ORIGINAL PAPER

Wintering forest birds roost in areas of higher sun radiation

Sara Villén-Pérez · Luis M. Carrascal · Oscar Gordo

Abstract We analyze environmental determinants of roost site selection by tree gleaning passerines wintering in a Mediterranean montane oakwood at a craggy area of high variation in altitude and hill-shading pattern. We hypothesize that in temperate latitudes of cold winter climate, birds should spend the night in areas of low altitudes, higher temperatures, and higher solar radiation in order to minimize thermoregulation costs during resting time and to improve foraging conditions just before and after roosting. We study night occupation of woodland locations by the presence of feces in 159 wooden nest boxes (i.e., under identical controlled roosting situations). We employ GIS methods to quantify solar radiation at each location surrounding the nest boxes and data loggers to measure air temperature in the field. Birds prefer to roost in forest patches with higher solar radiation, where the period of light available for foraging is extended and thermoregulation costs during daytime are minimized. They also selected woodland patches with taller trees, a pattern consistent with their foraging preferences for trunks and branches. Other environmental variables played a negligible role in determining the selection of roost sites. Here, we show, for the first time, the importance of sun radiation determining where to spend the night in wintering birds and call attention on considering the thermal space in forest management. Forest management should preserve woodland patches with taller trees more exposed to solar radiation to enhance winter habitat suitability for birds in these Mediterranean oakwoods.

S. Villén-Pérez (✉) · L. M. Carrascal
Department of Biogeography and Global Change,
Museo Nacional de Ciencias Naturales (CSIC),
C/José Gutiérrez Abascal 2, 28006 Madrid, Spain
e-mail: sara.villen@mncn.csic.es

O. Gordo
Department of Zoology and Physical Anthropology,
Universidad Complutense de Madrid,
José Antonio Novais 2, E-28040 Madrid, Spain

Introduction

Winter is the most severe season for small passerines of temperate and boreal latitudes. Long and cold winter nights become the most stringent period of the day, when birds have to cope with temperatures well below their thermoneutral zone (Calder and King 1974) while fasting for many hours. Thus, birds have developed several behavioral strategies in order to minimize thermoregulation costs and to ensure winter survival (Mayer et al. 1982; Swanson 1993; Carey 1996; McKechnie and Lovegrove 2002). Roost site selection is an important decision when facing harsh conditions of winter nights (Pinowski et al. 2006; Coombs et al. 2010; Grüebler et al. 2013). Birds select warmer forest areas and roost sites to reduce metabolic expenditure during resting time (Virkkala 2004; Velky 2006; Velky et al. 2010; Zabala et al. 2012), and they can further reduce the rate of heat loss by radiation and wind-forced convection by sheltering in dense vegetation (Lustick and Kelty 1979; Buttemer 1985; Webb and Rogers 1988), winter nests (Buttemer et al. 1987), tree cavities (Kendeigh 1961; Coombs et al. 2010), or artificial nest boxes (Pinowski et al. 2006).

After long fasting and energy-consuming winter nights, when fat reserves are at minimum level, finding food in the shortest possible time is also essential for survival (Houston and McNamara 1993). In addition, a successful and late foraging at the end of the day may be important in order to accumulate enough fat reserves to get through the following night, especially in those days of harsh weather conditions (Blem 1990; McNamara et al. 1994; Polo et al. 2007).

The environmental and foraging conditions of birds during the previous afternoon and the following morning might be determined by multiple factors. Harsh winter weather (e.g., snowstorms and wind) may make difficult or even impede food searching, and snow and ice can cover food resources limiting their availability, with dramatic consequences for fasting birds. Both unpredictable harsh weather and snow cover are strongly and directly related with altitude, and therefore, birds generally prefer to overwinter in lowlands (e.g., Herbers et al. 2004; Senar and Borras 2004). Temperature exerts a prominent role on bird metabolism below the critical minimum (usually around 20 °C for small passerine; Kendeigh et al. 1977) and is likely to improve the quality of the foraging environment (Robinson et al. 2007; Cresswell et al. 2009), so birds are expected to distribute accordingly, selecting areas with higher temperatures during winter at different spatial scales, all other things being equal (e.g., Root 1988; Meehan et al. 2004; Carrascal et al. 2012a). On the other hand, sun radiation has both illumination and thermal benefits with important consequences on winter bird distribution at local scales (Shields and Grubb 1974; Stapanian et al. 1999; Huertas and Díaz 2001; Carrascal and Díaz 2006). Diurnal birds need a minimum light intensity for foraging, and the length of direct sun incidence is the ultimate determinant of the available time for foraging each day. Moreover, received heat from sun radiation has a pronounced effect in reducing thermoregulatory costs at low temperatures in temperate and boreal latitudes (De Jong 1976; Lustick et al. 1978; Carrascal et al. 2001). Finally, direct sun radiation on clear days favors the activity of prey such as ectothermic arthropods, increasing food availability for birds (Honek 1997; Carrascal et al. 2001). Therefore, it is expected that small diurnal passerines will select sunlit areas (with high exposure to sunlight) in order to reduce the inactive nighttime period and to increase the accumulated benefits derived from solar radiation.

Vegetation structure also plays a prominent role in defining the space that provides roosting opportunities and feeding substrates for bird populations (Cody 1985; Wiens 1989). To survive winter conditions, birds must explore their environment in order to familiarize themselves with their habitat, tracking the changing food availability to reduce the risk of starvation (Naef-Daenzer 2000). Therefore, the previous knowledge of the area must also be of value for winter residency, considering social dominance and food storing behavior (Sandell and Smith 1991; Koivula et al. 1993; Brotons and Haftorn 1999; Broggi and Brotons 2001), so we expect that the pattern of winter roosting will somehow reflect the previous exploitation of the area (i.e., previous occupancy during the breeding season for sedentary species).

Winter is a hard period for birds living in montane oakwoods of continental cold Mediterranean climate (Senar

and Borras 2004), which need to find the most favorable forest patches in order to ameliorate the limiting conditions of winter weather. Here, we investigate factors associated with roost site selection, including both the environmental conditions at night and the foraging scenario just before and after roosting time. The specific goal is to test the predictions related to the influence of altitude, temperature, sun radiation, habitat structure, and the previous knowledge of the area summarized in Table 1. We study woodland passerines wintering in a montane Mediterranean forest of central Spain of cold continental climate within a heterogeneous forest according to habitat structure and topographic complexity that generates a high variability in the hill-shading pattern. We investigate the determinants of winter roost site selection by using nest boxes of identical characteristics, set on a regular basis throughout a study area that constitutes a combination of especially harsh environmental conditions depicting an energy-limiting winter scenario in which birds should use the habitat efficiently in order to minimize thermoregulation costs of winter residency.

Materials and methods

Study area and period

The study was carried out in a monospecific oak forest (*Quercus pyrenaica*) located in the Guadarrama Mountains, central Spain (40°53′N–3°50′W). The study area covers 61 ha of a craggy and predominantly north-facing slope ranging between 1,250 and 1,600 masl, the altitudinal superior limit of oak forests in the region (Blanco et al. 1997). The high altitude along with the orientation imposes harsh conditions during the winter, with the least possible hours of sun radiation, and temperatures usually bellow 0 °C. The area received a relatively low insolation during the winter study period (an average of 3 h and 21 min of sun per day, i.e., 36 % of light

Table 1 Predictions of bird preferences for night-roost sites and hypotheses related to predictions

Predicted higher occupation of roost sites	Related hypotheses
At lower altitudes	Harsh weather probability
With higher nocturnal temperatures	Thermoregulation costs
With higher diurnal temperatures	Thermoregulation costs
With higher potential sun radiation	Thermoregulation costs
	Foraging period length
	Prey activation–food availability
With higher development of tree crown	Habitat preferences
With higher previous breeding occupancy	Previous knowledge of resources

hours at winter solstice, with 36 % of days with >5 h of sun per day; average data from Navacerrada Pass and Colmenar Viejo meteorological stations, from 23th November to 13th January; Spanish Agencia Estatal de Meteorología - Ministerio de Medio Ambiente, Medio Rural y Marino).

The study was conducted on 52 days around winter solstice (from 23th November 2010 to 13th January 2011), i.e., the most stringent period of the winter considering the relative duration of day and night (9:14 h–14:46 h, respectively, at winter solstice). The study area has 159 wooden nest boxes installed in 2008 in a grid at a regular distance of c. 50 m between adjacent boxes (c. a density of 2.6 nest boxes per hectare; Fig. 1). These nest boxes have been used as regular breeding sites since 2008 by the pied flycatcher (*Ficedula hypoleuca*; transaharian migrant) and the following three resident species; blue tit (*Cyanistes caeruleus*), great tit (*Parus major*), and nuthatch (*Sitta europaea*). In a pilot survey outside the study period of 52 days, we observed that nest boxes were only used as winter roost sites by blue tits, great tits, and nuthatches and that each nest box was only used each night by one individual (i.e., communal roosting was never observed). We used wooden nest boxes (base 11 × 13 cm, height 20 cm, 15 mm thickness of walls, centered entrance of 30 mm diameter), with a plastic pipe of 9 cm long installed in the entrance to avoid predation by Mustelidae, the garden dormouse (*Eliomys quercinus*) and the great spotted woodpecker (*Dendrocopos major*). Nest boxes were hanged from branches with a metal hook at an average height of 3.76 m (0.49 SD). The occupation of nest boxes may be favored by the scarcity of natural cavities in this managed forest (Camprodon et al. 2008). Occupation of nest boxes by blue tit, great tit, and nuthatch was registered during the preceding breeding season (spring 2010; data obtained by OG in the context of other research program).

Two habitat measurements of 10 m around each nest box were obtained as follows: average oak height and number of oaks larger than 10 cm of trunk diameter at breast height. These habitat variables define tree crown characteristics and were obtained considering the habitat preferences of the studied species (Perrins 1998) and winter habitat use in the study region (Carrascal et al. 1987).
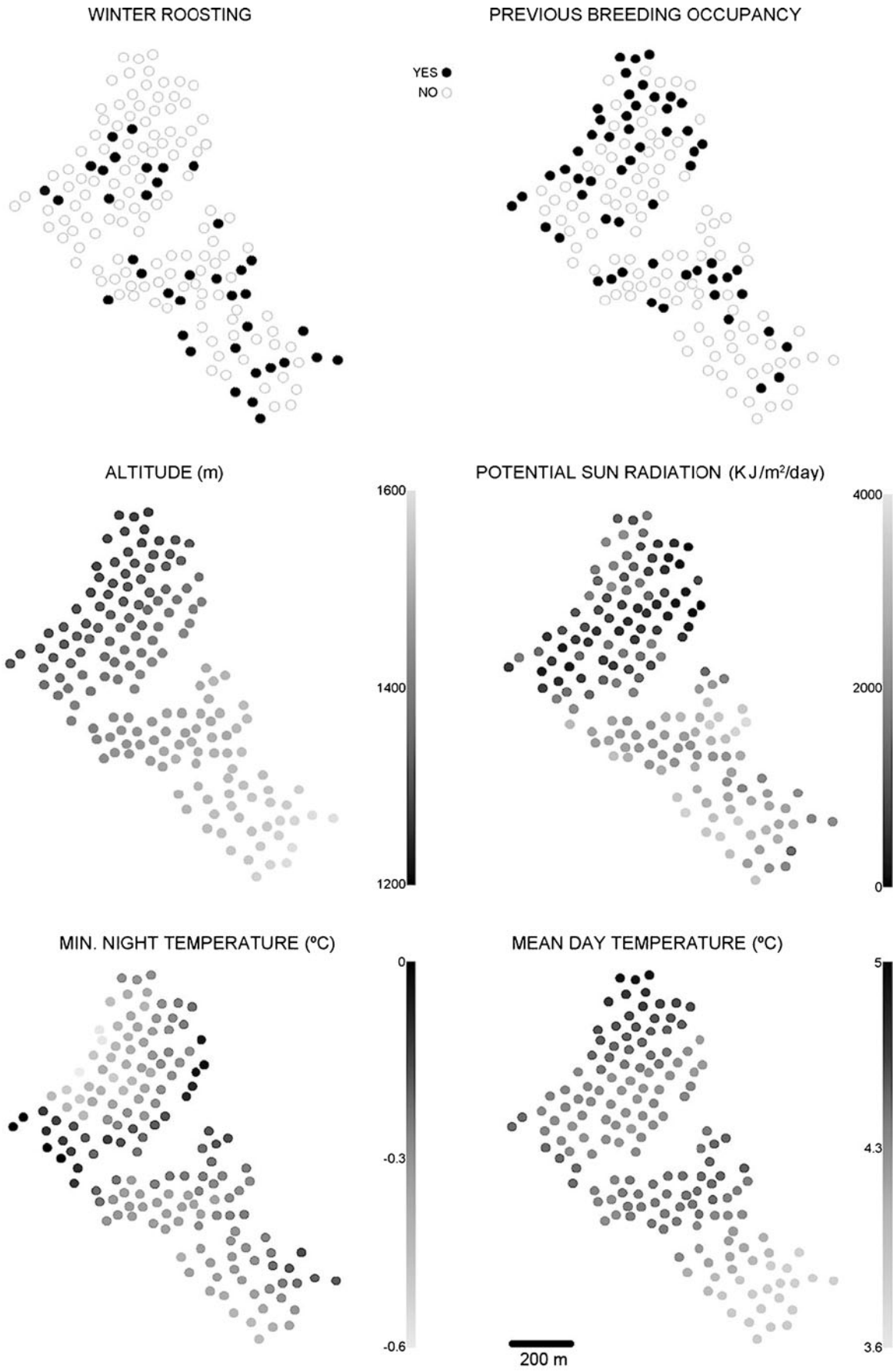
Air temperatures

To measure winter air temperature, we set 10 temperature data loggers (Onset HOBO® Pendant, model UA-002-64, resolution 0.1 °C) covering the whole spatial variability in altitude, cardinal orientation, and location (in the latitude–longitude plane) within the study area. In average, there was one logger in a circle of 126-m radius. Loggers were placed on thick oak trunks, oriented to the north and at approximately 1.5 m above ground, in such a manner that they never received direct solar radiation (i.e., air temperature was measured in the shade).

Data loggers recorded air temperature every 10 min from 1st December 2010 to 13th January 2011. For each recording day (144 measurements), we calculated average daytime temperature, average night temperature, maximum daytime temperature, and minimum night temperature. Temperatures for these 44 winter days were averaged for each sampling point. In order to avoid multicollinearity in data analyses and considering that these four temperature measurements were highly correlated across days and sampling points, we selected the two least correlated measurements as follows: minimum night and average daytime temperature. These two temperatures have a different functional meaning that is related to maximum thermoregulatory costs at night and average thermoregulatory costs at daytime, respectively.

To estimate the minimum night and average daytime temperature in the location of each of the 159 nest boxes, we used a weighted-averaging approach considering the temperatures registered in the 10 points where the temperature loggers were placed. The temperature for each nest box location was calculated considering the temperatures registered by all loggers located in a radius of 350 m, weighted by the inverse of their distances (this threshold leads to an average of 3.3 temperature loggers used for each nest box, which we considered appropriated for this scenario). This methodological approach is similar to the interpolation of weather variables into pixelated maps using the available small number of meteorological stations.

Sun radiation at nest boxes

Potentially received sun radiation at each nest box location was obtained using ArcMap® (v10) together with a digital elevation model of the terrain (30-m resolution ASTER Global Digital Elevation Model). Sun illumination raster layers accounting for sun position, terrain slope, cardinal orientation, and hill-shading effect were generated for the study area at the winter solstice, every 15 min of daytime (with values ranging from 0 to 254, where 0 is complete lack of sun radiation and 254 is perpendicular to solar radiation). Hill-shade figures were converted to incident solar radiation per area (KW/m^2). Required azimuth and sun elevation angles were obtained from a web application at http://www.sunearthtools.com, while incoming direct solar radiation was obtained from the Radiation On Collector Program (http://www.builditsolar.com). Based on these 15-min values, we calculated the duration of sun incidence at each nest box and an index of cumulative sun radiation during the whole day at winter solstice (kilojoules per square meter). These two measures were highly correlated in the study area ($r = 0.86$, $n = 159$). In order to avoid redundancy, in the analyses, we only considered the index of sun radiation, which is probably more informative. This index corresponds to the maximum amount of radiation potentially received at each site under

◀ **Fig. 1** Location of 159 nest boxes in the study area, and the spatial variation of night occupancy of nest boxes throughout 52 days around the winter solstice (*WINTER ROOSTING*) and five predictor variables used in the analysis shown in Table 2

anticyclonic sunny conditions. The influence of cloud cover related to regional meteorological conditions was homogeneous throughout our relatively small study area, and therefore, potential sun radiation is a good index of relative differences among nest boxes.

Winter nest box occupation

Nest boxes were carefully cleaned of feces at the end of the previous spring and at the beginning of the study (23–24th November) in order to set homogeneous initial conditions for all nest boxes in terms of parasitism infestation or predators traces (Christe et al. 1994; Ekner and Tryjanowski 2008). We put standard-sized filter paper (11 × 13 cm) covering the base of the nest boxes to facilitate the detection of feces. The presence of feces in nest boxes was checked only once, at the end of the study (12th/13th of January 2011). Nest boxes were only manipulated during daylight hours (2 h after sunrise and 1 h before sunset) to avoid disturbance and undesirable influence on occupation decisions (Tyller et al. 2012). We found no birds during the daytime in any of the 159 nest boxes revised both at the beginning and at the end of the study and we, consequently, assume that birds usually did not occupy nest boxes during daytime. Therefore, the presence of feces in nest boxes can be assumed as a reliable indicator of nocturnal occupation (Dhondt et al. 2012). Winter nest box occupation at night was defined by the presence of feces throughout the 52 days of study (from 23th/24th of November 2010 to 12th/13th of January 2011).

Data analyses

The comparison between occupied and unoccupied nest boxes was carried out by Monte Carlo analyses (Davison and Hinkley 2007). First, we obtained the t test statistics comparing the averages of occupied ($n = 38$) and unoccupied ($n = 121$) nest boxes, considering the seven original variables (altitude, potential sun radiation, average minimum night temperature and average diurnal temperature during the whole study period, average oak height and density 10 m around each nest box, and the occupation of nest boxes in the preceding breeding season of April–June 2010). Second, a randomization process was carried out maintaining the data in each row (i.e., the values of the seven predictor variables within each nest box location and the true associations between them), obtaining a bootstrap sample of 159 nest boxes, and defining a first group of null-occupied ($n = 38$) and null-unoccupied ($n = 121$) nest boxes. The aim of this randomization procedure was to preserve the spatial structure of the data, accounting for the spatial

autocorrelation of the data and for the possible pseudoreplication derived from the fact that the same individual bird may occupy more than one nest box on different nights. Third, seven t tests were carried out considering the null groups of occupied and unoccupied nest boxes, thus obtaining a null t statistic for the seven original variables. This process was repeated 9,999 times. Fourth, the actual figures of the t statistic testing occupied vs. unoccupied nest boxes were compared with 9,999 null t values obtained for each one of the seven predictors analyzed. Significance of t tests comparing the actual averages of occupied and unoccupied nest boxes was estimated considering the position of these true t statistics within the null distribution of t figures by means of the percentiles using a one-tailed approach according to predictions in Table 1. Analyses were carried out using the Resampling and Monte Carlo functions of "PopTools 3.0" (http://www.cse.csiro.au/poptools/) within Microsoft Excel 2010.

A principal components analysis (PCA) with a Quartimax rotation was carried out with the seven variables describing the 159 nest boxes to obtain a reduced number of factors that summarized the relationships among variables and defined environmental gradients within the study area. Four factors with eigenvalues larger than one were retained. The principal components analysis was carried out using STATISTICA 10.0 (StatSoft Inc., Tulsa, OK, USA). Using the factor scores of each nest box (i.e., position of each nest box in the principal components), the preceding testing approach based upon Monte Carlo analysis was repeated, on this occasion testing for the differences between the average position of occupied and unoccupied nest boxes in the four environmental gradients. Two-tailed ps were estimated because it was not possible to make a priori predictions about the structure of the relationships among variables in the principal components. Finally, a spatial eigenvector mapping analysis (SEVM) was carried out to account for spatial autocorrelation in nest box occupancy (Diniz-Filho and Bini 2005; Dorman et al. 2007). SEVM is based on the idea that spatial arrangement of sample locations can be translated into explanatory variables that capture spatial effects. Nest box occupancy was treated as a binomial variable and the four principal components obtained from the PCA as continuous predictors. The eigenfunction decomposition of the spatial connectivity matrix among the 159 nest boxes yield seven spatial autocorrelation filters that reduced spatial autocorrelation in the residuals of the model (nonsignificant according to Moran's I). SEVM was carried out using SAM package (Rangel et al. 2010).

Results

There was a very broad variation in environmental variables among nest box locations (range: min–max); potential cumulative sun radiation: 15–3,604 kJ/m^2 (on winter solstice),

altitude: 1,281–1,599 m, average minimum night temperature (from 1st December to 13th January): −0.60 to −0.01 °C, average diurnal temperature (from 1st December to 13th January): +3.80 to +4.90 °C, oak height: 4–15 m, oak density: 6–127 oaks per 314 m^2. Only 38 of a total of 159 available nest boxes were occupied for winter roosting (24 %). Most nest boxes chosen by birds for winter roosting were not occupied the previous breeding season (81 %), and only 12 % of nest boxes used for breeding were later used for winter roosting (Fig. 1).

According to predictions derived from the hypotheses explaining winter preferences for roost sites (Table 1), characteristics of woodland locations with occupied nest boxes significantly differed from those with unoccupied nest boxes in only the amount of potential sun radiation and average oak height (Table 2). Birds preferred woodland locations with higher potential sun radiation and taller oaks around nest boxes. Nest box occupancy in the preceding breeding season did not show the predicted effect: wintering birds preferentially roosted in nest boxes not used during the previous breeding season. Altitude and temperatures did not show the predicted effects: occupied roost sites were 52 m higher, had nearly identical minimum night temperatures, and were 0.13 °C colder during the day than unoccupied nest boxes (one-tailed ps > 0.85). Oak density around the nest boxes did not influence their occupancy. Therefore, selection of woodland locations to spend the night under identical controlled situations (i.e., roosting within the same wooden nest boxes) was only dependent on subtle variations in sun incidence related to topography and maturity of the oaks.

The principal component analysis (PCA) provides four factors with eigenvalues higher than one, which accounted for 80.1 % of original variance (Table 3). The first component accounts for one-third of original variance, defining a natural gradient of increase in potential sun radiation with increasing altitude and decreasing diurnal temperature and nest box

occupancy the previous breeding season. The second (16 %), third (16 %), and fourth (15 %) components order the nest boxes according to average tree height, oak density, and minimum night temperature, respectively. Thus, a large amount of variation in oak height and density was not related to altitude, temperatures, or potential sun radiation in our study area, as they entered in different orthogonal components. Average position of occupied and unoccupied nest boxes significantly differed in the first two components. Occupied nest boxes during winter received more sun radiation, were located at higher altitudes with lower average diurnal temperatures, and were less occupied for reproduction the previous breeding season, than unoccupied nest boxes. On the other hand, occupied nest boxes for winter roosting were surrounded by taller oaks than unoccupied ones. Nearly identical results were obtained using SEVM analysis as follows: only the first and second components of the PCA were positively and significantly related to nest box occupancy after accounting for spatial autocorrelation.

Discussion

To our knowledge, this is the first study relating sun radiation during daytime to winter night roosting preferences. The prominent influence of sun radiation just before and after the critical night-fasting period probably precluded the manifestation of other classical effects such as temperature or altitude. Wintering birds identified the fine-grained mosaic of radiation generated by the hill-shade effect and chose to roost at forest patches with higher sun radiation.

The great importance of sun radiation for wintering birds may respond to three complementary causes. First, a terrain with a longer sun incidence has greater illumination levels, even when the sky is cloudy, extending the time available for foraging. If small birds are strongly pressed to feed in order

Table 2 Mean and standard deviation (SD) of seven variables describing the characteristics of occupied (OCCUP, $n = 38$) and unoccupied (UNOCCUP, $n = 121$) nest boxes for winter roosting. Statistical significance of the differences between means were obtained using t tests and Monte Carlo analysis building null distributions of t statistics (9,999 randomization trials; see "Data analyses" for more details). Significance tests are one tailed according to predictions in Table 1. Potential sun radiation is the cumulative radiation obtained in an anticyclonic sunny day in winter solstice

	OCCUP		UNOCCUP			
	Mean	SD	Mean	SD	Prediction	One-tailed p
Altitude (m)	1,471.9	91.3	1,419.6	89.5	Lower	0.999
Minimum night temperature (°C)	−0.31	0.09	−0.29	0.12	Higher	0.856
Average day temperature (°C)	4.21	0.23	4.35	0.21	Higher	0.999
Potential sun radiation (KJ/m^2)	1,953.0	902.4	1,557.0	864.7	Higher	0.010
Oak height (m)	10.1	1.8	9.2	2.0	Higher	0.005
Oak density (#/314 m^2)	50.5	27.4	53.1	27.5	Higher	0.684
Previous breeding occupancy (%)	18.4	39.3	41.3	49.4	Higher	0.997

Table 3 Principal components analysis performed with seven variables defining environmental characteristics in 159 locations with nest boxes (factors PC1–PC4). In bold type are factor loadings >0.5. Mean and standard deviation (SD) of factor scores of occupied ($n = 38$) and unoccupied ($n = 121$) nest boxes in each principal component. Statistical significance of the differences between means were obtained using t tests and Monte Carlo analysis building null distributions of t statistics (9,999 randomization trials; see "Data analyses" for more details). Results of the spatial eigenvector mapping (SEVM) show the partial coefficients and significance of principal components after considering seven spatial autocorrelation filters

	PC1	PC2	PC3	PC4
Altitude	**0.92**	−0.03	−0.13	0.10
Minimum night temperature	0.03	−0.05	−0.01	**0.97**
Average day temperature	**−0.70**	−0.36	0.35	−0.09
Potential sun radiation	**0.79**	−0.32	0.04	−0.25
Oak height	0.00	**0.91**	0.06	−0.06
Oak density	−0.25	0.00	**0.85**	−0.04
Previous breeding occupancy	**−0.53**	−0.27	−0.48	−0.15
Eigenvalue	2.32	1.14	1.10	1.05
% variance accounted for	0.33	0.16	0.16	0.15
Factor scores of occupied nest boxes				
Mean	0.51	0.36	0.06	−0.15
SD	0.95	0.96	0.97	0.86
Factor scores of unoccupied nest boxes				
Mean	−0.16	−0.11	−0.02	0.05
SD	0.97	0.99	1.01	1.04
t test (two-tailed p)	0.0006	0.011	0.697	0.267
Coefficients of SEVM	0.239	0.077	−0.007	−0.038
Significance	<0.001	0.011	0.829	0.224

to cope with winter requirements because of their high metabolism relative to their small body masses, the low food availability, low temperatures, and the long fasting night period (e.g., Gibb 1954), they should prefer those woodland areas with longer day lengths and better foraging conditions (amount of sun radiation and duration of sun incidence were highly correlated: $r = 0.86$; see also Carrascal et al. 2012b for the importance of day length on tit abundance along a latitudinal gradient). Second, birds may benefit from the heating effect of sun radiation on cloudless days, accounting for a 10–15 °C increase in operative temperature under winter windless conditions (see Carrascal et al. 2001 and Carrascal et al. 2012a for the same woodlands in Guadarrama mountains). Several laboratory studies have shown the significant effect of sun radiation on passerines, dropping the lower threshold of temperature tolerance and reducing the metabolic costs of thermoregulation (Lustick et al. 1970; 1978; De Jong 1976; Wood and Lustick 1989; Wolf et al. 2000). Finally, sun radiation indirectly enhances foraging efficiency of birds by increasing the activity of ectothermic arthropods (Avery and Krebs 1984; Honek 1997; Carrascal et al. 2001).

Contrary to our prediction, wintering birds did not show any preference for roosting at lower altitudes

(Tables 2 and 3). Due to orographic effects in our study area, the patches located at higher altitudes turned out to be those with a higher sun incidence (Table 3, Fig. 1). This counterintuitive preference for high elevations due to increased sunshine was also shown in black-and-white snub-nosed monkeys wintering in the Trans-Himalayans (Quan et al. 2011).

Yet surprisingly, selection of roost sites was not influenced by environmental temperature, either nocturnal or diurnal (Table 2). Our results are in accordance with Thiel et al. (2007), who reported that microclimate does not influence selection of night roosts by the capercaillie in central Europe. Thermal properties of cavities for roosting may buffer environmental variation in outdoor night temperature (Paclik and Weidinger 2007; Coombs et al. 2010; Grüebler et al. 2013). This fact may reduce the importance of temperature in the selection of night roosts, allowing other factors such as habitat or resources surrounding the roost site to gain importance. Moreover, Polo and Carrascal (2008) demonstrated that temperature per se does not influence night body mass loss in a small passerine, the coal tit (*Periparus ater*), in the same region. Nocturnal body mass loss mainly depended on the level of body mass at dusk and daily body mass gain in the previous day, supporting the influence of proximate effects related to the regulation of body reserves the

preceding day, instead of the expected pure physiological energetic balance (i.e., lower temperature related to higher resting metabolism; Calder and King 1974; Carey 1996).

The preference for woodland patches with taller oaks is consistent with the preference of the studied species for mature oakwoods, considering they are tree canopy gleaners and trunk foragers (Perrins 1998; see Carrascal and Díaz 2006; Carrascal et al. 2012c for the study region). Overlapping this general pattern of habitat preferences with the selection of locations where cumulative solar radiation is greater, a practical recommendation may be derived from our results as follows: forest management practices should preserve the most mature forests considering their location on those slopes more exposed to solar radiation during winter, in order to enhance habitat suitability for woodland birds in these Mediterranean deciduous forests of continental cold climate.

Finally, the decoupling between occupancy of nest boxes in winter and the previous breeding season may reflect how birds adjust their distribution to the specific requirements of the season, imposed by both the environment and the phase of their life cycle. In spring, birds may avoid higher altitudes with more weather instability, where a sudden cold spell can drastically compromise parental investment (Sanz and Moreno 1995; Seoane et al. 2013).

The applicability of the habitat use pattern described in this paper cannot be generalized to every environmental condition or geographical location. Geographic and orographic variation in winter sun incidence defines the background where the phenomenon may be ecologically relevant for these species. For example, cloudiness and day length vary from less than 50 % of the 9–10 h of winter daylight in southern Europe to more than 70 % of less than 5 h of daylight at latitudes above 55° (Henderson-Sellers 1986). Thus, possibilities for minimizing costs of thermoregulation by selecting sunlit patches are scarce at higher latitudes with few clear days available in winter. Moreover, this behavior can only operate in mountainous areas where the hill-shade effect introduces a large variation in sun radiation at small spatial scales. For example, in the study area, the potential sun radiation received at different nest box locations varied enormously both in length (from 15 min to 7 h) and in magnitude (from 15 to 3,604 kJ/m^2 in the winter solstice day; Fig. 1). Therefore, selection of roost sites according to differential solar radiation received by a forest patch could play an important role at mountainous areas of cold climate with frequent anticyclonic conditions.

References

Avery HI, Krebs JR (1984) Temperature and foraging success of great tits *Parus major* hunting for spiders. Ibis 126:33–38

Blanco E, Casado MA, Costa M, Escribano R, García M, Génova M, Gómez A, Moreno JC, Morla C, Regato P, Sanz H (1997) Los bosques ibéricos. Una interpretación geobotánica. Planeta, Barcelona

Blem CR (1990) Avian energy storage. Curr Ornithol 7:59–113

Broggi J, Brotons L (2001) Coal tit fat-storing patterns during the non-breeding season: the role of residence status. J Avian Biol 32:333–337

Brotons L, Haftorn S (1999) Geographic variation of the storing behaviour in the Coal tit *Parus ater*: role of winter residency and environmental conditions. Ibis 141:587–595

Buttemer WA (1985) Energy relations of winter roost-site utilization by American goldfinches (*Carduelis tristis*). Oecologia 68:126–132

Buttemer WA, Astheimer LG, Weathers WW, Hayworth AM (1987) Energy savings attending winter-nest use by verdins (*Auriparus fiaviceps*). Auk 104:531–535

Calder W, King J (1974) Thermal and caloric relations of birds. In: Farner D, King J (eds) Avian biology, vol 4. Academic, London, pp 259–413

Camprodon J, Salvanya J, Soler-Zurita J (2008) The abundance and suitability of tree cavities and their impact on hole-nesting bird populations in beech forests of NE Iberian Peninsula. Acta Ornithol 43:17–31

Carey C (1996) Avian energetics and nutritional ecology. Chapman and Hall, New York

Carrascal LM, Díaz L (2006) Winter bird distribution in abiotic and habitat structural gradients. A case study with Mediterranean montane oakwoods. Ecoscience 13:100–110

Carrascal LM, Potti J, Sánchez-Aguado FJ (1987) Spatio-temporal organization of the bird communities in two Mediterranean montane forests. Holarct Ecol 10:185–192

Carrascal LM, Díaz JA, Huertas DL, Mozetich I (2001) Behavioral thermoregulation by treecreepers: trade-off between saving energy and reduced crypsis. Ecology 82:1642–1654

Carrascal LM, Villén-Pérez S, Seoane J (2012a) Thermal, food and vegetation effects on winter bird species richness of Mediterranean oakwoods. Ecol Res 27:293–302

Carrascal LM, Santos T, Tellería JL (2012b) Does day length affect winter bird distribution? Testing the role of an elusive variable. PLoS One 7(2):e32733

Carrascal LM, Seoane J, Villén-Pérez S (2012c) Temperature and food constraints in wintering birds—an experimental approach in montane Mediterranean oakwoods. Community Ecol 13:221–229

Christe P, Oppliger A, Richner H (1994) Ectoparasite affects choice and use of roost sites in the great tit, *Parus major*. Anim Behav 47:895–898

Cody ML (1985) Habitat selection in birds. Academic Press, London

Coombs A, Bowman J, Garroway C (2010) Thermal properties of tree cavities during winter in a northern hardwood forest. J Wildl Manag 74:1875–1881

Cresswell W, Clark JA, Macleod R (2009) How climate change might influence the starvation–predation risk trade-off response. Proc R Soc Lond B 276:3553–3560

Davison AC, Hinkley DV (2007) Bootstrap methods and their application. Cambridge University Press, Cambridge

De Jong AA (1976) The influence of simulated solar radiation on the metabolic rate of white-crowned sparrows. Condor 78:174–179

Dhondt AA, Blondel J, Perret P (2012) Why do Corsican blue tits *Cyanistes caeruleus ogliastrae* not use nest boxes for roosting? J Ornithol 151:95–101

Diniz-Filho JA, Bini LM (2005) Modelling geographical patterns in species richness using eigenvector-based spatial filters. Glob Ecol Biogeogr 14:177–185

Dorman CF, McPherson JM, Araújo MB, Bivand R, Bolliger J, Carl G, Davies G, Hirzel A, Jetz W, Kissling D, Kühn I, Ohlemüller R, Peres-Neto P, Reineking B, Schröder B, Schurr FM, Wilson R (2007) Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. Ecography 30:609–628

Ekner A, Tryjanowski P (2008) Do small hole nesting passerines detect cues left by a predator? A test on winter roosting sites. Acta Ornithol 43:107–111

Gibb JA (1954) Feeding ecology of tits, with notes on treecreeper and goldcrest. Ibis 96:513–543

Grüebler M, Widmer S, Korner-Nievergelt F, Naef-Daenzer B (2013) Temperature characteristics of winter roost-sites for birds and mammals: tree cavities and anthropogenic alternatives. Int J Biometeorol. doi:10.1007/s00484-013-0643-1

Henderson-Sellers A (1986) Cloud changes in a warmer Europe. Clim Chang 9:25–52

Herbers J, Serrouya R, Maxcy K (2004) Effects of elevation and forest cover on winter birds in mature forest ecosystems of southern British Columbia. Can J Zool 82:1720–1730

Honek A (1997) The effect of temperature on the activity of Carabidae (Coleoptera) in a fallow field. Eur J Entomol 94:97–104

Houston AI, McNamara J (1993) A theoretical investigation of the fat reserves and mortality levels of small birds in winter. Ornis Scand 24:205–219

Huertas D, Díaz JA (2001) Winter habitat selection by a montane bird assemblage: the effects of solar radiation. Can J Zool 79:279–284

Kendeigh SG (1961) Energy of birds conserved by roosting in cavities. Wilson Bull 73:140–147

Kendeigh S, Dol'nik V, Gavrilov V (1977) Granivorous birds in ecosystems. In: Pinowski J, Kendeigh S (eds) Avian energetics:127–204. Cambridge University Press, Cambridge

Koivula K, Lahti K, Orell M, Rytkonen S (1993) Prior residency as a key determinant of social-dominance in the willow tit (Parus montanus). Behav Ecol Sociobiol 33:283–287

Lustick S, Kelty M (1979) Effects of the roost site on the energetics of blackbirds and starlings. Bird Control Seminars Proceedings, pp 260–272

Lustick S, Talbot S, Fox E (1970) Absorption of radiant energy in redwinged blackbirds (Agelaius phoenicelus). Condor 72:471–473

Lustick S, Battersby B, Kelty M (1978) Behavioral thermoregulation: orientation toward the sun in herring gulls. Science 200:81–83

Mayer L, Lustick S, Battersby B (1982) The importance of cavity roosting and hypothermia to the energy balance of the winter acclimatized Carolina chickadee. Int J Biometeorol 26:231–238

McKechnie AE, Lovegrove BG (2002) Avian facultative hypothermic responses: a review. Condor 104:705–724

McNamara JM, Houston AI, Lima SL (1994) Foraging routines of small birds in winter: a theoretical investigation. J Avian Biol 25:287–302

Meehan TD, Jetz W, Brown JH (2004) Energetic determinants of abundance in winter landbird communities. Ecol Lett 7:532–537

Naef-Daenzer B (2000) Patch time allocation and patch sampling by foraging great and blue tits. Anim Behav 59:989–999

Paclik M, Weidinger K (2007) Microclimate of tree cavities during winter nights-implications for roost site selection in birds. Int J Biometeorol 51:287–293

Perrins CM (1998) The complete birds of the Western Palearctic on CD-ROM, version 1.0. Oxford University Press, Oxford

Pinowski J, Haman A, Jerzak L, Pinowska B, Barkowska M, Grodzki A, Haman K (2006) The thermal properties of some nests of the Eurasian tree sparrow Passer montanus. J Therm Biol 31:573–581

Polo V, Carrascal LM (2008) Nocturnal body mass loss in coal tits Periparus ater: the combined effects of ambient temperature and body reserves. Acta Zool Sin 54:615–621

Polo V, Carrascal LM, Metcalfe NB (2007) The effects of latitude and day length on fattening strategies of wintering coal tits (Periparus ater L): a field study and aviary experiment. J Anim Ecol 76:866–872

Quan R-C, Ren G, Behm JE, Wang L, Huang Y, Long Y, Zhu J (2011) Why does Rhinopithecus bieti prefer the highest elevation range in winter? A test of the sunshine hypothesis. PLoS Biol 6:e24449

Rangel TF, Diniz-Filho JAF, Bini LM (2010) SAM: a comprehensive application for spatial analysis in macroecology. Ecography 33:46–50

Robinson RA, Baillie SR, Crick HQP (2007) Weather-dependent survival: implications of climate change for passerine population processes. Ibis 149:357–364

Root T (1988) Energy constraints on avian distributions and abundances. Ecology 69:330–339

Sandell M, Smith HG (1991) Dominance, prior occupancy, and winter residency in the great tit (Parus major). Behav Ecol Sociobiol 29:147–152

Sanz JJ, Moreno J (1995) Experimentally-induced clutch size enlargements affect reproductive success in the pied-flycatcher. Oecologia 103:358–364

Senar JC, Borras A (2004) Surviving to winter: strategies of wintering birds in the Iberian Peninsula. Ardeola 51:133–168

Seoane J, Villén-Pérez S, Carrascal LM (2013) Environmental determinants of seasonal changes in bird diversity of Mediterranean oakwoods. Ecol Res 28:435–445

Shields WM, Grubb TC (1974) Winter bird densities on north and south slopes. Wilson Bull 86:125–130

Stapanian MA, Smith CC, Finck EJ (1999) The response of a Kansas winter bird community to weather, photoperiod, and year. Wilson Bull 111:550–558

Swanson DL (1993) Cold tolerance and thermogenic capacity in dark-eyed juncos in winter: geographic variation and comparison with American tree sparrows. J Therm Biol 18:275–281

Thiel D, Unger C, Kery M, Jenni L (2007) Selection of night roosts in winter by capercaillie Tetrao urogallus in Central Europe. Wildl Biol 13:73–86

Tyller Z, Paclik M, Remes V (2012) Winter night inspections of nest boxes affect their occupancy and reuse for roosting by cavity nesting birds. Acta Ornithol 47:79–85

Velky M (2006) Patterns in winter-roosting and breeding of birds in nest-boxes. Tichodroma 18:89–96

Velky M, Kanuch P, Kristin A (2010) Selection of winter roosts in the great tit Parus major: influence of microclimate. J Ornithol 151:147–153

Virkkala R (2004) Bird species dynamics in a managed southern boreal forest in Finland. For Ecol Manag 195:151–163

Webb DR, Rogers CM (1988) Nocturnal energy expenditure of dark-eyed juncos roosting in Indiana during winter. Condor 90:107–112

Wiens J (1989) The ecology of bird communities. Volume I: foundations and patterns. Cambridge University Press, Cambridge

Wolf B, Wooden K, Walsberg G (2000) Effects of complex radiative and convective environments on the thermal biology of the white-crowned sparrow (Zonotrichia leucophrys gambelii). J Exp Biol 203:803–811

Wood J, Lustick S (1989) The effects of artificial solar-radiation on wind-stressed tufted titmice (Parus bicolor) and Carolina chickadees (Parus carolinensis) at low-temperatures. Comp Biochem Physiol 92:473–477

Zabala J, Zuberogoitia I, Belamendia G, Arizaga J (2012) Micro-habitat use by bramblings Fringilla montifringilla within a winter roosting site: influence of microclimate and human disturbance. Acta Ornithol 47:179–184