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Microclimate in the snow burrows of willow grouse (Lagopus lagopus)

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Temperature, relative humidity, and CO_2 content were recorded experimentally in artifical snow burrows of penned willow grouse in northern Finland. The rapidity of warming was inversely proportional to the temperature and original density of the snow. At air temperatures below —35°C the burrow temperature might rise continuously for as long as 8 h, but usually it reached a constant level within 2—3 h. The final temperature of closed burrows was not essentially affected by snow density, and was nearly always higher than the lower critical temperature for the willow grouse (—6 °C). CO_2 did not accumulate in the burrows, and the relative humidity was always 100 %.

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1. Introduction

Birds of the grouse family (*Tetraonidae*), in spite of their excellent insulation, shelter against cold and wind in open or closed snow burrows. There are numerous descriptions of this roosting behaviour and of the structure of the snow burrows (e.g. Formozov 1946, Teplova & Teplov 1947, Johnson 1954, Dulkeit 1960, Siivonen 1963, Sulkava 1969, Marjakangas 1979). According to Kuzmina (1961), snow burrowing is an adaption to the poor nourishment during wintertime; the birds can survive only if they can collect their food very quickly and burrow into the snow for the rest of the time. In this way, they minimize their energy consumption. There is only scanty published evidence that tetraonid birds depend on snow shelters, but in cold winters with a hard snow crust and icing they may starve to death (Teplova & Teplov 1947, Kuzmina 1961, McGowan 1969). Birds with a full crop have a reserve that will provide energy for at least 2 days (Irving et al. 1967). Capercaillies (*Tetrao urogallus*) may spend 2 or 3 days and nights in their snow burrows, and the hazel hen (*Tetrastes bonasia*) does not leave the burrow if the outside temperature is below —33 °C (Donaurov 1947, Kuzmina 1961). Alaskan willow ptarmigan (*Lagopus lagopus*) lose weight during the coldest period of winter (West & Meng 1968). In penned ring-necked pheasants (*Phasianus colchicus*) the reduction in body weight may affect the outcome of reproduction (Breitenbach et al. 1963, Gates & Woehler 1968, Barret & Bailey 1972).

The first measurements of the temperatures in the snow burrows of tetraonid birds were presented by Volkov (1968). He found that the closed burrows of the hazel hen and the black grouse (*Lyrurus tetrix*) were 2.8—8.4 °C warmer than the snow at the same depth. Volkov (1968) also discusses factors influencing the warming process.

The purpose of this study was to determine how snow density, temperature, and burrow structure affect the microclimate of the burrow, and to estimate the energetic advantage of snow shelters for willow grouse (*Lagopus l. lagopus*).

2. Methods

The research was carried out at Simo (65°37′N, 25°00′E) in 1975, at the Meltaus Wildlife Research Station (66°55′N, 25°15′E) in 1976, and at the Kilpisjärvi Biological Station (69°03′N, 20°49′E) in 1977. The mean weight of the 6 willow grouse captured with nets and used in the experiments was 536 g (range 485—700 g). In the cages (2.4 × 1.2 × 0.6 m) the birds were exposed to the local conditions and could burrow in the snow. They were fed with willow branches, cowberries, and red whortleberries.

The burrow temperatures were measured by the method described by Volkov (1968). Experimental pens of size 12 × 25 × 12 cm were made of 12-mm cotton net stretched on a wire frame. The size of the experimental pen was based on measurements of 357 natural snow burrows of willow grouse. A thermocouple or thermistor was inserted into a plastic tube tied inside the pen. The tube was partly open at the side in the lower part. Thus the thermocouple or thermistor was not in contact with either the snow or the bird, and was protected against any falling snow. The roof above the closed burrow was always about 5 cm thick (the mean of measurements in 117 closed burrows). Temperature was measured with a Wallac EP-400 thermohygrometer (a thermistor) or with a thermocouple connected to a Honeywell electronik Y 153 recorder. When used simultaneously in 1977 the two methods gave the same readings. Because the bird might shift its position during the measurement and so cause some temperature variation, readings were made to the nearest 0.5 °C only.

The CO$_2$ content was analysed with a Scholander micro-gas analyser to the nearest 0.001 vol. % (Scholander 1947). Relative humidity was measured with a Vaisala HM-11 hygrometer.

Density and temperature of snow were measured layer by layer in the uppermost 30 cm of snowpack. The grain size in every layer was determined by visual inspection on a graduated plate etched with a 1-mm spaced grid. Snow was classified according to IUGG (International Union of Geodesy and Geophysics, Commision on Snow and Ice), except that new snow was grouped into two classes:

1) newly fallen, flake-like snow, grain diameter more than 1 mm (Fa$_1$),
2) newly fallen, dense, wind-driven snow, grain diameter less than 1 mm (Fa$_2$),
3) old, fine-grained snow, grain diameter less than 2 mm (Db),
4) old, coarse-grained snow, grain diameter more than 2 mm (Dd).

3. Results

3.1. Temperature in snow burrow

Temperature changes are slower in snow than in air. At the start, however, the temperature may be lower in the burrow than in the snow, for cold air flows in when the burrow is open. In the experiments that lasted more than 1 h, 70—80 % of the variation in the burrow temperature could be explained by changes in snow temperature alone. If the snow was colder than —4 °C the relation between the temperatures in the burrow and in the snow could be described by a linear regression line. If the snow was warmer than —4 °C, the burrow often warmed up to the melting point. The willow grouse then got wet and tried to escape from the pen.

In density classes I and II the burrow temperature (y) after 1 h was about half the snow temperature (x). Between density classes III and IV the burrow temperatures did not differ significantly, and the burrow temperature was about 2/3rds of the snow temperature (Table 1). The differences between the burrow temperatures in the different snow density classes were further reduced when the measurement lasted 2 h. Usually the burrow temperatures rose only during the first 2 or 3 h, but at air temperatures below —35 °C the burrows dug in old coarse snow might continue to warm up for as long as 8 h. The final temperature was nearly always above —11 °C. The coldest air temperature measured during the experiments was —44 °C. In density classes I, II and III the burrows remained below —6 °C only when the air temperature was below —39 °C, and in density class IV when the air temperature was below —31 °C.

Table 1. Linear regression for snow burrow temperature (y) in relation to snow temperature (x). Measurements during 1 and 2 h.

Density class (g/cm^3)		Regression equation	F	n	R^2 %
1 h.					
I	0.051—0.100	$y = 0.198+0.418\ x$	0.001	14	89
II	0.101—0.150	$y = 0.307+0.559\ x$	0.001	24	89
III	0.151—0.200	$y = 0.411+0.646\ x$	0.001	14	95
IV	0.201—0.250	$y = 0.030+0.067\ x$	0.001	17	92
2 h.					
I	0.051—0.100	$y = 0.299\ x$	0.001	6	97
II	0.101—0.150	$y = 0.840+0.390\ x$	0.001	9	86
III	0.151—0.200	$y = 0.246+0.576\ x$	0.001	21	86

Open burrows were as warm as the snow or only 2—3 °C warmer. Because the bird did not stay so still in open burrows as in closed ones, the air was cooled by snow that fell from the walls.

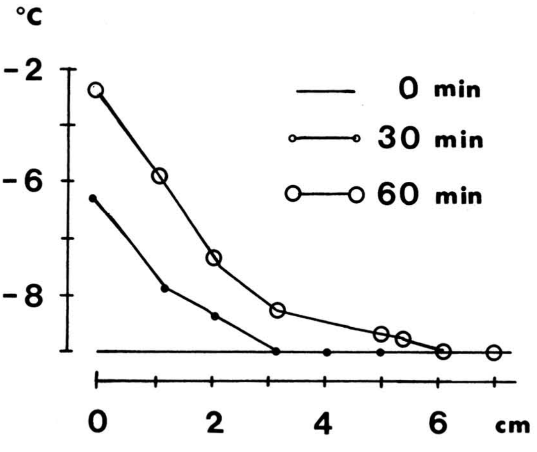

Fig. 1. Temperature distribution in the wall of the closed snow burrow during 1 h. Snow density 0.130 g/cm^3 (Fa$_1$ + Fa$_2$), and air temperature —24 °C.

3.2. Temperature and density in the snow walls of the closed burrows

A temperature rise could be shown in the 5- to 7-cm layer of compacted snow lining the walls of the burrow (Fig. 1). If a bird spent many hours in the burrow, ice formed on the floor. As a result of warming and mechanical stress, flake-like snow (Fa$_1$) and new fine-grained snow (Fa$_2$) became like hard »cemented» snow. Small differences in the final densities might explain why the final temperatures were not strongly dependent on the original snow density (Table 2). Homogeneous snow was seldom found in the uppermost 15- to 20-cm-thick layer that is needed for a closed burrow; usually a burrow wall consisted of two or three snow qualities differing clearly in density and grain size.

3.3. CO$_2$ content and relative humidity in the closed snow burrow

The roof of the burrow was thin enough (5 cm) to prevent accumulation of CO$_2$. Thus the air must have been exchanged at least 1.4—2.0 times per hour if O$_2$ consumption is calculated from the data given by West (1972). The air volume in the burrow where the bird was sitting was about 1 800 cm^3. In grouse burrows, as in all snow holes, the relative humidity was always 100 %.

3.4. Snow burrows as heat shelters

The thermal advantage of snow burrowing can be estimated by comparing heat loss at burrow temperatures and at the snow surface. If, for example, the energy expenditure (including activity) at —30 °C is about 22 kJ/h/bird (West 1968), and at rest about 12 kJ/h/bird in the closed burrow in new snow, where the final temperature is about —5 °C, then the saving would be about 45 %. Evans (1971) has measured the energy expenditure for the sharp-tailed grouse (*Pediocetus phasianellus*) at different temperatures and wind velocities. He found that these data could be used for estimating the effect of wind on the heat loss in *Lagopus lagopus,* too. If the air temperature is —20 °C and wind velocity 0.5 m/s the willow grouse would save 46 % of its heat loss on the snow surface by burrowing. The heat loss in air would then be about 481 kJ/h/m^2 and in the burrow, where the temperature is — 5 °C, about 258 kJ/h/m^2 (Evans 1971).

Table 2. Compaction os snow in the wall of the closed burrows in the 10-cm-thick layer in experiments lasting more than 2 h.

	Density class (g/cm^3)	Original density	Final density	n	Snow quality
I	0.051—0.100	0.090±0.009	0.191±0.063	28	Fa$_1$+Fa$_2$ or Db
II	0.101—0.150	0.130±0.002	0.196±0.063	35	Fa$_1$+Db or Fa$_2$ or Fa$_2$+Db
III	0.151—0.200	0.174±0.007	0.212±0.020	25	Fa$_1$+Db or Fa$_2$

4. Discussion

The microenvironment of the roosting willow grouse and the other tetraonids is obviously warmer in very cold but snowy winters than in mild winters with occasional periods of thaw and hard crust. It could be estimated that in snowy winters the total time spent in snow would amount to 1—2 months (about the diurnal activity see West 1968, Wolterink et al. 1968). Tetraonid birds, including willow grouse, diminish their activity during hard frost (Kuzmina 1961, West 1968). In their closed snow burrows willow grouse will usually be in a thermoneutral environment, for the lower critical temperature for the willow ptarmigan is —6 °C (West 1972). Warming of the burrows is limited by the fact that the temperature of snow walls cannot exceed 0 °C. Data on the metabolic rate measured calorimetrically are not quite applicable to burrow conditions, for the heat loss from an animal in snow and in air may differ even if the temperature is the same, because of the different thermal conductivities of the media. The values for energy saving presented in section 3.4, however, are presumably fairly realistic estimates.

The rate at which the snow burrow warms up is evidently related to the surface temperature of the bird. Although comparisons are made difficult by differences between the methods used for measuring burrow temperature, the snow burrows of willow grouse appear to be slightly colder than those of the hazel hen or black grouse (Volkov 1968, Andreejev 1977) (Fig. 2). Well-insulating plumage may be an advantage for birds that use closed snow shelters, because the temperature in their burrows does not rise too high.

The water vapour in the burrow may also affect the temperature of the burrow (Volkov 1968). The water lost from the bird by various routes freezes on the roof and walls of the burrow because, even in an empty burrow, the relative humidity is 100 %. Water loss has not been measured, but at 0 °C the

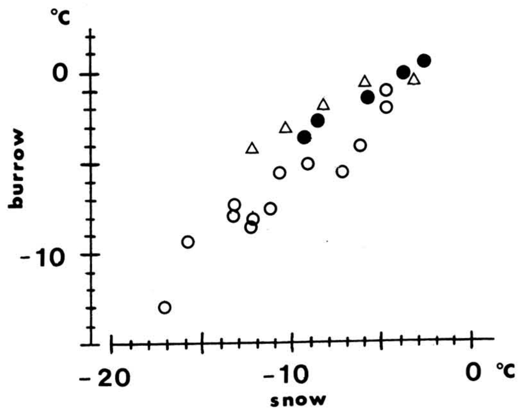

Fig. 2. Comparison of the burrow temperatures (2 h) of three tetraonid birds, black grouse (*Lyrurus tetrix*) (●), hazel hen (*Tetrastes bonasia*) (Δ) (Volkov 1968) and willow grouse (*Lagopus lagopus*) (○) as a function of snow temperature.

white-tailed ptarmigan (*Lagopus leucurus*) evaporated about 2 mg/h/g (Johnson 1968). Thus a willow grouse weighing 500 g would evaporate about 1 g of water per hour, which would produce 2991 J on cooling from +40 °C to 0 °C, condensing, and freezing. Droppings (about 4 g/h) on the bottom of the burrow contained about 60 % water. This water would produce 1205 J on cooling and freezing. The total excretory water would produce an amount of heat (4196 J) corresponding to about 35 % of total heat loss from the inactive willow grouse (about 12 kJ/h) at —5 °C (West 1972). Freezing of the water excreted by the bird in the burrow may warm the burrow, but diffusion of water vapour will also transfer heat. Yosida et al. (1955) have calculated that if diffusion of water vapour through the snowpack were prevented the thermal conductivity of snow of the density 0.1 g/cm^3 would diminish by 37 %. If the thermal conduction coefficients presented by many authors (summarized by Mellor 1964) include both conduction and convection, then convection via water vapour diffusion in the burrow conditions would be 50—80 % of the total heat flux through the roof because of the relatively great temperature gradient in the burrows compared with that in a natural snowpack. Heat transfer via water vapour diffusion has been calculated here from the equation given by Mellor (1964) and temperature gradients measured in closed burrows.

Air flow through snow does not perhaps have much effect on the rate of heat transfer if the mass flux density of air through the roof is only from 0.03 $\times$ 10^4 to 0.04 $\times$ 10^4 g/cm^2/s or 2 500—3 500 cm^3/h (Yen 1962).

West (1968) did not observe any signs that willow ptarmigan in Alaska suffered from cold even when the birds could not seek shelter in snow in their cages. They had about the same energy consumption in summer and winter, and for short times could tolerate extremely low temperatures (—60 °C) in the metabolic chambers (West 1972). However, it is not known to what extent cold tolerance may be affected by such factors as simultaneous cold, food shortage, and the increased activity needed for seeking buds. In fact, it is not known whether in natural conditions the birds are able — or need — to maintain the same level of energy consumption in winter as in summer.

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