only for very short periods of time. In principle activity curves thus show two essential activities: feeding and grooming. During the two daily activity periods early in the morning and in late afternoon birds are completely occupied with acquiring food. As grooming was never observed during these two periods, it is assumed that this is carried out during the passive periods in the snow burrow or outside at a hidden place. Feeding activity during the passive period was also possible when

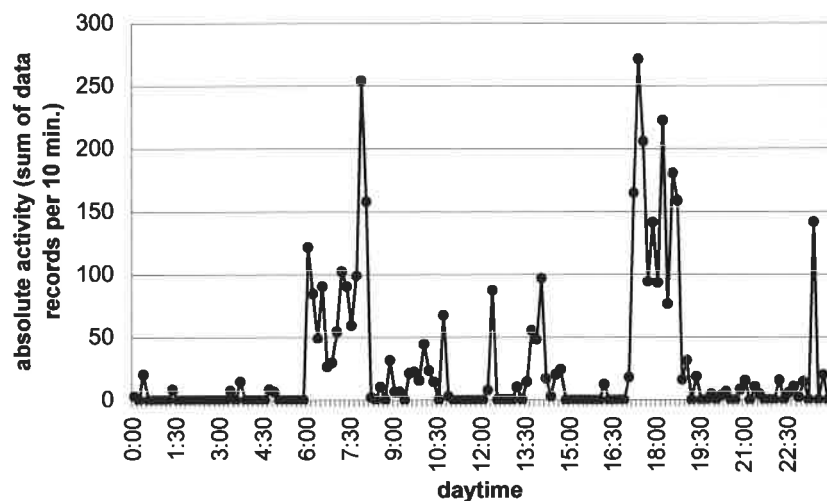


Fig. 1. Example of an absolute activity curve from bird # 522 in Les Diablerets on 12<sup>th</sup> March. Presented are the 144 daily data points (10 min periods).

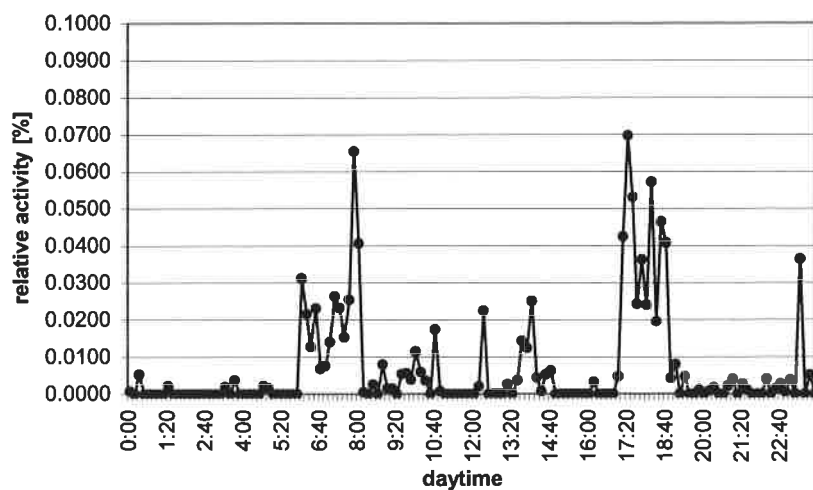


Fig. 2. Example of a relative activity curve from bird # 522 in Les Diablerets on 12<sup>th</sup> March. The Y-axis presents proportions (sum of all 144 data points = 1)

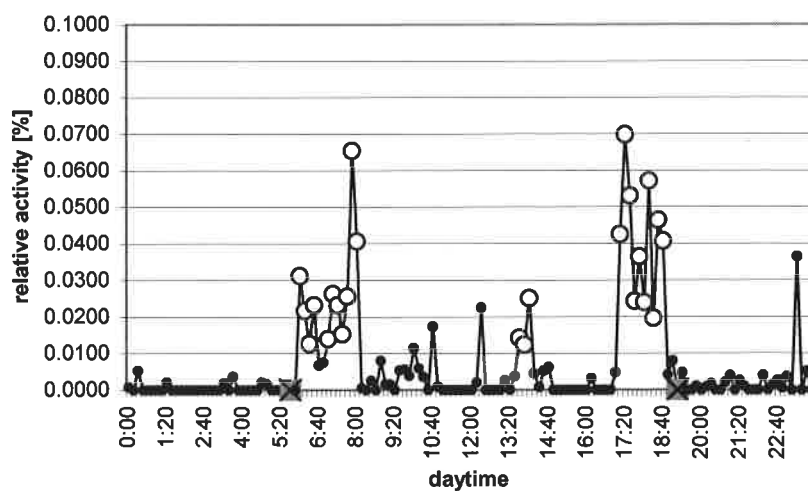


Fig. 3. Example of a feeding activity curve (marked data points depict feeding sequences) from bird #522 in Les Diablerets on 12<sup>th</sup> March. The two crosses show daylight interval boundaries.

birds roost on branches or on the ground. But in such cases activity could be recognized as high peaks in the activity curve. Therefore we assumed that in most cases feeding and grooming can be separated. Feeding activity thus corresponds to all activity that is higher than the activity during the passive periods. Criteria to determine **feeding activity** from baseline resting activity were set arbitrarily as follows:

- any cluster of  $\geq 3$  data points in succession above the 0.01 (1%) line of the relative activity;
- all points above the 0.04 (4%) line of relative activity (Fig. 3).

In some activity curves high peaks appeared at night ( $> 0.04$ ), indicating that feeding may take place then. We therefore decided to consider only **daylight activity**. Dusk and dawn were characterised by sudden and clear-cut activity changes. For each week we calculated the means of all starting and end times of birds' activity. Afterwards, only data points laying within this **daylight interval** were referred to (Fig. 3).

#### 2.3.2.1 Revised activity patterns

Sometimes transmitters produced "false" active signals maybe due to abnormal position of the tag around bird's neck. This is recognizable on activity curves as high and constant values (Fig. 4). When this happened at night only, data from the daylight interval could still be used. If this happened during the day, activity curves were not further considered in the analyses. Four out of 27 activity curves contained false active signals at night and had to be "adjusted". These erroneous data points contain a very huge amount of data records. Because data points represent relative values, erroneous sequences reduce the height of all other data points. Therefore, the criteria to determine feeding activity are no longer usable. So the error had to be completely removed as shown in Fig. 5.

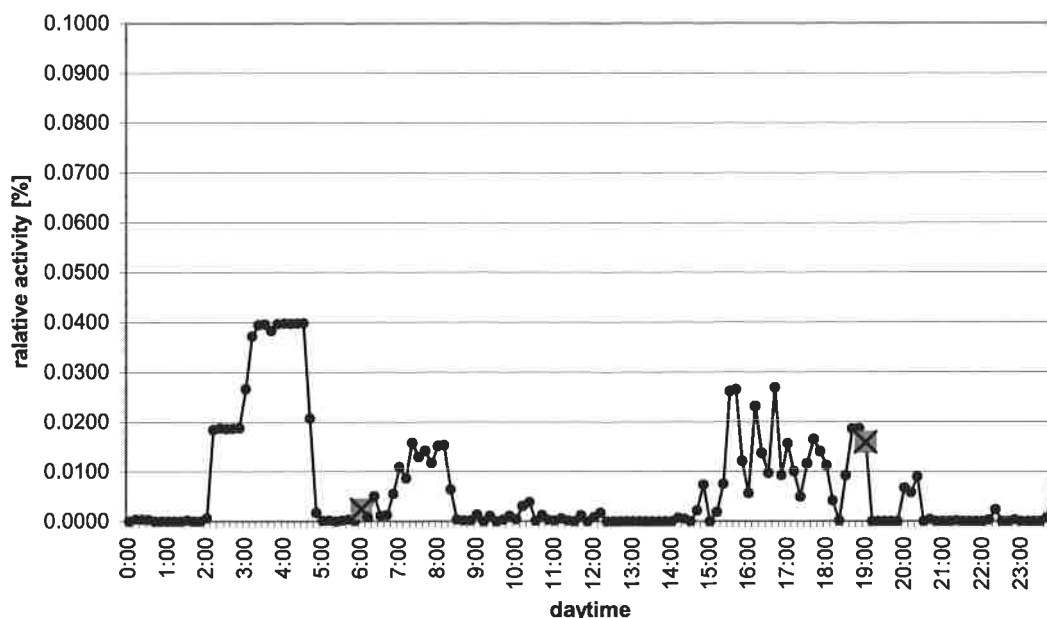


Fig. 4. Example of an activity curve from bird # 687 in Verbier on 17<sup>th</sup> February. This activity curve contains false active signals between 2 and 5 AM, The two crosses define daylight interval boundaries.

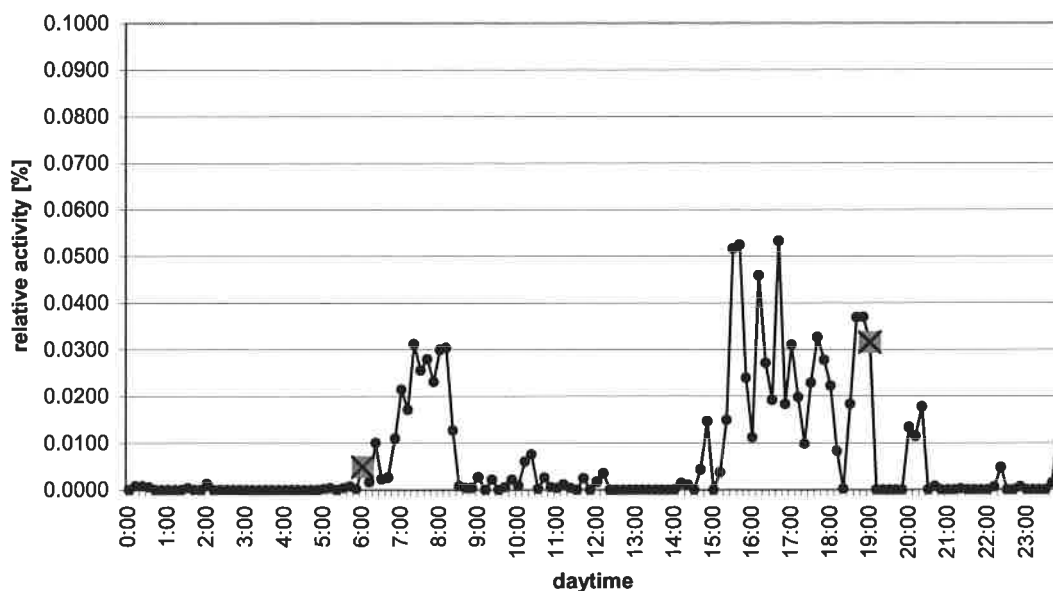


Fig. 5. Activity curve from bird # 687 in Verbier on 17<sup>th</sup> February with removed false active signals between 2 and 5 AM. The two crosses define daylight interval boundaries.

### 2.3.2.2 Night activity

Activity curves where activity seems to take place at night, as shown in Fig. 6, were recorded on 2 out of 29 nights in total (6.9 %). They have not be considered in our analyses.

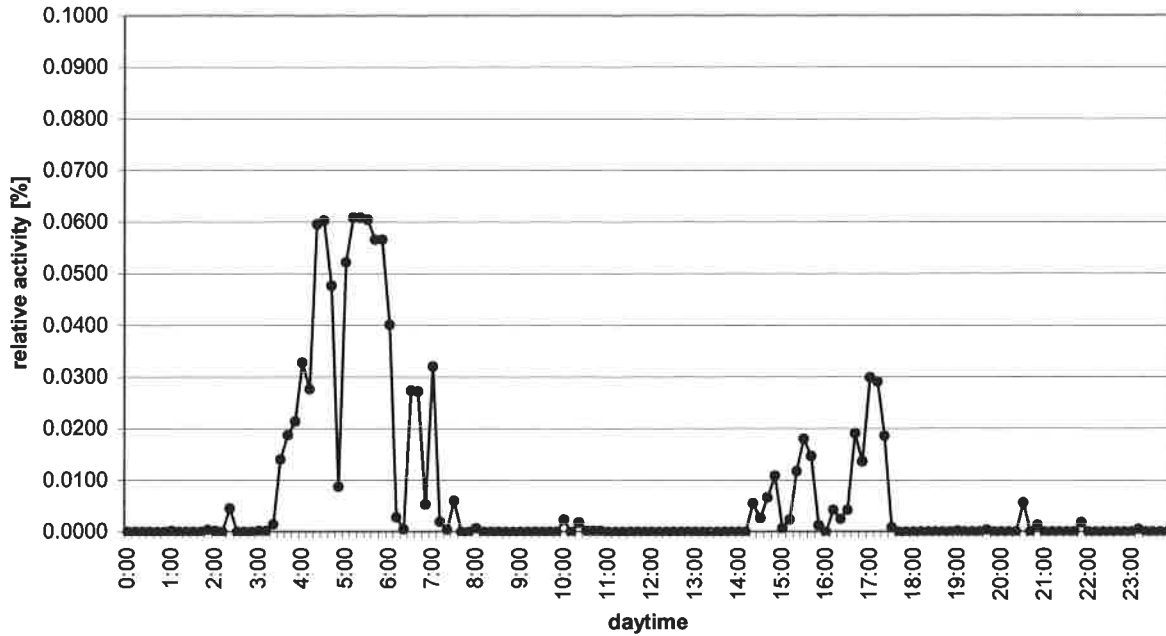


Fig. 6. Example of an activity curve from bird # 755 in Verbier on 28<sup>th</sup> January. The morning activity period seems to be switched to night.

### 2.3.3 Temperature measurements

Temperatures of air and snow were measured and recorded every thirty minutes by stationary equipment (Logger, Squirrel Meter, Typ 1006, Eltec), and every week downloaded onto a portable computer. Snow temperature was measured in 15 cm depth (approximate middle snow burrow depth). Air temperature was measured directly on snow surface and 200 cm above it. The equipment was placed in a waterproof box and burrowed into the snow in order to hide the material and to avoid low temperatures during the night.

### 2.3.4 Burrow temperatures

To be able to calculate bird's daily energy expenditures it was necessary to estimate burrow temperature. In his study of black grouse, Voklov (1968) measured iglu, snow, snowsurface, and air temperature. According to him there is a very narrow positive linear relationship between iglu and snow temperature ( $r = 0.998$ ,  $p = 0.0001$ ; Fig. 11; snowsurface temperature:  $r = 0.948$ ,  $p = 0.0141$ ; air temperature:  $r = 0.946$ ,  $p = 0.0149$ ). We therefore used the following equation to estimate iglu temperatures from our data on snow temperature:

$$T_i = 1.784 + 0.567 * T_s$$

where  $T_i$  is iglu temperature and  $T_s$  is snow temperature ( $r^2 = 0.996$ ,  $p < 0.0001$ ).

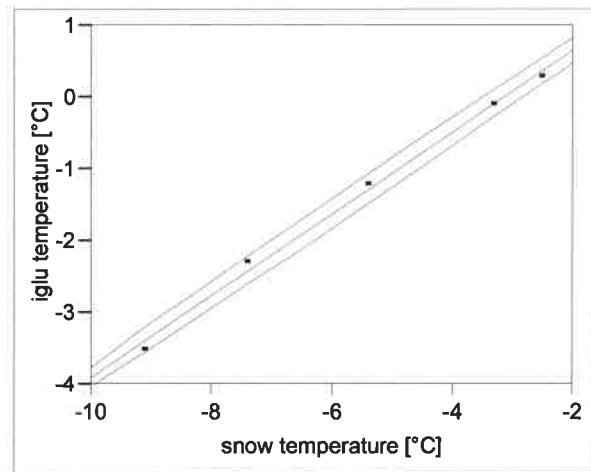


Fig. 11. Product moment correlation of iglu vs. snow temperature. Density ellipse shows 90 % confidence intervals. The linear regression line is also presented.

### 2.3.5 Visual observation of behaviour

Birds were observed, whenever weather and topography allowed, during the two active periods early in the morning (7-9 AM) and in late afternoon (4-8 PM), in order to recognize whether birds were inside or outside snow burrows. When available, sequences of simultaneous recorded data (activity curve via radioequipment, on one side, and visual observation of behaviour, on the other side) were used to interpret complete activity curves and therefore to reconstruct daily **time budgets**.



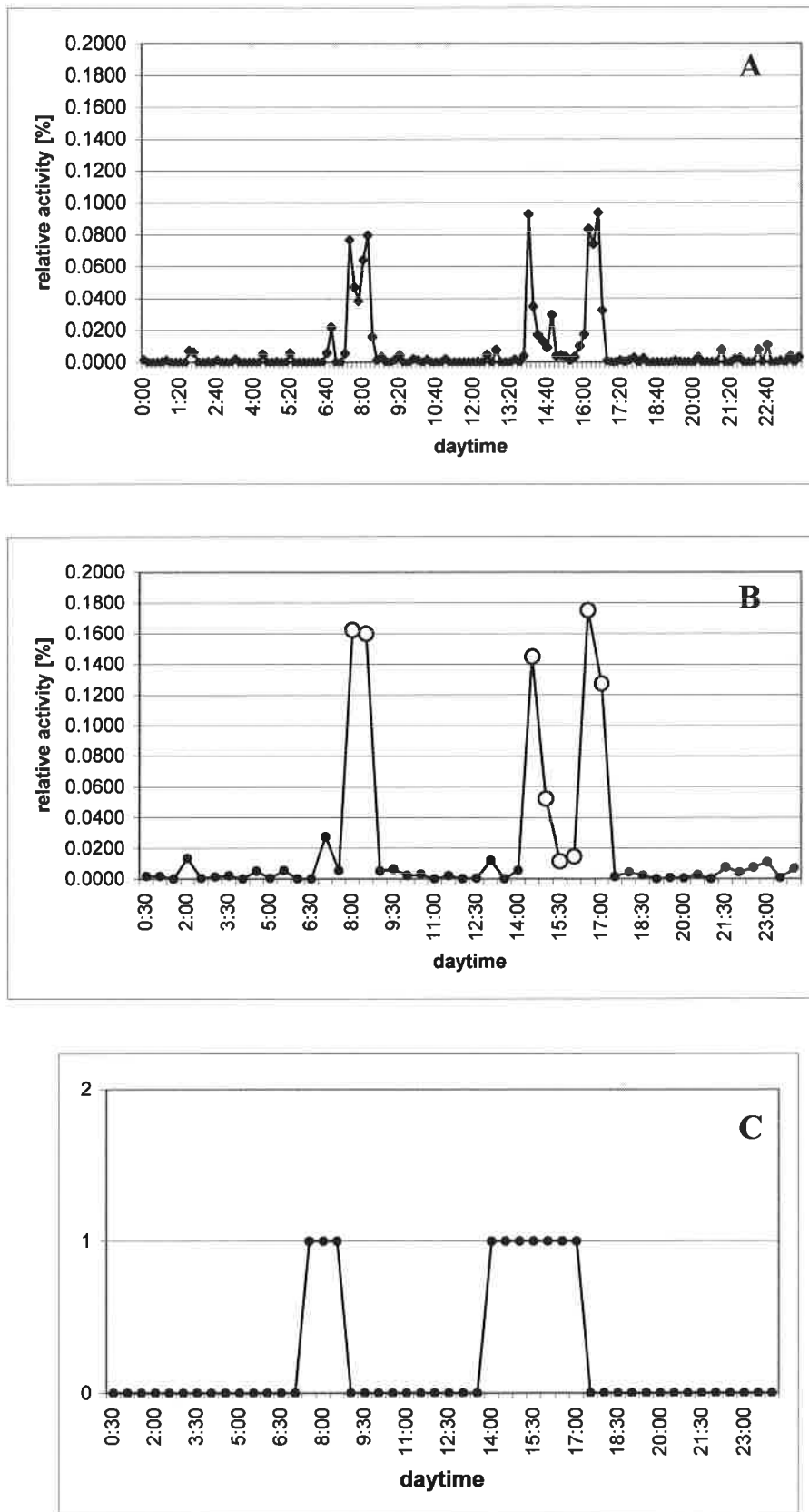


Fig. 7. Progression from an activity curve (A) towards its time budget (C) from bird # 755 in Verbier on 30<sup>th</sup> January. A) Activity curve with 10 min time interval; B) Activity curve reduced to 30 min time interval; open circles indicate activity outside iglu; C) Final time budget ( 0 = "bird inside iglu", 1 = "bird outside iglu").

## 2.4 Time budget

Time budgets considered two major behaviours: inside or outside snow burrow. Therefore a time budget can be presented like a dichotomic curve with 0 = “bird inside snow burrow” and 1 = “bird outside snow burrow”. To achieve time budget analyses, only those activity curves could be used which showed a clear fragmentation between active and passive periods, in order to be able to define the two mentioned behaviours. Activity curves consist of data points that represent ten minute intervals each. As temperature data were recorded every 30 min., 3 successive ten minute periods were grouped together. Finally, a bird was considered as outside a snow burrow by determining at each of the two activity periods: first two points in succession above the 0.02 (2%) activity line, the last point above the 0.02 (2%) activity line, and all points in between (Fig. 7).

### 2.4.1 Energetic quantification of daily time budget

Time budgets were used to calculate **daily energy expenditures** of a given bird on a given day. Using the oxygen consumption equation, obtained from respirometric measurement in the lab, energy expenditures for each 30 minute period (starting with time interval 0:00 - 0:30 and ended with interval 23:30 – 24:00) was calculated. Therefore, depending on the behaviour of the bird (visible on time budget), either temperature of air or iglu was used to estimate daily energy expenditures. To know how much energy a bird was saving on a particular day, energy expenditure of a burrowing bird was compared with an hypothetical bird which would have stayed that day outside the iglu, other things being equal.

## 2.5 Statistical analyses

Because data were not normally distributed and sample size was small, the additive effect of disturbance was tested by means of Spearman's rank correlation test. The relationships between saved energy vs air temperature, as well as oxygen consumption vs burrow temperature were calculated by regression analyses. Analyses were performed using the program JMP4 (SAS Institute Inc. 2001, Cary, NC, USA).

### 3 Results

#### 3.1 Oxygen consumption

Oxygen consumption increased linearly with decreasing temperatures. The female did not differ strikingly from the males (Fig. 8). Raw data are presented in Appendix 1.

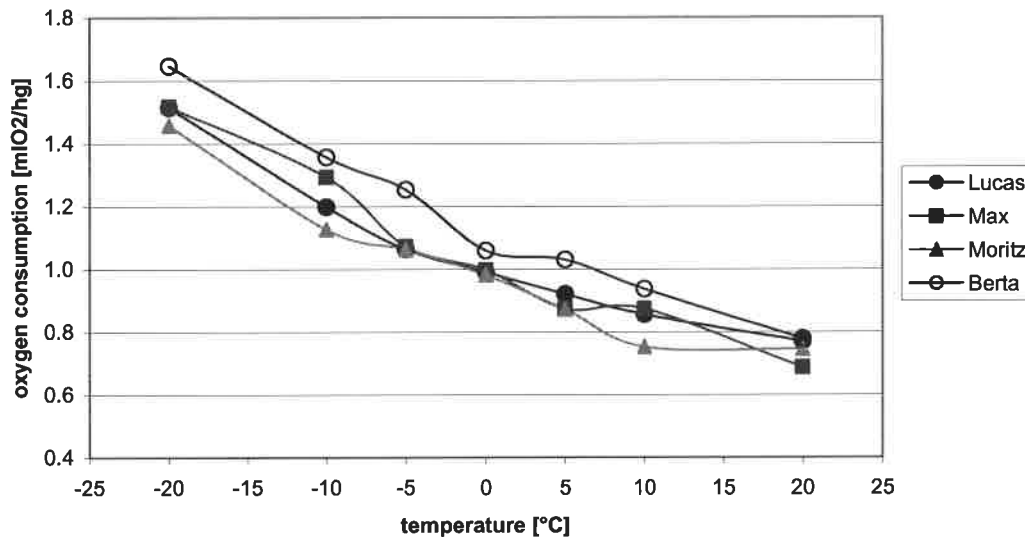


Fig. 8. Mass relative metabolism ( $\text{mlO}_2/\text{h}\cdot\text{g}$ ) at seven different temperature levels for three males and one female.

As we restricted field observations to males, the female was excluded from subsequent regression analyses. Figure 9 shows the relationship between absolute metabolism and ambient temperature. Its equation is:

$$\text{Oxygen consumption} = 1000.65 - 19.4 \cdot T + 0.365 \cdot T^2$$

with oxygen consumption being measured as  $\text{mlO}_2/\text{h}$  and  $T$  being temperature in  $^{\circ}\text{C}$  ( $r^2 = 0.975$ ,  $p < 0.0001$ ).

An analysis performed on average values yielded a better relationship ( $r^2 = 0.998$ , Fig. 10), but we used the former equation for estimating metabolism in free-ranging birds.

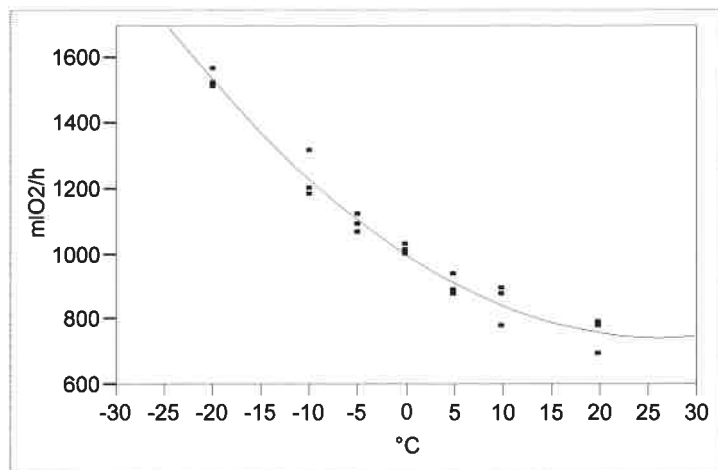


Fig. 9. Absolute metabolism vs ambient temperature.  
Regression curve drawn through all data points (n=3 birds).

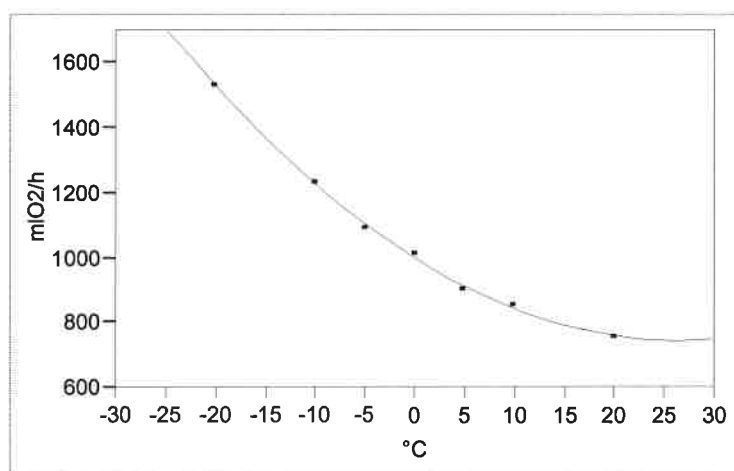


Fig. 10. Absolute metabolism vs ambient temperature.  
Regression curve drawn using mean values.

### 3.2 Feeding activity and energetic expenditures

Feeding activity seemed to increase from day 0 (first flushing day) to day 3 (last flushing day) suggesting that disturbance may have an additional effect (Fig. 12). But this trend was not significant ( $r_s = 0.454$ ,  $n = 8$ ,  $p = 0.259$ ). This however, was due to an outstanding point on day 3. If removed, the trend became significant ( $r_s = 0.954$ ,  $n = 7$ ,  $p = 0.0009$ ). Despite data independency was not achieved (one bird was measured more than once), we ran Mann-Whitney U-tests to see if control values differed from experimental day values. There is no significant difference between control I days and experimental days ( $z = 0.66238$ ,  $n = 12$ ,  $p = 0.5077$ ). Also no significant difference was found between experimental days and control II days ( $z = -0.77630$ ,  $n = 14$ ,  $p = 0.4376$ ).

Estimated energy expenditures of days 0-3 showed no trend at all during flushing experiments ( $r_s = 0.358$ ,  $n = 8$ ,  $p = 0.386$ ; Fig. 13). There was no significant difference between experimental days and control I days ( $z = 1.39066$ ,  $n = 12$ ,  $p = 0.1643$ ) and between control II days and experimental days ( $z = 0.96931$ ,  $n = 14$ ,  $p = 0.3324$ ).

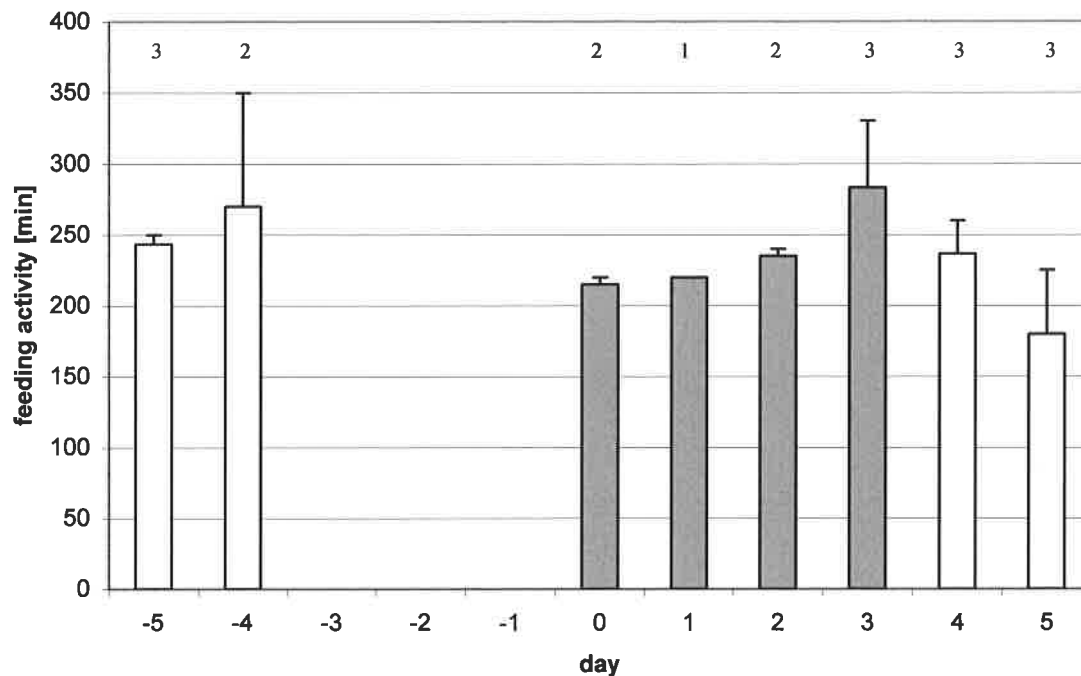


Fig. 12. Mean ( $\pm$  se) feeding activity of 4 birds on undisturbed days (white bars = controls) and disturbed days (grey bars = flushing experiments). Numbers above the columns represent the sample size (Appendix 1).

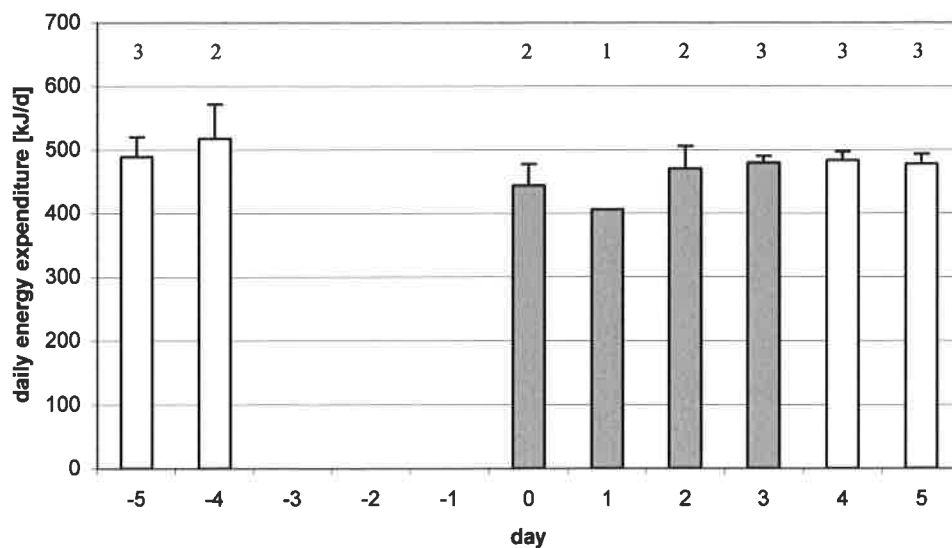


Fig. 13. Mean ( $\pm$  se) daily energy expenditure of 4 birds on undisturbed days (white bars = controls) and disturbed days (grey bars = flushing experiments). Numbers above the columns represent the sample size (Appendix 1).

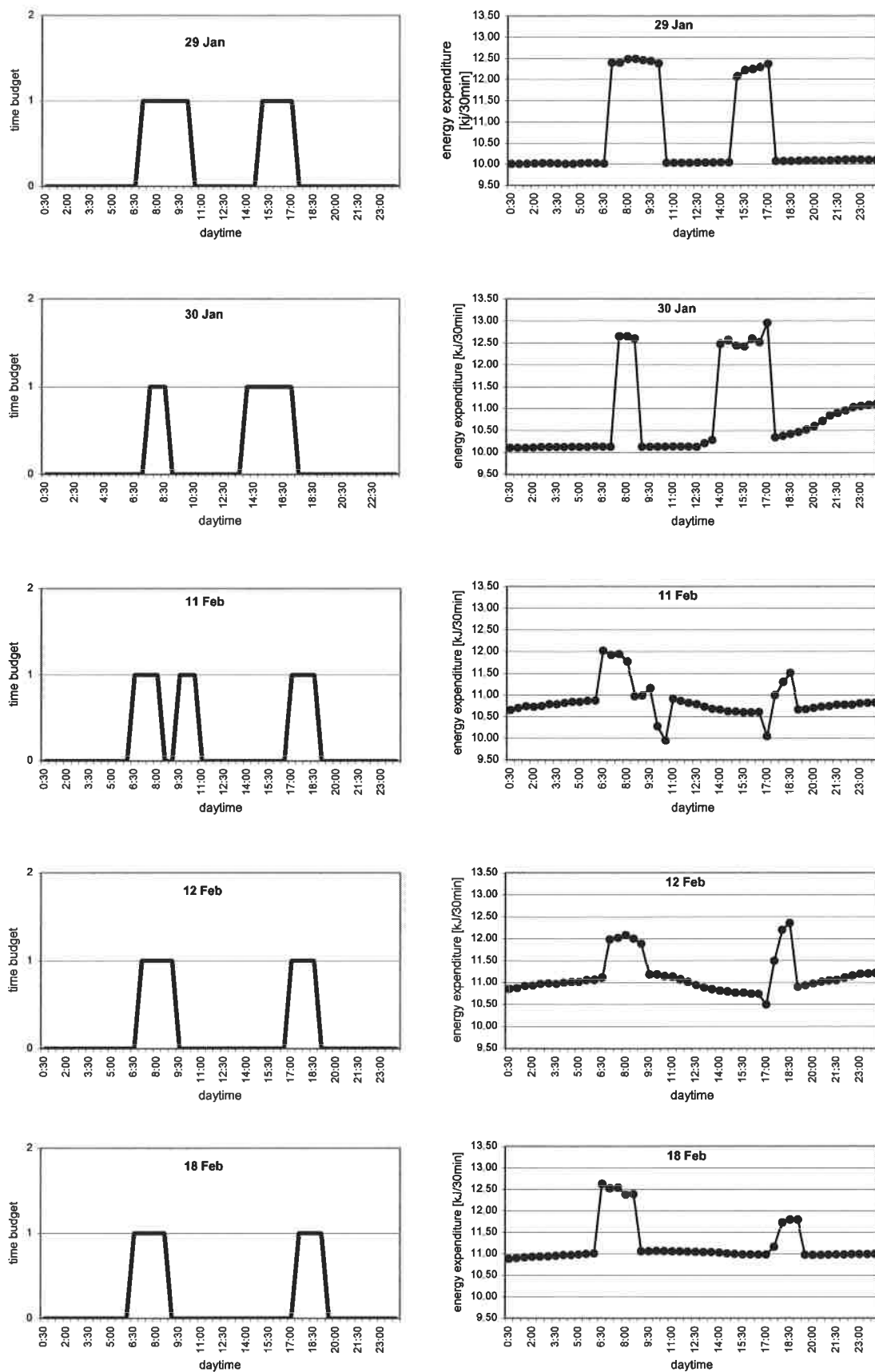


Fig. 14. Time budgets (left) and related energy expenditure (right). For time budget: 1 = bird outside iglu; 0 = bird inside iglu.

Fig. 14 shows an example of conversion of time budget into energy expenditure data for bird # 755 in Verbier. Diagrammed are five days when bird showed his typical bimodal behaviour (snow burrowing) due to ideal snow condition. The mean duration of morning activity was  $2.1 \pm 0.57$  h (range: 1.5 – 3h) while afternoon activity lasted on average  $1.9 \pm 0.65$  h (range: 1.5 – 3h).

Fig. 15 shows, for the same bird and days as in Fig. 14, the differential between atmospheric and iglu temperatures. Fig. 16 shows the hypothetical energetic gain achieved by the bird if it would have stayed within its iglu instead of roosting outside at atmospheric temperatures. If the bird had spent this time outside the iglu, the mean ( $\pm$  SD) daily energy expenditures would have been  $568.1 \pm 33.8$  kJ vs  $524.6 \pm 11.5$  kJ if it would have used its snow burrow.

Black grouse can save up to 15 % energy if snow burrowing on cold days (Fig.17). A relationship between estimated energy savings and air temperatures shows that energy savings through the iglu strategy are much greater at lower air temperatures (29 and 30 January).

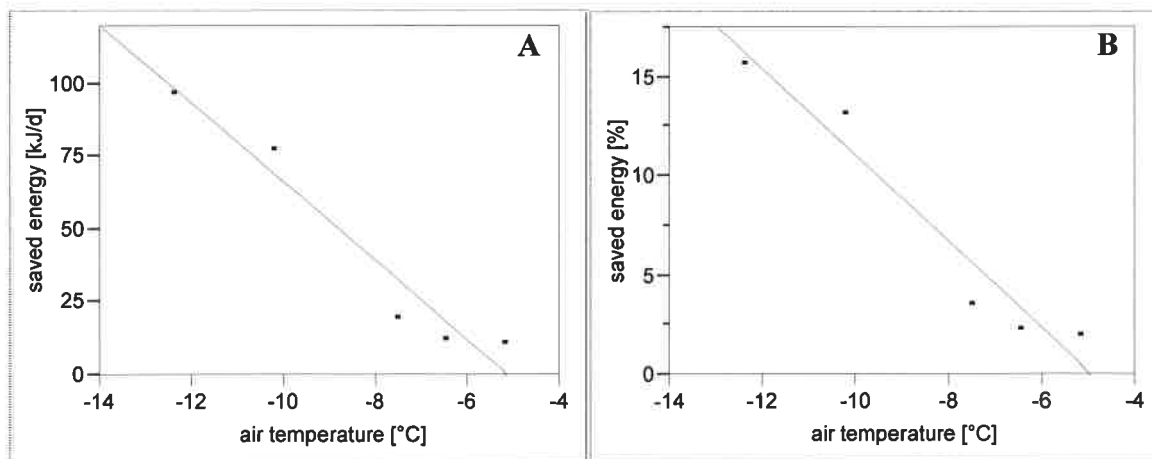


Fig. 17. Estimated energy savings with respect to air temperature expressed in kJ (A) and percent (B).

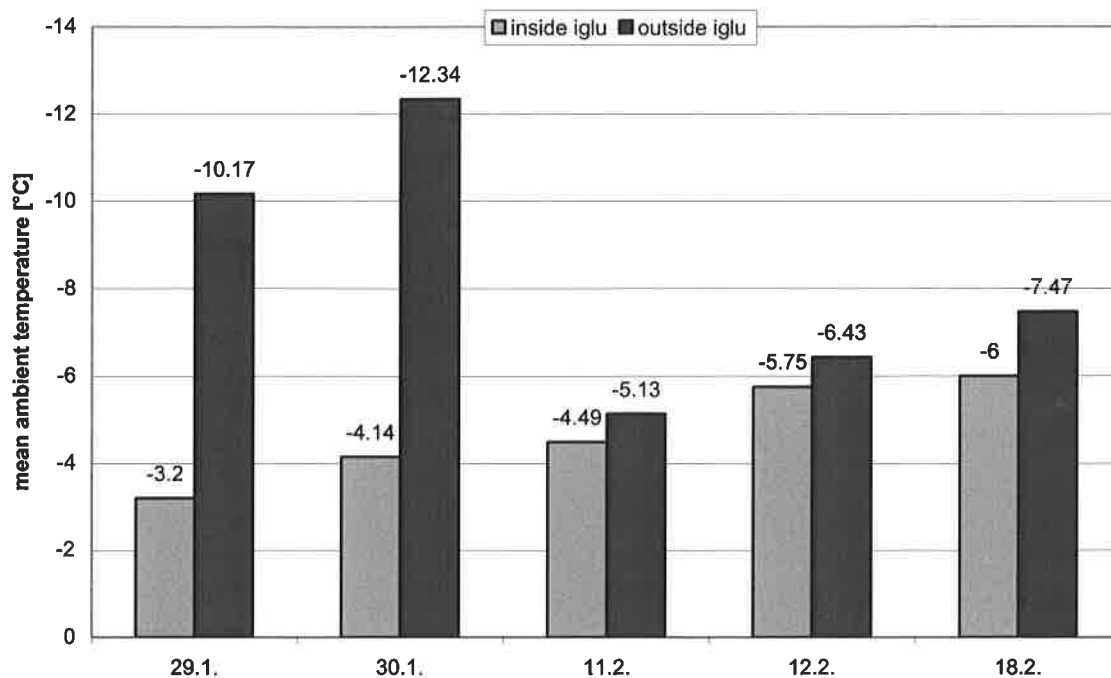


Fig. 15. Measured (inside iglu) and hypothetical (outside iglu) mean ambient temperatures on five days in bird # 755.

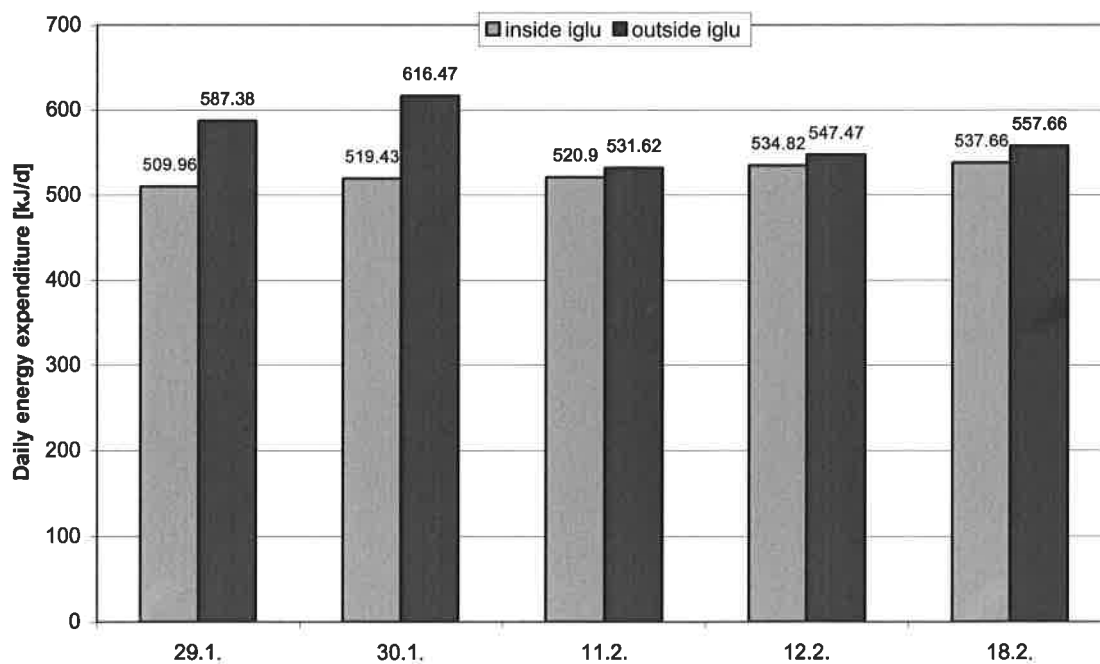


Fig. 16. Measured (inside iglu) and hypothetical (outside iglu) daily energy expenditures on five days in bird # 755.



## 4 Discussion

We compared our results with Rintamaki's data (1983) on oxygen consumption of black grouse in Finland. The shape of both (his and ours) oxygen consumption curves looks similar, without distinct inflection point and no thermoneutrality in the range of temperatures measured. Yet, Rintamaki's birds consumed about 50% more oxygen and the increase in oxygen consumption at lower temperatures was more pronounced. This discrepancy can have several causes: variation in measurement procedures or differences in acclimatization or adaptation to cold of birds. Weathers (1979) calculated that, in birds, metabolic rate changes, on average, by 1% per degree in latitude. This could explain a 20% lower metabolic rate in birds from the Swiss Alps compared with birds from Finland (Oulu, 65°N). The remaining variation remains difficult to interpret, however.

Based on data presented by Volkov (1968), we calculated an equation to estimate iglu temperatures so as to draw estimations of birds' oxygen consumption during resting period in snow burrow. However, in Volkov's experiments (1968) the birds were placed in small metal cages burried in snow, which possibly disrupted snow structure and heat conductance. Therefore our calculations about energy expenditure and energy-saving could be either over- or underestimated. According to our results, birds can save during cold days up to 15 % of daily energy expenditures by resting in iglus during the passive periods. It would be wise to repeat Volkov's experiments with a more appropriate experimental set up (no metal cage, etc.) to better quantify potential energy savings in wintering Black grouse. In order to achieve this, we could refer to a study by Andreev (1977). His birds carried an electric sensor on the back, connected by fine wires to a measuring device. Placed in fresh snow and exposed to cold they readily burrowed a cavity. Data on iglu and snow temperature collected in such a manner would be more realistic than our extrapolations from Volkov's data (1968).

We could not firmly demonstrate that the feeding activity in a disturbed bird was higher than in an undisturbed bird, although a trend was recognizable (Fig. 12). Albeit not differing from experimental results, high values on control I days could be due either to birds otherwise disturbed or to colder weather. As regards control II days, high daily feeding activity following days of disturbance could still be an effect of compensating for extra energetic costs. In this case declining feeding activity would occur only later on.

Despite the fact that a trend to higher feeding activity occurred during experimental days (Fig.12), pointing to a possible additive effect of our flushing experiments, this was not paralleled by a trend to higher energy expenditures (Fig. 13). Several other factors like snow

quality, air temperature, precipitation, or additional disturbance by tourists or ski lift employees may be accounted for. Also it seems that some birds can really get used to regular human presence, which may have further reduced the effect of our flushings. A larger sample size is required to get a better picture.

Under some circumstances night activity was recorded, indicating that night feeding might take place. In this case night feeding activity should be included in our analyses, otherwise daily feeding would be underestimated. Yet, some night activity seems to be normal and relates probably mostly to grooming and not to feeding. In the laboratory we observed that birds have not a continuous sleep. They were sleeping most of the time but woke up regularly, about every 7-10 min, staying awake for about one minute. When birds were awake they changed their position by walking around a little bit, fluffed up their plumage, gaped and cleaned their feathers. This behavior could also be proceeded under natural conditions in iglu or on trees. Waking up regularly during sleep could be a way to prevent being surprised by predators. Long activity bouts during the night (Fig. 6), might coincide with intense feeding on bright nights. As far as these long feeding bouts are concerned they should be considered in our future analyses.

In the wild, Black grouse might actually not respond to disturbance by increasing feeding activity and therefore energy expenditures. Disturbance might in the end merely affect condition and fitness without provoking immediate compensatory strategies (Hüppop & Hagen 1990). The measurement of heart beat rate might be a better indicator of stress (Jungius & Hirsch 1979; Hüppop & Hagen 1990). Heartbeat-rate radio-transmitters can be fixed on birds' body or can be implanted. Through telemetric acquisition it would be possible to assign individual stress to a specific input of disturbance (Hüppop 1995). Hubert & Hüppop (1993) found a duplication in rate of heartbeat under excitation for black-legged kittiwake *Rissa tridactyla*. Rate of heartbeat and oxygen consumption are, in general, linearly correlated, which offers another method for measuring actual energy expenditures (Webster 1967; Johnson & Gessaman 1973; Hayes et al. 1992). Together with heartbeat-rate, the level of stress hormones (adrenalin, noradrenalin, corticosteron for birds) increases when an animal is disturbed (Harlow et al. 1987). Hormone excretion incurs specific energy expenditures (Siegel 1980; Axelrod & Reisine 1984; Moen 1973). The quantification of stress hormones appears thus to be one of the most promising avenues for the study of human-generated disturbances on animals.

During our flushing experiments droppings were collected from snow iglus. Analyses of stress hormone (corticosteron) metabolites in this faecal material (Baltic, unpublished) showed that there was a significant difference in corticosteron level between control day and experimental days. This proves that disturbance was actually effective during our field experiments. It appears that a combination of several methods (time budget, energy output, heartbeat frequency, stress hormones) might be the best way to quantify the actual impact of human activities, in particular winter sports, on alpine Black grouse populations.

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## 6 References

- Arlettaz, R., Ruchet, C., Aeschimann, J., Brun, E., Genoud, M. & Vogel, P. 2000. Physiological traits affecting the distribution and wintering strategy of the bat *Tadarida teniotis*. *Ecology* 81: 1004-1014.
- Aschoff, J. 1966. Circadian activity patterns with two peaks. *Ecology* 47: 657-662.
- Andreev, A.V. 1977. Temperature conditions in snow-holes of *Tetrastes bonasia kolyomensis* But. *Ekologija* 8(5): 93-95.
- Axelrod, J. & T. D. Reisine 1984. Stress hormones: their interaction and regulation. *Science* 224: 452-459.
- Bertram, B.C.R. 1978. Living in groups: predators and prey. An evolutionary approach. Blackwell Scientific Publications pp. 64-96.
- Bossert, A. 1980. Winterökologie des Alpenschneehuhns *Lagopus mutus Montin* im Aletschgebiet, Schweizer Alpen. *Orn. Beob.* 77: 121-166.
- Calder, W.A. & King, J.R. 1974. Thermal and caloric relations of birds. Academic Press, New York and London pp. 259-413.
- Depocas, F. & Hart, S. J. 1957. Use of the Pauling oxygen analyser for measurement of oxygen consumption of animals in open-circuit systems and in a short-lag, closed-circuit apparatus. *J. Appl. Physiol.* 10: 388-392.
- Ellison L.N., Leonard, P & Menoni, E. 1988. Effect of shooting on a black grouse population in France. *Supplemento alle Ricerche di Biologia della Selvaggina* 14:117-128.
- Fransilla, M. 1949. Mikroilmasto-oppi. Otava, Helsinki pp. 257.
- Giorgi, M.S., Arlettaz, R., Christe, P. & Vogel, P. 2001. The energetic grooming costs imposed by a parasitic mite (*Spinturnix myoti*) upon its bat host (*Myotis myotis*). *Proc. R. Soc. Lond. B*, 268: 1-5.
- Glutz von Blotzheim, U.N., Bauer, K.M. & Bezzel, E. 1973. Handbuch der Vögel Mitteleuropas 5. Akademische Verlagsgesellschaft, Frankfurt am Main, pp. 700.
- Harlow, H. J., E. T. Thorne, E. S. Williams, E. L. Belden & W. A. Gern 1987. Cardiac frequency. *Can. J. Zool.* 65: 2028-2034.
- Hayes, J. P., J. R. Speakman & P. A. Racey 1992. Sampling bias in respirometry. *Physiol. Zool.* 65: 604-619.
- Hjorth, I. 1970. Reproductive behaviour in *Tetraonidae* with special reference to males. *Viltrevy* 7: 181-596.

- Hubert, B. & O. Hüppop 1993. The influence of excitement on heart rate and oxygen consumption of Kittiwakes (*Rissa tridactyla*). Proc. Int. Congr. Appl. Ethol., Berlin 1993: 541-543.
- Hüppop, O. & K. Hagen 1990. Der Einfluss von Störungen auf Wildtiere am Beispiel der Herzschlagfrequenz brütender Austernfischer. Vogelwarte 35: 301-310.
- Hüppop, O. 1995. Störungsbewertung anhand physiologischer Parameter. Der Ornithologische Beobachter 92: 257-268.
- Ingold P., Huber B., Mainini B., Marbacher H., Neuhaus P., Rawyler A., Roth M., Schnidrig R. & Zeller R. 1992. Freizeitaktivitäten – ein gravierendes Problem für Tiere ?. Der Ornithologische Beobachter 89: 205-216.
- Johnson, S. F. & J. A. Gessaman 1973. An evaluation of heart rate as an indirect monitor of free-living energy metabolism. In : J.A. Gessaman (Ed.): Ecological energetics of homeotherms. Monogr. Ser. Utah State Univ. Press. Logan 20: 44-54.
- Jungius, H. & U. Hirsch 1979. Herzfrequenzänderungen bei Brutvögeln in Galapagos als Folge von Störungen durch Besucher. J. Orn. 120: 299-310.
- Kauhala, K., Helle, P. & Helle, E. 2000. Predator control and the density and reproductive success of grouse populations in Finland. Ecography, 23: 161-168.
- Korhonen, K. 1980. Microclimate in the snow burrows of willow grouse *Lagopus lagopus*. Ann. Zool. Fennici 17: 5-9.
- Lindström, J., Ranta E., Kaitala V. & Lindén H. 1995. The clockwork of Finnish tetraonid population dynamics. Oikos 74: 185-194.
- Lindström, A. & Kvist, A. 1995. Maximum energy intake rate is proportional to basal metabolic rate in passerine birds. Proc. R. Soc. Lond. B, 261: 337-343.
- Marjakangas, A. 1980. Snow roosting in tetraonids *Tetraonidae*. Memoranda Societatis Pro Fauna et Flora Fennica 56: 65-70
- Marjakangas, A. 1986. On the winter ecology of the black grouse, *Tetrao tetrix*, in central Finland. Acta Universitatis Oulensis, Series A, No 183, pp. 34.
- Marti, C. 1985. Unterschiede in der Winterökologie von Hahn und Henne des Birkhuhns *Tetrao tetrix* im Aletschgebiet (Zentralalpen). Orn. Beob. 82: 1-30.
- Marti, C. 1980. Die Energieversorgung des Birkhuhns im Winter. Wildtiere 4/86
- Moen, A. N. 1973. Wildlife ecology. Freeman, San Francisco. 16 + 458 S.
- Pauli, H. R. 1980. Nahrungsökologische Untersuchungen am Birkhuhn in den Schweizer Alpen. Beih. Veröff. Naturschutz Landschaftspflege Bad. Württ. 16: 23-35.

- Pauli, H. R. 1974. Zur Winterökologie des Birkhuhns *Tetrao tetrix* in den Schweizer Alpen. Orn. Beob. 71: 247-278.
- Porkert, J. 1969. Zum Übernachten unserer Waldhühner im Schnee. Opera Corcontica 6: 93-102.
- Potapov, R.L. 1985. Otrjad kuroobraznye (Galliformes). Fauna SSSR, Pticy Tom III, Vyl. 1. Leningrad.
- Pulliainen, E. 1981. Weights of the crop contents of *Tetrao urogallus*, *Lyrurus tetrix*, *Tetrastes bonasia* and *Lagopus lagopus* in Finnish Lapland in autumn and winter. Ornis Fennica 58: 64- 71.
- Ricklefs, R.E., Konarzewski, M. & Daan, S. 1996. The relationship between basal metabolic rate and daily energy expenditure in birds and mammals. The American Naturalist, 147: 1047-1071.
- Rintamäki, H., Saarela, S., Marjakangas, A. & Hissa, R. 1983. Summer and winter temperature regulation in the black grouse *Lyrurus tetrix*. Physiological Zoology, 56: 152-159.
- Semenov-Tjan-Šanskij, O.I. 1960. Die Ökologie der Birkhuhnvögel (*Tetraoniden*). 5: 1-304.
- Siegel, H. S. 1980. Physiological stress in birds. BioScience 30: 529-534.
- Svensson, E., Råberg, L., Koch, C. & Hasselquist, D. 1998. Energetic stress, immunosuppression and costs of an antibody response. Functional Ecology, 12: 912-919.
- Volkov, N.I. 1968. An experimental study of thermal conditions in snow burrows of tetraonid birds. Zool. Žurnal 47: 283-286
- Webster, A. J. F. 1967. Continuous measurement of heart rate as an indicator of the energy expenditure of sheep. J. Nutr. 21: 769-785.
- West, G.C. 1968. Bioenergetics of captive willow ptarmigan under natural conditios. Ecology, 49: 1035-1045
- Weathers, W.W. 1979. Climatic adaptation in avian standard metabolic rate. Oecologia (Berlin), 42: 81-89

## 7 Appendices

Appendix 1. Oxygen consumption at seven different temperature levels for three males and one female. Body mass was measured before experiment.

Lucas	ml O <sub>2</sub> /h	mass	mlO <sub>2</sub> /hg
-20	1513.5	999.2	1.515
-10	1200.5	1001.1	1.199
-5	1067.6	1003.1	1.064
0	1010.0	1019.6	0.991
5	941.7	1022.7	0.921
10	879.2	1027.4	0.856
20	792.9	1028.7	0.771

Max	ml O <sub>2</sub> /h	mass	mlO <sub>2</sub> /hg
-20	1565.6	1031.2	1.518
-10	1319.5	1019.8	1.294
-5	1092.8	1018.5	1.073
0	998.7	1000.5	0.998
5	876.1	1002.2	0.874
10	894.1	1022.6	0.874
20	692.8	1008.4	0.687

Moritz	ml O <sub>2</sub> /h	mass	mlO <sub>2</sub> /hg
-20	1525.9	1046.9	1.458
-10	1186.6	1053.1	1.127
-5	1122.2	1055.4	1.063
0	1029.7	1049.4	0.981
5	887.5	1018.3	0.872
10	782.5	1039.7	0.753
20	783.2	1051.6	0.745

Female	ml O <sub>2</sub> /h	mass	mlO <sub>2</sub> /hg
-20	1329.9	808.0	1.646
-10	1080.2	795.9	1.357
-5	1003.1	800.2	1.254
0	826.8	780.0	1.060
5	826.2	802.0	1.030
10	748.6	798.6	0.937
20	622.1	799.0	0.779



Appendix 2. Daily total feeding activity (minutes) for the four radiomonitorred, free-ranging birds. Note that bird # 755 was used in two separate flushing experiments. Underlined are the days when birds stayed in iglus during the passive periods.

day:

bird #	undisturbed							disturbed				undisturbed															
	-6	-5	-4	-3	-2	-1	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16				
389										320	200	270															
522		250	190				220	220	240	340	280	130															
687		250	350				290		260	180		140															
755							140		230	190	230																
755		230					210		170	160											180	140					