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Winter activity patterns of the Black Grouse *Tetrao tetrix*

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The winter activity patterns of wild, mostly artificially fed Black Grouse *Tetrao tetrix* were studied in central western Finland in 1976–82 and 1987–88. The commencement of the diel activity followed the time of sunrise. For most of the winter, the Black Grouse confined their activity to the morning and spent the rest of the day, 94% on average, in snow roosts. The length of activity was correlated with ambient temperature, but not with photoperiod. In December–February, the activity peaked in the morning, even when snow roosting was not possible. In late March and April, when the snow cover was hard, the activity was clearly bimodal, with the major peak in the morning. In concentrating activity to the morning ("bigeminus" pattern) in winter, Black Grouse differ from most other grouse, which show a major activity peak in the evening. Short diel activity, and snow-roosting and flocking behaviour may constitute a successful energetic and antipredator option in this species.

1. Introduction

Northern grouse (subfamily Tetraoninae) are adapted to subsisting on food plants available above the snow in winter (e.g. Leopold 1953, Bryant & Kuropat 1980, Moss & Hanssen 1980, Pulliainen 1981, Andreev 1988). Due to the relatively low nutritive value and digestibility of their diets (Moss 1983, Andreev 1988), grouse do not generally accumulate substantial fat reserves in winter, and must therefore feed regularly (Thomas 1987). This kind of feeding option evidently favours behavioural adjustments that reduce energy consumption (see Lindén 1984). The most important ways grouse can conserve energy in cold winter weather include reduction of activity (Semenov-Tjan-Sanskij 1960, Pulliainen 1981, Gjerde & Wegge 1987) and snow-roosting behaviour (Andreev 1977, Korhonen 1980, Marjakangas et al. 1984, Thompson & Fritzell 1988). On the other hand, or additionally, these behavioural patterns may serve as a means of avoiding predators (Bergerud & Gratson 1988, Marjakangas 1990).

Grouse of several species and populations share an "alternans" pattern of diel activity (Aschoff 1966) in winter, with a secondary peak in the morning and a major peak in the evening (e.g. West 1968, Bossert 1980, Höglund 1980, Pulliainen 1981, Gjerde & Wegge 1987, Mossop 1988). Most authors attribute the adoption of the "alternans" pattern to energetic reasons, i.e. the birds endeavour to fill their crops just before starting the nocturnal resting period (Höglund 1980, Pulliainen 1981), or to avoid high energy loss during the coldest morning hours (Gjerde &

Wegge 1987). In addition, Mossop (1988) argued that Willow Grouse (*Lagopus lagopus*) feed in twilight to reduce the risk of predation.

However, Black Grouse *Tetrao tetrix* in the Swiss Alps show a "bigeminus" (see Aschoff 1966) activity pattern during winter, with the major peak in the morning (Pauli 1974). According to the inquiry data collected by Seiskari (1962) in Finland, Black Grouse feed throughout the winter day, though the main feeding period may occur before noon. Captive Black Grouse fed steadily during the daylight hours from January to late February, when they began to show a bimodal activity pattern (Seiskari 1962).

Several features make this perhaps the most conspicuous of the grouse species when feeding in winter. Black Grouse show intensive flocking behaviour (Koskimies 1957) and dwell in relatively open habitats, and in contrast to the Willow Grouse, they are dark and feed mostly in trees when there is a snow cover (mainly on staminate catkins of birch *Betula* spp.; e.g. Seiskari 1962, Pulliainen 1982). Black Grouse are smaller than Capercaillie (*Tetrao urogallus*), and are therefore more vulnerable to predation by the Goshawk *Accipiter gentilis* (Huhtala 1976), and possibly more sensitive to cold (see Rintamäki et al. 1983, 1984). These features are likely to have affected the evolution of winter activity patterns in Black Grouse.

The aim of this paper is to document the diel activity patterns of Black Grouse in winter in Finland using field data, mainly from artificially fed birds, to analyse the relative importance of abiotic factors affecting them, and to compare these with the factors affecting other grouse species and populations.

2. Material and methods

Data on the activity patterns of Black Grouse were collected during 232 field days at three study sites in central western Finland; at Lampinjärvi and Kauhaneva, 4 km apart, in Ylivieska (64°N, 25°E) during winter in 1976–82 and 1987–88 (only at Kauhaneva), and in Oulu (65°N, 26°E) in 1978–82. The study sites are located on slightly undulating terrain, and the major habitats are bogs, forests, clearcuts and plantations. The dominant tree species are Scots pine *Pinus sylvestris*, Norway spruce *Picea abies*, and birches *Betula pubescens* and *B. pendula*.

At each site, the field work was focused upon a feeding station installed on an open bog (at Kauhaneva from 1978 onwards). Feeding Black Grouse with oats in winter has been a fairly common game management technique in Finland since the late 1960s (Marjakangas 1986). Virtually all Black Grouse within 2–3 km of the feeding station join the feeding flock (Valkeajärvi & Ijäs 1989). Feeding helped me to study these birds, but did not affect their vigilance. There is no significant difference in the crude protein content between oats and birch catkins, but the digestibility of oats is higher than that of catkins (see Marjakangas 1986). However, Black Grouse visiting feeding stations also eat their natural winter foods, the proportion of these in the diet being about 14% (Marjakangas 1986).

I began watching the sites one hour before sunrise, i.e. in good time before the Black Grouse left their night quarters (Hjorth 1968). The birds were observed from a hide placed 50 m from the feeding station, or sometimes from the surrounding heaths about 500 m away, with the aid of binoculars or a spotting scope. The hide did not seem to influence their behaviour, because they could even sit on the roof. Visibility was fairly good, 0.5–1 km in most directions, and the Black Grouse mostly dwelt within 1 km of the feeding station (Marjakangas 1986). When the birds disappeared from sight, they were followed on skis, every effort being made to avoid disturbing them. In these cases, after 10–20 minutes' searching, the birds were mostly found feeding in trees. I always tried to see the birds settling to roost. Flushing Black Grouse from their roosting sites was accidental and the majority of the observations on snow roosting refer to Black Grouse flushed from snow roosts. The study sites were usually left at dusk.

In accordance with Pauli (1974), the time of activity includes here the short inactive bouts that the birds spent in places other than their actual roosting sites (e.g. on tree tops). The diel distribution of activity and snow roosting is presented as the number of occasions per half-hour intervals when Black Grouse were observed being active or roosting in the snow, irrespective of the number of birds present. For instance, when birds were observed being active on 19 days in February at 9.00–9.30, this means 19 observations for that half-hour interval. Eighty-eight per cent of the observations refer to flocks (≥ 2 inds.), and Black Grouse in flocks tend to behave similarly.

The ambient temperature and the velocity and direction of the wind were recorded continuously at the study site in Oulu and instantaneously at the sites in Ylivieska. During the field days, the ambient temperature ranged from –34°C to +3°C, the mean temperature being about –12°C. The depth and structure of the snow cover were recorded to study the snow-roosting possibilities for Black Grouse.

Goshawks were often observed attempting to kill Black Grouse at the study sites, and carcasses of Black Grouse killed by Goshawks were sometimes found. Eagle Owls *Bubo bubo* and red foxes *Vulpes vulpes* were other potential predators of Black Grouse observed, though much less frequently than Goshawks. No Black Grouse were found that had been killed while roosting in the snow.

3. Results

The flocks observed at the Oulu, Lampinjärvi and Kauhaneva sites consisted of 21–46, 16–45 and 16–65 individuals, respectively. The lowest numbers were recorded in November and early December. The mean proportion of females was 35%. The length of the diel activity of Black Grouse did not differ significantly between the study sites in Ylivieska and Oulu ($t = 0.51$, $df = 14$, $P > 0.5$), and hence the data were pooled.

From December through February, the activity of the Black Grouse clearly peaked in the morning (Fig. 1). In March, and especially in April, the birds showed two activity peaks, separated by a resting period around noon, when they were not seen. There are only 34 activity records from November, 76.5% of which were made before noon.

The major factor found by me to affect the activity patterns of the Black Grouse was the suitability of the snow for roosting. When the quality and quantity of snow allowed roosting,

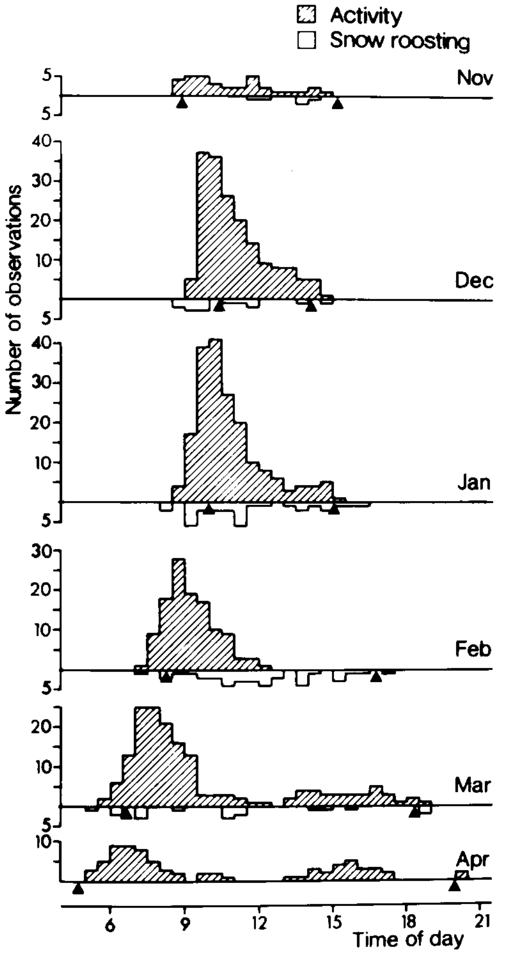

Fig. 1. The diel distribution of activity and snow roosting at the Oulu and Ylivieska (Kauhaneva and Lampinjärvi) study sites during winter in 1976–82 and at the Kauhaneva site in 1987–88. The black triangles show the times of sunrise and sunset in the middle of each month.

the Black Grouse confined their activity to the morning, and spent the rest of the day in snow roosts. The period between 21 December 1976 and 3 February 1977 at Lampinjärvi provided a representative case of the effect of snow-roosting conditions on the length of diel activity (Fig. 2). At the beginning of the period, icy snow prevented burrowing, and the Black Grouse roosted in coniferous trees or on the snow. Frequent snowfalls increased the depth of the soft surface

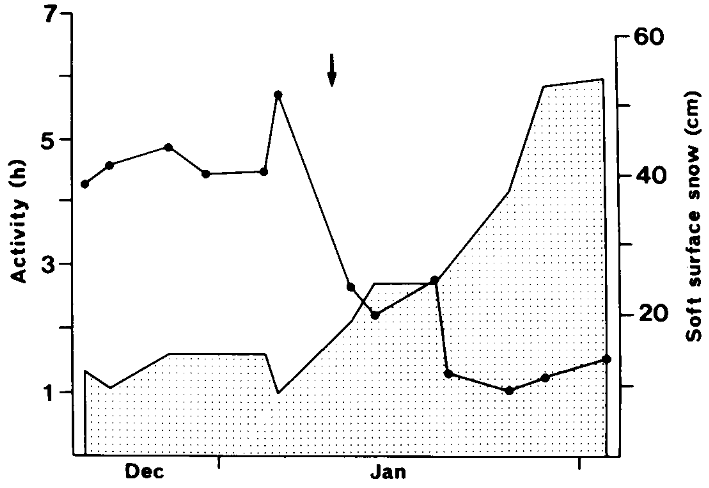

Fig. 2. The relationship between the duration of the diel activity of Black Grouse (large dots) and the depth of the soft surface snow available for roosting (hatched area) at Lampinjärvi between 21 December 1976 and 3 February 1977. The arrow shows the date after which only snow roosting was observed.

snow from early January onward, and after about 10 January the birds started to shift to roosting within the snow. At the same time, they gradually reduced the length of their diel activity. There was no corresponding trend in the ambient temperature during this period. The negative correlation between the depth of the soft surface snow and the length of the diel activity of Black Grouse was statistically significant (Spearman rank correlation, $r_s = -0.88$, $P < 0.001$).

The exact time from the appearance of the first individuals in the morning to the commencement of snow roosting of the individuals seen last was recorded on 16 days between 25 November and 6 March during the study years. The length of the activity ranged from 42 min to 3 h 5 min, averaging 1 h 30 min (SD = 38 min), and it was significantly and positively correlated with the ambient temperature ($r_s = 0.52$, $P < 0.05$; Fig. 3). The length of activity was not correlated with the photoperiod ($r_s = 0.18$, $P < 0.1$).

On the six occasions when Black Grouse were seen burrowing after the morning activity, they were watched leaving their roosting site the next morning. The number of snow roosts corresponded to the number of birds in the flock. This confirmed that there was no afternoon activity that might have escaped attention.

The snow conditions usually allowed the Black Grouse to start regular snow roosting in December or early January. The restriction of activity to the morning hours was most pronounced in February (Fig. 1), when the soft surface snow was deepest every year. Successive thaws and frosts hardened the snow, making it unsuitable for roosting, mostly in early March, and the Black Grouse then started to show a bimodal activity pattern. Winter 1980–81 provided the Black Grouse with unusually favourable roosting conditions, because of heavy snowfalls and powdery snow conditions. The birds were able to roost continuously in the snow from about 20 November almost until the end of March, when they still showed only morning activity (Fig. 4). The photoperiod was then about 12 hours. Afternoon activity was observed only at the end of January, when the ambient temperature hovered above zero for a few days, and at least some of the birds roosted in trees or on the snow.

The birds visited the feeding stations every field day, except between 22 January and 8 March 1977 at Lampinjärvi. The reason for their absence at Lampinjärvi is unknown. During this period they dwelt in the same area, feeding on natural foods, and were easily observed. The length of their diel activity during the period did not differ from that shown by the Black Grouse visiting the feeding stations during the later years ($t = 0.66$, df = 12, $P > 0.5$). Observations made by hunters during the winter shooting season for Black Grouse in January 1981 also suggest that they are able to fill their crops with natural food as rapidly as when visiting the feeding stations. For instance, a bird shot at 9.20 had an empty crop, as is usual after the night (Moss 1983), but another, probably belonging to the same flock, shot at 10.15 had its crop full of birch catkins (Antero Kinnunen, pers. comm.).

4. Discussion

I found that in favourable burrowing conditions, Black Grouse confine their winter activity to the morning and spend the rest of the day in snow. Thus the Black Grouse may be classified as a time minimizer in winter in terms of feeding strategies (Schoener 1971). My results support Seiskari's (1962) conclusion that a filled crop satisfies the food requirements of a Black Grouse for one winter day, and that the main feeding period occurs before noon. At a study site 200 km south of Ylivieska, Valkeajärvi & Ijäs (1989) also found that, when able to roost in the snow, Black Grouse may show only morning activity. Artificial feeding did not appear to affect activity patterns significantly, probably because Black Grouse are more restless and scan more at the feeding station than when feeding in trees (Marjakangas 1986). Thus the artificial food may not reduce foraging time and costs.

How then do Black Grouse manage to take enough food for a whole day during such a short activity period, even without artificial feeding? First, Black Grouse prefer staminate catkins of birch to birch twigs and buds and needles of Scots pine (Seiskari 1962, Pulliainen 1982). Catkins fill the crop relatively rapidly, because they are many times larger than the other winter food items. Second, catkins are the most nutritious food in grouse winter diets in the Palaearctic boreal forest (Andreev 1988), with a crude protein content of 12.6–17.1% (dry matter; Salo 1973, Pulliainen & Iivanainen 1981), which is superior to that of Scots pine needles (7.0–7.3%), for instance, selected by Capercaillie (Pulliainen 1979). This is an important advantage, because the digestibility of natural diets of grouse is largely dependent upon their protein content (Andreev 1988). Consequently, the bulkiness resulting from the relatively low quality of the winter diets consumed by Capercaillie and Willow Grouse (Pulliainen 1979, Moss 1983) may force these birds to alternate between feeding and resting

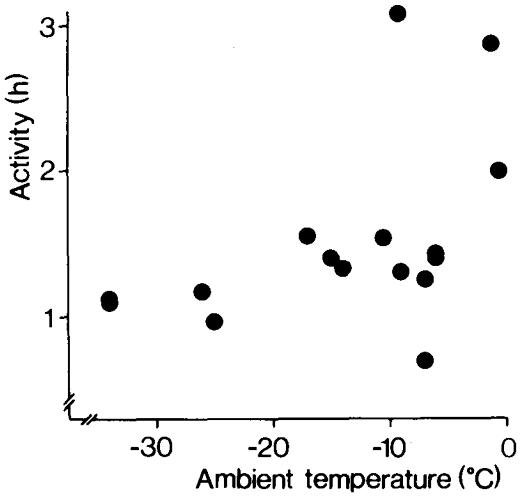

Fig. 3. The relationship between the length of the diel activity of the Black Grouse and the ambient temperature at the study sites during winter in 1976–82 and 1987–88.

during a winter day (Höglund 1980, Pulliainen 1981, Gjerde & Wegge 1987). Third, snow roosting serves to reduce energy demands (Thompson & Fritzell 1988) and thus the time needed for feeding. Finally, intensive flocking in birds generally increases the feeding efficiency of participating individuals, because they can allocate more time to foraging and less to their individual vigilance (e.g. Caraco 1979, Barnard 1980).

Black Grouse seem to adopt the diel activity pattern with only one peak in the northern parts of their range. In central Sweden (61°N), Black Grouse showed two activity peaks, separated by a rest of a few hours in snow roosts, in early March (Willebrand 1988), while in the present study sites they showed only a morning peak in March when able to roost in the snow. Pauli's (1974) substantial data on the activity patterns of Black Grouse in the Swiss Alps (46°N) reveal two major differences in comparison to my study. First, the Black Grouse in the Alps show a bimodal pattern, with the major peak in the morning, throughout the winter, roosting in the snow both at night and around noon. In the present study sites the photoperiod of 3.5–6 hours in December–January might be too short for a simi-

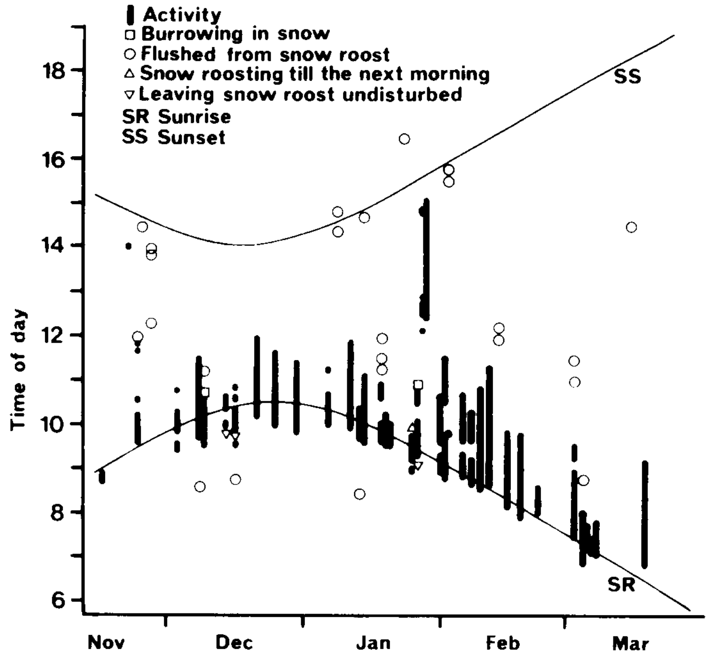

Fig. 4. Observations of the diel rhythm of Black Grouse at Oulu during winter in 1980–81.

lar pattern, since Black Grouse confine their activity rather strictly to the light hours of the day. Even so, the Black Grouse kept the unimodal pattern under suitable burrowing conditions until the end of March, when the photoperiod was as long as 12 hours. Second, the Black Grouse in the Alps are active for a longer period than those in Finland. In mid winter the morning activity of Swiss Black Grouse lasted 1.5–2.5 hours and the afternoon activity 1–2 hours, the total diel activity time increasing with increasing photoperiod (Pauli 1974). In my study, activity merely followed the occurrence of sunrise, without any response to increasing photoperiod, until roosting in the snow became impossible.

These differences may ultimately be attributed to climatic differences. In the Black Grouse, the total daily intake of fresh winter food is about 10% of its body mass (e.g. Keller et al. 1979). A crop loaded with that much food may increase the vulnerability of the bird to raptors (see Kenward 1978). Black Grouse in the south may avoid this risk by consuming the daily amount of food in two phases, with some hours of digestion between them. In the north, in contrast, Black Grouse take the risk of predation, possibly because the climate is more severe and they have more need for shelter against the cold. Moreover, warming up a snow roost entails an energy investment (see Korhonen 1980, Marjakangas et al. 1984), and northern Black Grouse may not be able to afford warming up two roosts a day. The difference in the duration of diel activity between southern and northern Black Grouse may be explained by three factors. First, due to the milder climate, the southern birds are less exposed to cold than the birds in the north. Swiss Black Grouse also feed in smaller flocks or singly (Pauli 1974, Marti 1985), and may have to allocate more time to scanning. Second, the diets are different: the most important winter food of Black Grouse in Switzerland is larch *Larix decidua* twigs (Zettel 1974). This food is relatively low in protein (Keller et a. 1979), and the birds may have to fill their crops twice a day to satisfy their need of nutrition. It is more difficult to explain why Swiss Black Grouse increase the level of activity during the snow-roosting season, whereas Finnish Grouse do not. Rock Ptarmigan in the Swiss Alps also show fairly constant duration of activity from January to April (Bossert 1980). Third, males may start displaying earlier in the south, which tends to increase the duration of activity as the season proceeds.

Why do Black Grouse in Finland not concentrate activity to the evening during winter, like most other grouse? It is typical of Black Grouse cocks that they sporadically display in the morning throughout the winter. When they have a short display period in the morning, they combine it with a feeding bout, and thus a "bigeminus" pattern may have evolved. Also, if the birds only feed once a day, in the morning, they may be hungry by the next morning and have to forage earlier than if they had eaten twice the day before.

Gjerde & Wegge (1987) suggested that Capercaillie avoid high energy loss during cold morning hours by postponing activity to the afternoon. This pattern does not fit the Black Grouse, but they tend to reduce activity at low temperatures (Keller et al. 1979, this study). On the other hand, they seem to prefer feeding in good light conditions, unlike Willow Grouse (e.g. Mossop 1988). This pattern is in accordance with their antipredator option during activity in winter, in that while being conspicuous, they are also able to observe and flee from predators at a considerable distance (Koskimies 1957).

Once Black Grouse have buried themselves in the snow, they are virtually safe from raptors. Grouse roosting in large flocks enjoy a further advantage against mammalian predators: canids at least find it difficult to locate a target bird among the dense group of individuals roosting in the snow (Marjakangas 1986, Mossop 1988). Short diel activity and intensive snow-roosting and flocking behaviour seem to constitute a successful energetic and antipredator option (see Marjakangas 1990), in view of their generally low winter mortality (Willebrand 1988, Valkeajärvi & Ijäs 1989).

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Selostus: **Teeren vuorokausirytmi talvella**

Havaintoja teeren aktiivisuuden ja lumikiepissä oleskelun vuorokautisesta ajoittumisesta ja kestosta kerättiin Oulussa ja Ylivieskassa sijaitsevilla ruokinta-alueilla talvina 1976–82 ja 1987–88. Teeriparvea havainnoitiin tavallisesti ruokintapaikalle pystytetystä piilokojusta, mutta lintujen hävittyä näkyvistä niitä seurattiin pyrkien kuitenkin välttämään häiritsemistä.

Marraskuusta helmikuuhun teeret olivat selvästi aktiivisimmillaan aamulla (kuva 1). Tärkein vuorokausirytmiin vaikuttava ulkoinen tekijä oli lumipeite (kuva 2): kun kieppiin oli mahdollista kaivautua, teeret rajoittivat vuorokautisen aktiivisuutensa keskimäärin 1.5 tuntiin. Helmikuu oli joka talvi pehmeälumisin kuukausi, ja niinpä teeriä tavattiin silloin puolenpäivän jälkeen vain lumikiepistä (kuva 1). Linnut eivät pidentäneet aktiivisuusaikaansa päivän pidentyessä mutta olivat liikkeellä sitä lyhyemmän aikaa, mitä alhaisempi oli lämpötila (kuva 3). Pehmeälumisena talvena 1980–81 iltapäiväaktiivisuutta havaittiin vain suojapäivinä (kuva 4).

Lumipeitteeseen syntyi kaivautumista haittaavia hankikerroksia yleensä maaliskuussa, jolloin teerien aktiivisuus muuttui kaksihuippuiseksi. Sveitsissä, missä teeret myös lepäävät lumikiepissä, niiden aktiivisuus on kaksihuippuinen läpi talven mutta keskittyy sielläkin aamuun, kun taas useimmilla muilla metsäkanalintulajeilla iltahuippu on tärkeämpi. Yhtenä syynä tähän eroon saattaa olla koirasteerien tapa soida silloin tällöin myös talviaamuisin.

Teeri näyttää sopeutuneen talveen hyvin, sillä lyhyt vuorokausiaktiivisuus, oleskelu lumikiepissä ja parvikäyttäytyminen vähentävät energiankulutusta ja suojaavat erityisesti petolinnuilta.

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