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The winter roosting and diet of Black Grouse *Tetrao tetrrix* in the north-western Italian Alps

Massimo Bocca¹, Enrico Caprio^{2*}, Dan Chamberlain² and Antonio Rolando²

¹ Parco Naturale Mont Avic, località Fabbrica 164, 11020 Champdepraz (Aosta), Italy

² Dipartimento di Scienze della Vita e Biologia dei Sistemi, via Accademia Albertina 13, 10123 Torino, Italy

*Corresponding author: email enrico.caprio@gmail.com, tel. +39 011 6704534

Abstract The factors influencing the selection of Black Grouse winter roost sites and choice of roosting strategy (open-air roosts versus snow burrows, or ‘igloos’) were assessed in The Alps, including the influence of winter diet, snow conditions and habitat at different scales. Of 337 roosts detected, 31% were igloos and 69% were open-air roosts. At the larger scale (30x30m), ground curvature, altitude, slope, southerly aspect and mountain pine *Pinus montana uncinata* cover were positively correlated with roost presence. At the smaller scale (10m radius), roost presence was positively correlated with a northerly aspect, cover of green alder *Alnus viridis*, and a low cover of vegetation downslope from the roost. Roosting strategy was related to temperature and snow conditions (with more igloos when snow depth was greater, but fewer igloos when a hard snow crust had formed). The winter diet of the Black Grouse mostly comprised mountain pine needles (84% of droppings). The results suggest that a range of factors influence choice of roost site, including predator avoidance, food availability and topography. The latter showed contrasting effects at different scales, suggesting that Black Grouse select colder sites (with deeper snow) within warmer areas (energetically more favourable). Management to encourage the mountain pine, whilst maintaining scattered green alder in the understorey, is likely to improve Black Grouse winter habitat quality. Choice of roosting strategy is however dictated by weather conditions. If the reduction in precipitation and snow cover continues as forecast, open-air roosting might be more frequent in the future. However, open-air roosting might increase predation risk, which could be deleterious for the species’ conservation.

Keywords: Black Grouse, diet, habitat selection, landscape selection, roosting strategies, snow conditions

Introduction

The majority of bird species which breed at high latitudes or altitudes migrate to warmer climates, including short-distance altitudinal movements, in winter. The few species that remain all year require particular physiological and behavioural adaptations to enable them to cope with the harsh environmental conditions, i.e. low temperatures and snow cover (Martin 2001). The Black Grouse *Tetrao tetrix* is one such species that has developed a survival strategy that includes digging burrows under the snow, also called igloos, for both diurnal and nocturnal roosting (Cramp and Simmons 1979; Marjakangas 1986). Furthermore, they are able to subsist on food plants available above the snow but, because of the relatively low nutritive value and digestibility of their diet, they do not generally accumulate substantial fat reserves, and so must feed regularly (Marjakangas 1992; Ponce 1985; Zettel 1974). The Black Grouse therefore has a finely balanced daily energy budget in winter (Andreev 1988), and disruptions may have important implications for its survival (Arlettaz et al. 2007). However, the species has an unfavourable conservation status in Europe (BirdLife International 2004), is listed in the Annex I of the EU Birds Directive (2009/147/EEC) and many populations are declining (e.g. Storch 2000a, 2007a, 2007b; Ludwig et al. 2006; Sim et al. 2008). The causes of the decline are unclear, but they may include habitat changes, anthropogenic pressure, predation or climate change (Storch 2000b, 2007a, 2007b; Sim et al. 2008; Braunisch et al. 2011). Recent studies have shown that winter sports may represent a threat for the Black Grouse (Zeitler 1995, Arlettaz et al. 2007) and there is the need to identify refuge areas where human access is limited to prevent disturbance (Braunisch et al. 2011). Climate change may also pose a threat as reductions in winter snowfall (Brunetti et al. 2009) may impact on the species' roosting ecology.

Roost site selection and choice of roosting strategy (i.e. igloos or open-air roosts) may be influenced by four main factors: snow quality, energy conservation, predator avoidance and food availability. Black Grouse have been reported to need a minimum snow depth of 30cm to construct igloos (Cramp and Simmons 1979; Marjakangas 1986), although the moisture levels (powdery snow is preferred) and the presence of a snow crust also seem important. In moist snow for instance, there is a risk of becoming imprisoned after the surface snow freezes, and several reports of imprisoned grouse are documented (Porkert 1969; Marjakangas 1990). Furthermore, a snow crust may be too hard to excavate an igloo, so birds are forced to roost in the open (Cramp and Simmons 1979). Igloos may serve to conserve energy during colder periods. Powdery snow in particular has a high thermo-insulative capacity, and thermal responses of Black Grouse individuals roosting in the snow have shown marked energy savings (Marjakangas et al. 1984). However, given that the Black Grouse may use igloos even in relatively mild weather, when it may not be necessary for energetic reasons, an anti-predator function has also been suggested (Bergerud and Gratson 1988; Marjakangas 1990). This hypothesis seems rational because predation mortality, mainly due to large birds of prey, is particularly high (Angelstam 1984; Caizergues and Ellison 1997). Furthermore, an increased vulnerability to predation during years with little snow has been detected (Spidsø et al. 1997). Roost

site location may also depend on food availability and distribution and there is evidence that Black Grouse roosting sites are placed near recently used feeding areas (Cramp and Simmons 1979). Black Grouse diet varies according to seasonal and local availability. Needles and buds of many conifers (*Pinus montana* group, *P. cembra*, *Larix decidua*), catkins of birch *Betula* spp., leaves, shoots and twigs of *Vaccinium* spp. and *Rhododendron* spp. are very common food items in winter when, because of snow cover, birds are forced to feed in trees and taller shrubs (Cramp and Simmons 1979; Marti 1985; Ponce 1985, 1992; Filacorda et al. 1997, Borchtchevski 2000).

This study is, to our knowledge, the first undertaken to identify ecological factors influencing winter roosting behaviour and roost site choice (i.e. igloos or open-air roosts) of the Black Grouse in the Alps. We tested the effect of habitat and topographic variables on roost location at two different spatial scale extents (30m and 10m) in order to assess whether there are particular physical characteristics of roost sites relative to unused locations. Snow conditions may be important in determining roosting strategy, and given the potential energy-saving and predator-avoidance benefits of igloos, we expected that there would be an effect of weather on whether grouse roost in igloos or in the open air. We therefore tested the effect of snow conditions and temperature on roosting strategy. Finally, we assessed winter diet through the analysis of droppings in order to determine if roost sites were influenced by the proximity of preferred food plants. The over-arching goal was to use our results to better understand the factors that influence roost site selection and choice of roosting strategy, and so better understand the function of roosts and hence make provision for management that will provide improved winter roosting habitat for the Black Grouse.

Methods

Study area

The research was carried out in Mont Avic Natural Park (Chalamy Valley, Valle d'Aosta, 45°40'N, 7°35'E) in the north-western Italian Alps (Fig. 1), which belongs to Nature 2000, a protected area network of the European Union (Special Conservation Site IT1202000 Parco Naturale Mont Avic, Special Protection Area IT1202020 Mont Avic and Mont Emilius). The study area, of about 20 km², includes forests dominated by mountain pine *Pinus montana uncinata*, but also frequent larch *Larix decidua* and Scots pine *Pinus sylvestris*, some subalpine pastures, peat-bogs, small lakes and scree slopes. Ericaceae (mostly *Rhododendron ferrugineum*, *Vaccinium myrtillus*, *V. vitis-idaea*, *V. gaultherioides*), juniper *Juniperus communis*, green alder *Alnus viridis*, and dwarf mountain pines constitute the

main understory and also scrub above the treeline. The study area is characterized by an endalpic climate, with scarce precipitation and a pronounced annual temperature range. Precipitation is on average below 1200 mm/year, and is concentrated in autumn and spring, with a relative summer minimum and a winter maximum (the average winter precipitation in the study years was 147 mm, the minimum year was 2003 with 51 mm, and the maximum year was 2004 with 238 mm). Black Grouse are present from 1400 up to 2350 m asl, with spring densities varying from a minimum of 2.5 to a maximum of 4.5 displaying males/km² in the years 1986–2010 (Chamberlain et al. 2012). Human disturbance is virtually absent in winter (and only light in the summer months).

Black Grouse survey

The study area was systematically surveyed during seven winters (December-March 1992-95, 2002-04, 2009-11). The presence of roosts was determined along ten transects (Fig. 1) with a total length of 52.5 km, with an altitudinal range of 1400m to 2400m asl. Surveys were conducted in any snow depth conditions, roosts being located by visual contacts or indirect signs within a fixed width of 30 m from the transect line. Igloos were identified on the basis of the characteristic excavations made by Black Grouse when digging into the snow to create an igloo, whereas open-air roosts were identified on the basis of: i) the presence of concentrations of droppings on branches and ii) the presence of concentrations of droppings on the ground, usually sheltered by bushes, rocks or logs. This included searching potentially suitable locations within 30m when it was considered detection was unlikely from the transect line. Droppings of a roosting individual have a characteristic 'pyramidal' form below the roost, and it is usually evident that a particular location has been used as an open-air roost. We therefore did not take into account isolated droppings or those dispersed over a wide area that could be ascribable to feeding activities.

A stratified random selection of transects was made which ensured that a transect covered a range of habitat types, altitudes and slopes that were broadly representative of the study site as a whole, although some subsequent adjustments to transect routes were made on the ground according to accessibility. To reduce the risk of pseudoreplication of data (i.e. including roosts from the same individuals), we randomly selected sections of transects, constraining the selection so as not to include adjacent sections in the same winter. Each section was visited only once per winter (so n = 10 for each winter, total sample size = 70). All roosts were geo-referenced (a GPS e-Trex Garmin personal navigator was used from 2000) and later mapped and layered on vegetation and topographic maps through GIS (ESRI-ArcView 9.2).

Diet

A total of 153 droppings were collected along the transects within a fixed width of 30 metres from the transect line and at the roosting sites in 2003 and 2004. Only a single dropping was collected from the same location on the same day to reduce potential pseudoreplication in the sample. Zettel's methodology (1974) was used to obtain microscope preparations from remains containing plant epidermis. The main scope of this technique is to separate the plant epidermis from the remains and it is widely used for diet analysis in tetraonids (Lieser 1996; Siano et al. 2011). We were able to obtain epidermis separation by boiling the droppings in a water-glycerine solution; therefore all other treatments suggested by Zettel (i.e. use of solutions of KOH, HNO₃, HCrO) were avoided to preserve leaf fragments. Coloured (Sudan III) epidermis samples were prepared on a slide and examined under a microscope. Coniferous needles were identified by analyzing histological transversal sections after boiling. In all instances, to identify items (even non-epidermic ones), we compared dropping remains with reference collections that were set up by Prof. Passerin D'Entrevès and are hosted at the Life Sciences and Systems Biology Department of Turin University. The collection was created with several specimens and plant parts (i.e. *Arctostaphylos uva-ursi*, *Betula pendula*, *Juniperus communis/nana*, *Pinus cembra*, *Picea abies*, *Pinus sylvestris*, *Pinus cembra*, *Pinus mugo uncinata*, *Larix decidua*, *Vaccinium myrtillus*, *V. vitis-idaea*, *V. gaultherioides*, *Rhododendron ferrugineum*, *Sorbus aucuparia*, etc.) obtained in the study area. Pine needles were counted individually, while for other remains (i.e. larch brachiblasts or broadleaf remains) we estimated the surface covered in mm² after spreading the remains evenly on a graduated Petri dish.

Statistical analysis

Roost location

The location of the roosts was studied using both variables derived from digital maps of the study area (GIS analysis), and field variables measured at the roosting point (field analysis).

i) GIS data analyses

All roost data were mapped and layered on vegetation and topographic maps through GIS (ESRI-ArcView 9.2). Land cover data digitised from 1:10000 aerial photographs were used to identify forest types (Morra di Cella U & Cremonese E, 2004, technical report). Topographic variables were derived from a Digital Elevation Model (DEM) at a spatial resolution of 10 m. A strip of 30 m on either side of the transect line (i.e. a 30 m buffer on digital maps) was considered, and a 30 x 30 m grid map was superimposed on it. Variables were measured for every 30 x 30 m sample

square (N = 4240). For each sample square, we calculated the proportion of area covered by each habitat type category. Six major habitat types were thus identified on the basis of tree species prevalence in each square: mountain pine, bare ground, Scots pine, larch, mixed larch-mountain pine with understory (mostly alpenrose and small mountain pines) and broad-leaved trees.

Four major topographic variables were considered: mean altitude, mean slope, mean general curvature (where depressions and valleys are considered concave and have negative values, peaks and high points are considered convex and with positive values and flat areas have values of zero; Jenness 2011) and aspect. Both easting and northing were considered, expressed as an index equal to $-\cos(A)$, where A is the aspect (east or south) expressed in radians (Bradbury et al. 2011). A value of 1 represents facing directly south or east, and -1 represents facing directly north or west. We also took into account slope, aspect and ground profile heterogeneity. To do so, coefficients of variation ($CV = SD/mean \times 100$) were computed for the continuous variables (i.e. slope, aspect and curvature). For topographic variables, the average value of the nine 10 m pixels enclosed within each 30 x 30 m square was derived.

We analysed roost presence on each transect section in each year using binomial logistic regression with a logit link. To avoid collinearity, variance inflation factors (VIFs) were calculated for the variable set (Zuur et al. 2009; Dormann et al. 2013). The variable with the highest VIF was sequentially removed until all variables had a $VIF < 2.0$. Once the final model variable set had been identified, GLMs were compared using the R package MuMIn (Multi Model Inference; Burton 2011) to identify topographic and landscape variables associated with the roosting site locations using Aikaike's Information Criterion adjusted for small sample sizes (AICc), and by calculating the model-averaged coefficients and relative importance (calculated as a sum of the Akaike weights over all of the models in which that particular covariate is included) for each covariate using the function `model.avg` (MuMIn). Model averaging was performed on the subset of models with a cumulative weight $> 95\%$ of the total weight of all models (termed the 95% subset).

ii) Field analyses

To ascertain whether roosting sites were chosen according to particular, fine-grained habitat characteristics, we used GLMs to model roost presence/absence as a function of habitat variables measured in the field at 75 roosting sites, and the same number of random control sites. We used a stratified random design to ensure that control sites were randomly located in the same landscapes where roosting sites had been found previously (i.e. the same vegetation type, altitude and aspect). At the sampling point, we considered a restricted area within a 10 m radius

circular plot around the true/control roost, divided into two semicircles of higher and lower altitude to assess the role of vegetation above and below the sampling point. We recorded the following set of variables: 1) number of trees below the roost (i.e. trees with trunk diameter larger than 10 cm which were inside the lower semicircle), 2) number of trees above the roost (i.e. those inside the upper semicircle), 3) hindrance of vegetation (the circular plot was subdivided into 16 sectors from S1 to S16, sectors being numbered according their position following the slope of the area, with S4 and S5 directed above the sampling point and S12 and S13 directed below the sampling point. Each of the 16 sectors was scored 0 for the absence and 1 for the presence of significant hindrance, i.e. sectors where the vegetation had no openings to allow birds to flush) and 4) ground cover (percentage of bushes, green alder and no vegetation, covering at least 20% of the area). We also addressed microtopography, assessing from the Digital Elevation Model (DEM) the values of mean altitude, mean slope, mean general curvature and aspect (easting and northing) as described in the previous paragraph for a pixel of 10x10 m. Variable selection was carried out using VIFs and data were analysed using a multi-model inference approach, as described above.

Roosting types

The choice of roosting strategy (igloo vs. open-air) was studied in relation to temperature and snow conditions. The climate data were provided by Aosta Valley Snow and Avalanches Department and were collected from a meteorological station c. 4 km distant from the study site at Champorcher, which had a comparable exposition and altitude to the study site. Model predictors for the presence of roosts were: daily minimum and maximum temperatures, daily temperature range, snow depth and presence of snow crust (defined as being able to support the weight of a person, Ager 1967) on the survey day and 1, 2, and 3 days prior to the survey. Snow data were gathered following the International Classification for Seasonal Snow on the Ground (Fierz et al. 2009). Roost types were expressed as dichotomous variables (where igloo = 1 and open-air roost = 0) and were analyzed using GLMs specifying binomial errors, following the procedure described in the previous section for variable reduction and model averaging.

Food preferences

In addition to the general diet, we also studied food preferences in relation to the consumption of needles and buds of coniferous trees using both Bonferroni confidence intervals (Neu et al. 1974; Byers et al. 1984) and Compositional Analysis (Aebischer et al. 1993). Up-to-date digital maps of coniferous forest types were used to calculate food availability (percentages of the area covered by mountain pine, larch and Scots pine in a 100 m buffer around each transect), while food use was calculated as percentage frequencies (F%), obtained by dividing the

number of times a particular item was observed in droppings by the total number of times every item was observed in droppings.

Birds also fed upon sources whose availability was not known. The general diet was therefore described as percentages of occurrence (O%, i.e. the number of times a particular item was found in droppings by the total number of droppings examined).

Results

Roosts of Black Grouse were found between 1467 m and 2345 m asl. Snow was always present on the ground throughout all sampling periods, and the depth exceeded 30cm on 93% of all roosts located. Along transects, a total of 337 roosts were located, 231 open-air roosts and 106 igloos. 215 roosts were found with no snow crust (104 igloos and 111 open air roosts), 122 roosts were found with a snow crust (2 igloos and 120 open-air roosts; Figure 2). There was no evidence to suggest that any roosts were occupied by more than one individual (based on droppings accumulated beneath open-air roosts, and tracks in the snow around igloos, in addition to observations of roosting birds), except for one occasion when three individuals roosted in very close proximity in an open-air roost. Igloos were found when snow conditions were suitable for digging, i.e. relatively thick (average = 74.4 cm, minimum = 30cm, maximum = 119 cm). Often, the igloo had been constructed in fresh snow that had settled on an older layer with a hard frozen surface.

Roost location

GIS data analysis

There were seven variables included in the reduced model set after removing highly correlated variables. Model averaging based on the 95% subset (which comprised only three models) showed that roost presence was most closely associated (i.e. weight = 1.0) with a greater ground curvature (i.e. when roosts were placed in convex areas), a higher average altitude, a steeper slope, a more southerly orientation (i.e. south-facing slopes locations preferred) and a higher mountain pine abundance (Table 1).

Field analysis

Seven variables were subject to model averaging after variable reduction. The highest variable weights were for green alder cover, the number of trees below the sampling point, hindrance of S12 and southerly aspect (Table 2). The presence of roosting points was negatively correlated with the hindrance of vegetation measured in sectors below the roosting point (S11 and S12). Analogously, the presence of roosting sites was negatively correlated with the number of trees below the sampling point. Contrary to results of the GIS analysis (Table 1), the presence of roosting sites was less likely on southerly slopes (i.e. a negative effect of a southerly aspect). Vegetation ground cover of the

roosting sites also differed from that of control sites: large alder and *Juniperus communis* bushes were found more often at roosting than at control sites (Table 2).

Roosting strategy

The MuMIn procedure for roost site type selected only a single model, which accounted for over 95% of total model weight. The probability of finding an igloo rather than an open-air roost was higher when two days before the day of sampling, no snow crust was present, minimum temperature was lower and daily temperature range was greater.

Diet

The two measures of diet composition (%O and %F) showed a high level of consistency, demonstrating that mountain pine needles were by far the most frequent item in the diet, followed by larch brachiblasts and Scots pine needles (Table 4). *Vaccinium* sp. leaves and vegetative apexes, and emergent *Juniper* sp. needles were recorded infrequently (< 3.7% combined). Bonferroni analysis carried out on needles and buds of coniferous trees indicated that, among conifers, birds positively selected mountain pine needles and negatively selected Scots pine needles and larch brachiblasts during winter. Compositional analysis confirmed the same pattern, mountain pine scoring the highest rank, followed by Scots pine and larch (Table 5).

Discussion

Black Grouse roost characteristics have largely been ignored from a management point of view, yet they are likely to be very important given the species' energy budget, especially during harsh climatic conditions when the species' daily activity in winter can be as low as 140 minutes/day in the Alps (Marti and Pauli 1985). In addition, the species is likely to need roosting areas that provide for food needs close to the roost site and that are less affected by human disturbance. Furthering our understanding of Black Grouse winter roosting ecology should therefore ultimately help to make informed management decisions in order to safeguard this species of conservation concern, especially in the light of changing climatic conditions and increased human pressure on Black Grouse winter habitat (Arlettaz et al. 2007). In this study, we found a range of factors that appeared to affect roost site choice and roosting strategy, including altitude, vegetation cover, tree species, snow conditions and topography at different scales of resolution. This suggests a complex of factors that are important for Black Grouse habitats in winter. The possible mechanisms underpinning these relationships are discussed below.

Correlates of roost location

In the GIS analysis, variables positively affecting roost site location were altitude (the highest altitudes were preferred), vegetation type (pure mountain pine stands were preferred) and aspect (southerly aspects were preferred). The Black Grouse is a species which shows a preference for forested areas close to open habitats and is mainly

associated with treeline habitats in the Alps (Patthey et al. 2011), occupying a relatively narrow altitudinal range. Optimal altitudes for the Black Grouse change along the Alpine chain in relation to changes in the vertical distribution of the timber line (Ozenda 1985; Leonelli et al. 2010). As cover of different vegetation types was included in our models, the results suggest an effect of altitude that is in addition to forest cover. This could be related to climate (e.g. snow conditions may be more favourable at higher altitudes) or to more subtle variations in vegetation composition or structure that are correlated with altitude and which are not well-described by our relatively simple measures of vegetation cover. Vegetation type may be correlated with aspect as well, especially in valleys characterized by scarce summer rainfall.

Considering field variables in the immediate vicinity of the roost site (i.e. the field analyses), roosting Black Grouse seemed to prefer sites within forest vegetation, but with at least some vegetation-free space below the roost. In particular, they preferred sites with an understorey made up of large bushes (i.e. scattered green alders and junipers) and avoided open sites. Field variables *per se* had a stronger relevance in describing roost site selection, southerly aspect being the only topographic variable entering the model. We suggest that the selection of certain environmental variables (for both the GIS and habitat analyses) may depend upon the need to feed and for protection from predators. Food preferences are likely to be major determinants of habitat selection in birds (Rolando 2002), and there is evidence that local movements of Black Grouse may be dictated by wider variations in food availability: Radio-tagged grouse that frequented larch forests from spring to autumn in the French Alps tended in fact to move to mountain pine forests in winter (Ellison et al. 1989), likely because of the larch loss of needles in that season. In our study area, Black Grouse preferred to feed on mountain pine needles, and we suggest the positive selection of mountain pine stands for roosting derives, at least partially, from this trophic preference. In winter, Black Grouse diet reflects mainly the availability of resources, and they commonly feed on bushes (*Ericaceae* and *Juniperus sp.*) when there is limited or no snow cover, and on trees when the ground is covered with abundant snow (using conifers in the Alps and birch in Central-Northern Europe) (Ponce 1987). Mountain pine represents a dominant part of the diet in the French and Bernese Alps, while Larch is dominant in Valais. Food availability is important in reducing energy consumption. Ponce (1992) reported that some individual grouse moved 9 km in winter in a valley where mountain pine was abundant. Based on these facts, our study area likely represents an extremely favourable situation that embodies the most important ecological factors for winter roosts, since the most important food source is widely distributed and does not represent a limiting factor. Food availability and roosting sites are likely interconnected since an optimal strategy requires that birds roost where they feed – separating out the main driving factor (predation or food availability) would however require a very detailed study, possibly with experimental habitat manipulations.

Predator avoidance is also likely to play a relevant role in roost site selection. Black Grouse populations may be significantly affected by predation (Angelstam 1984; Caizergues and Ellison 1997) - even though most of the Black Grouse's predators prey upon eggs and chicks (Summers et al. 2004), there were several species of predator in the study area that could be capable of taking adults, including Eagle Owl *Bubo bubo*, Goshawk *Accipiter gentilis*, Golden Eagle *Aquila chrysaetos*, Pine Marten *Martes martes* and Red Fox *Vulpes vulpes*. Furthermore, remains of several adults killed by unidentified birds of prey were found during our study period. It therefore seems reasonable

to assume that predation risk may be a significant influence on adult Black Grouse habitat (and hence roost site) selection. The location of roosts, which were generally in fairly thick cover (especially in areas with scattered green alder), but with open areas downslope, may indicate that the Black Grouse tries to avoid predators by concealment, whilst maintaining an escape route by ensuring the possibility of rapid and unimpeded downhill flight. The positive selection for mountain pine stands might also be associated, at least in part, by predator avoidance tactics, given that this conifer also grows as an understorey bush, hence potentially providing cover. In other alpine areas, spruce (*Picea abies*) could play a similar anti-predation role, as several Black Grouse roosts have been documented sheltered by thick branches of this species where mountain pine is absent in the Aosta Valley (M. Bocca pers. obs.), as has also been documented for the Capercaillie *Tetrao urogallus* in the Pyrenees and in Norway (Gjerde 1991; Catusse 1989; Finne et al. 2000).

A further factor which may dictate preference for certain topographic features is the suitability of snow conditions for anti-predator refuges, since a higher slope and greater curvature offer higher probabilities of finding powdery snow suitable for digging igloos. Our results showed a clear preference, for all roosts, for a southerly aspect (42 % of sites, against 9 % exposed to the north) in the GIS analysis, but conversely, a clear preference for a northerly aspect at a smaller scale in the habitat analysis. We suggest that these contradictory results, which are also in contrast to the landscape level results of Braunisch et al. (2011), arise because Black Grouse prefer southerly slopes in general, which can offer generally warmer climatic conditions providing birds with physiological advantages, but they look for sites orientated away from southerly aspects at a micro-topographic scale for their roosts, as these offer better snow conditions for excavating igloos. This selection of colder winter roosting sites within warmer landscapes suggests that the Black Grouse has very precise habitat requirements for roost sites.

Igloos vs open-air roosts

It is assumed that when snow reaches a depth of about 30 cm, the Black Grouse excavates igloos (Cramp and Simmons 1979). Snow roosting is so common in certain northern areas that winter survival may depend strongly upon the thermo-insulative and/or anti-predation functions of these igloos. However, results of our extensive survey suggest that alternative, open-air roosts are common in our study area, representing 69% of the sampled roosts. Moreover, the relative frequency of open-air roosts may have been underestimated in our study, given the likely differences in detectability of the two roost types. Igloos are easily detected due to signs of excavations on the relatively homogenous snow surface. Open-air roosts are typically placed in less open habitats, hence identifiable signs (e.g. among rocks, in bushes or under over-hanging branches) may be less easily detected, although an effort to actively search for such locations was made.

An insufficient depth of snow due to local climatic conditions could be one cause of the prevalence of open-air roosts. Inner east-to-west oriented alpine valleys like Aosta Valley are known to be less snowy than others because they are more sheltered from weather systems both from the Atlantic and from the Mediterranean (Bätzing and Rougier 2005). Igloos can be excavated only in thick snow, which may be rather rare below 2000 m in the Southern Alps. Furthermore, formation of a snow crust, which apparently discourages the use of igloos as roosts (Table 3), may be relatively common in our study area. Snow crusts develop when surface snow melts and then re-freezes, a situation often associated with relatively warm foehn winds which frequently occur in the Southern Alps. Higher daytime temperatures, but freezing at night, might therefore decrease suitability even in the presence of adequate snow depth. In our analysis, we addressed effects of the surface snow crust, but it is likely that the situation is far more complex with regards to the snow stratigraphy, as several crusts may be formed as a consequence of melting and freezing events, which may also affect the snow's suitability for excavating igloos. We found igloos which had been excavated down to a hard 'floor' of a former snow crust, which further suggests that snow depth alone is not a good predictor of roost availability.

High mountains are particularly vulnerable to climate change: the rate of warming in mountains has been twice the global average (Brunetti et al. 2009) and increasing temperatures, higher snow lines and lower snowfall, evident over the past century, are expected to continue (EEA 2010). A reduction in precipitation and in the duration of snow cover have been detected over the last 40 years in the Italian Alps, with the greatest rate of decrease during the 1990s (Valt & Cianfarra 2010) as a consequence of climatic changes. Between 1992 and 2011, the minimum temperature has fallen below -15°C only 23 times at the Champorcher meteorological station, suggesting that the climate situation that Black Grouse has to face is totally different compared to northern populations in Scandinavia and Siberia, where temperatures can often reach below -40°C (Marjakangas 1990). This suggests a modest thermoregulatory role of igloos in our study area with respect to northern populations (Marjakangas 1990), and probably also to continental areas of the Alps (Bätzing and Rougier 2005, map on page 47). We therefore hypothesize that in the relatively mild climatic conditions of the Southern Alps under a warming climate, igloos may be no longer of capital importance for energy saving and, therefore, winter survival. Similarly, climate warming is also showing its effects on another tetraonid species, the Capercaillie. According to the research of Watson and Moss (2008), deep snow is less frequent and icy crusts are now more common, leading to the disappearance of suitable snow for roosts in Scottish woodland, where no igloos have been detected since 1984. However, it should be kept in mind that open-air roosting might increase predation risk for the Black Grouse (Spidsø et al. 1997) and therefore the effect, in the long term, might be deleterious for the species' viability. In this context, the importance of vegetation cover with an anti-predatory role close to potential roost sites is of high relevance to our particular study area, compared to those where climate allows good snow conditions for digging igloos.

Management implications

Addressing the unfavourable conservation status of the Black Grouse in Europe requires special conservation measures concerning its habitat, although many of these concern breeding habitat (Storch 2007a, 2007b). Those

conservation recommendations that are relevant to winter have focussed on impacts of disturbance, especially that caused by skiing (Zeitler 2000; Arlettaz et al. 2007; Braunisch et al. 2011). The present study stresses the fact that environmental variables controlling winter roosting ecology should also be considered in any management strategy. In our study area, the mountain pine is essential to the Black Grouse both with regard to roost location and diet. Our results also suggest that understorey vegetation is relevant for winter roosting and, therefore, preservation of tall scattered shrubs and bushes within alpine forests is essential for effective grouse management. Black Grouse clearly preferred mountain pine stands for roost sites, and preferred mountain pine needles for food. In the alpine regions that may be potentially colonized by this tree species (and everywhere that it already occurs), forest management could therefore plan interventions that secure its presence and possibly promote its expansion, which would include development of stands of uneven age so that it also occurs as an understory shrub. At the same time, disturbance at sites characterized by a complex microtopography should be minimised. Ideally, the value of these measures in securing conservation of the Black Grouse should be tested experimentally, through coordinated management and improved cooperation between hunting and land-management agencies, which should have the mandate to maintain the original tetraonid avifauna while simultaneously managing land for commodity production and recreation.

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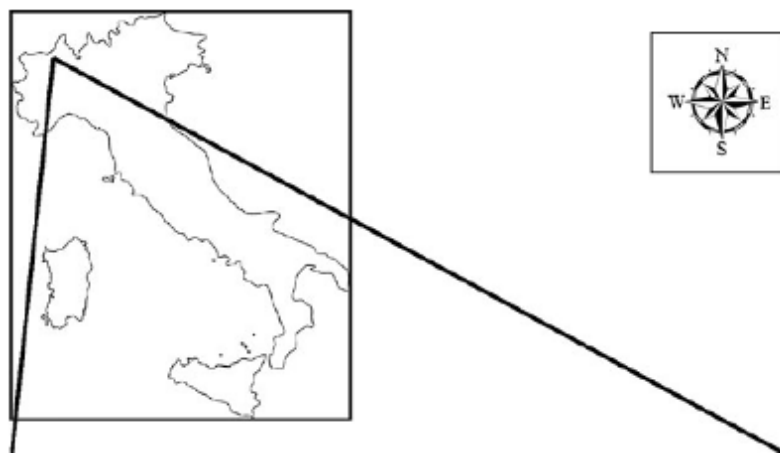
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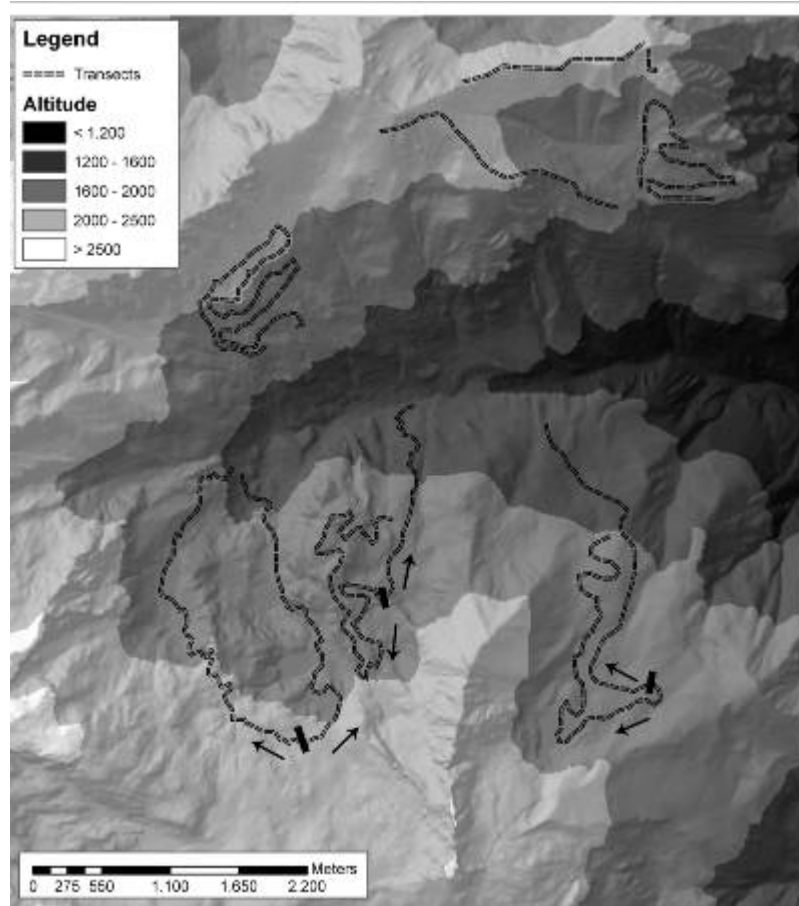


Fig. 1 The study area showing its location in northern Italy (upper panel), and the site boundary and survey locations (lower panel). Dotted lines indicate transects. Bold lines and arrows indicate starting points and direction of survey in longer transects.

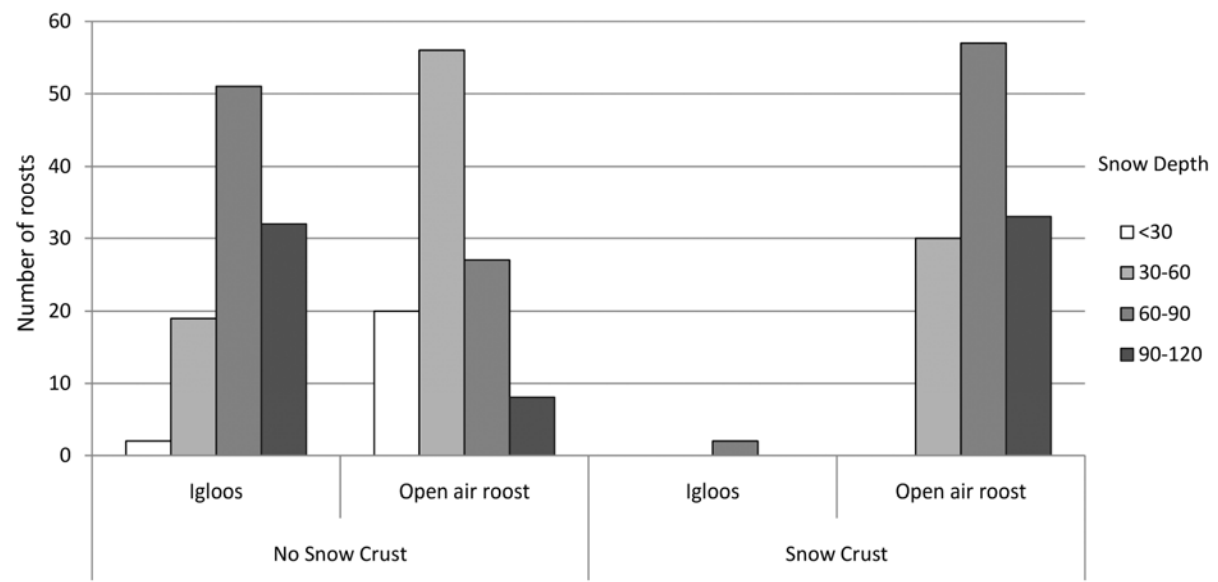


Fig. 2 Distribution of igloos and open air roosts according to snow conditions (classes of snow depth - < 30, 30-60, 60-90 and 90-120 cm), with and without a snow crust

Table 1 Model-averaged parameter estimates predicting the probability of occurrence of roosts on transect sections in the study area in relation to GIS-derived data (topography and habitat cover) at a 30m x 30m scale. Roost presence was modelled with binomial logistic regression. The average model for 95% of summed model weights is reported. Parameter estimates, standard errors, confidence limits and model variable weights are shown. Altitude was expressed in m, slope in angular degrees and habitat cover (forest, scrub, sparse vegetation and rock) as arcsine-square root transformed proportions. ASPECT_E, ASPECT_S = aspect as an index from 1 (directly facing east or south) to -1 (directly opposite to the aspect in question), H_CURV = heterogeneity of ground surface, MEAN_DEM = average altitude in meters, MEAN_SLOPE = average slope, MPA = percentage of mountain pine forest area. N = 4240.

Variable	Parameter estimate	Standard Error	LCL	UCL	Model weight
(Intercept)	-9.8521	1.2516	-12.3060	-7.3983	1.0000
MEAN_CURV	0.2108	0.0245	0.1629	0.2588	1.0000
MEAN_DEM	0.0030	0.0006	0.0018	0.0043	1.0000
MEAN_SLOPE	0.0284	0.0068	0.0151	0.0416	1.0000
MPA	0.0010	0.0002	0.0007	0.0013	1.0000
ASPECT_S	0.9565	0.1025	0.7556	1.1574	1.0000
H_CURV	0.0000	0.0000	0.0000	0.0000	0.2270
ASPECT_E	0.0304	0.0867	-0.1395	0.2003	0.2168

Table 2 Model-averaged parameter estimates predicting the probability of occurrence of roosts in the study area in relation to habitat data collected in the field, and topography at a 10m x 10m scale. Actual roost site locations were tested against randomly generated pseudo-absences. The average model for 95% of summed model weights is reported. Parameter estimates, standard errors, confidence limits and model variable weights are shown. Predictors were measured considering the position of the centre of the sampling site (i.e. the true or hypothetical roosting point). See methods for further details. AV = *Alnus viridis* percentage cover, GR = bare ground and rock percentage cover, JC = *Juniperus communis* percentage cover BE_TREE = number of trees below the roost, S11, S12 = hindrance of vegetation for sector 11, 12 (expressed as presence or absence of hindrance). N=150.

Variable	Parameter estimate	Standard Error	LCL	UCL	Model weight
(Intercept)	-0.243	0.647	0.651	1.034	
AV	3.001	1.108	1.117	5.191	1.000
GR	-1.386	0.501	-1.506	-0.395	0.969
JC	0.972	0.486	0.491	1.933	0.738
BE_TREES	-0.080	0.026	-0.126	0.029	1.000
S11	-1.324	0.501	-2.314	-0.580	0.930
S12	-1.863	0.575	-3.021	-0.504	1.000
ASPECT_S	-1.175	0.405	-1.908	-0.675	1.000

Table 3 The probability that a roost was an igloo (1) rather than an open-air roost (0), in relation to temperature and snow condition variables recorded two days before the day of sampling. There was only a single top model which explained >95% of total model weight, so parameter estimates (beta) and standard errors (SE) are not derived from model averaging. N = 337.

Variables	Beta	SE
Intercept	-4.603	0.780
Snow crust presence	-2.829	0.426
Minimum Temperature	-0.185	0.038
Daily Temperature Range	0.160	0.062
Snow Thickness	0.026	0.007

R-sq.(adj) = 0.588 Deviance explained = 58.9%

Table 4 Monthly winter food preferences. O% are frequency percentages obtained by dividing the number of times a particular item was found in droppings by the total number of droppings examined. N=153.

Month	O% Mountain Pine	O% Scots Pine	O% Larch	O% <i>Vaccinium</i> sp.	O% <i>Juniperus</i> sp.	N
December	33.3	0.0	66.7	3.7	5.6	18
January	93.8	0.0	0.0	2.3	1.5	65
February	90.7	11.6	0.0	0.0	2.3	43
March	85.2	7.4	7.4	2.3	0.0	27
Total	84.3	4.6	9.2	2.0	2.0	153