Winter habitat selection by a montane forest bird assemblage: the effects of solar radiation

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Abstract: A relationship between sunlight and bird abundance in cold climates may seem intuitive and perhaps obvious. However, there is, surprisingly, little or no evidence to support it. We investigated the effects of solar radiation on the winter abundance of insectivorous birds inhabiting a Mediterranean montane forest with a high frequency of cold, cloudless days. We censused birds by ear in 20 different forest tracts in which we simultaneously quantified a number of variables related to the availability of solar radiation, vegetation structure, arthropod abundance, and altitude. All variables related to solar radiation were reduced to a single principal component that attained high scores for south-facing transects, where many tree trunks received direct sunlight for a long period daily. The abundance of all bird species was positively related to the scores of transects on this component after the effects of vegetation structure, altitude, and prey availability were controlled for. Solar radiation was the main predictor of overall abundance and species richness of bird assemblages. Body mass and diet (insectivorous vs. mixed) explained 94.6% of interspecific variation in the strength of the relationship between solar radiation and bird abundance. We hypothesize that selecting forest sectors with a higher availability of sunlit patches allows birds to improve their winter survival by reducing the metabolic costs of thermoregulation, decreasing movement rates, and (or) increasing the time spent motionless in safe locations.

Résumé : Une relation entre la lumière solaire et l'abondance des oiseaux dans les climats froids peut sembler logique, même évidente, mais il existe peu de documentation à l'appui de cette hypothèse. Nous avons étudié les effets des radiations solaires sur l'abondance des oiseaux insectivores qui ont passé l'hiver dans une forêt méditerranéenne de montagne caractérisée par de nombreuses journées froides sans nuages. Nous avons recensé les oiseaux à l'oreille le long de 20 parcelles de forêt dans lesquelles nous avons en même temps quantifié un certain nombre de variables reliées à la disponibilité de la radiation solaire, à la structure de la végétation, à l'abondance des arthropodes et à l'altitude. Toutes les variables reliées à la radiation solaire ont été réduites à une seule composante principale accordant un pointage élevé aux transects orientés vers le sud qui comportent de nombreux troncs éclairés, directement exposés au soleil pendant une grande partie de la journée. L'abondance des oiseaux de toutes les espèces est en corrélation positive avec la position des transects sur cet axe principal éclairés une fois qu'on a tenu compte des effets de la structure de la végétation, de l'altitude et de la disponibilité des proies. La lumière solaire était également la principale variable prédictive de l'abondance globale et de la richesse en espèces au sein des peuplements d'oiseaux. La masse totale et le régime alimentaire (insectivores vs. omnivores) expliquent 94,6 % de la variation interspécifique de la force de la relation entre la radiation solaire et l'abondance des oiseaux. Nous croyons que le choix de secteurs qui comptent de nombreux coins éclairés dans la forêt donne aux oiseaux de meilleures chances de survie en hiver parce que cela leur permet de diminuer les coûts métaboliques de leur thermorégulation, de réduire leurs déplacements et (ou) de consacrer plus de temps au repos dans un endroit protégé.

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Introduction

The endothermy of birds is energetically expensive. Small birds have very high energy requirements, owing to their high surface/volume ratio and the metabolic costs of flight (Tatner and Bryant 1986; Carlsson and Moreno 1992; Hedenström 1992). These requirements increase in cold environments and (or) during the winter as a consequence of the inverse relationship between metabolic rate and ambient temperature (Calder and King 1974). The long winter nights at temperate latitudes cause some small passerines to lose up to 9–15% of their body mass (Bednekoff et al. 1994 and references therein), and adverse meteorological conditions (e.g., snowstorms) may have a serious impact on bird populations (Graber and Graber 1983; Hendricks and Norment 1992).

Any behavioural or physiological strategy that facilitates thermoregulation might therefore enhance winter survival. Different groups of birds use several types of physiological strategies, and previous studies have documented the advantages of selecting thermally appropriate roosts (Walsberg 1986; Webb and Rogers 1988; Jenni 1991), but the diurnal cost of thermoregulation can also be reduced behaviourally. By selecting appropriate diurnal microhabitats, small birds

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can reduce their energy expenditure (Walsberg 1985; Wachob 1996). For example, small passerines can take advantage of solar radiation, which has a pronounced effect in reducing their metabolic rate (Hamilton and Heppner 1967; Lustick 1969; Lustick et al. 1970; Ohmart and Lasiewski 1971; Wolf and Walsberg 1996). By exploiting environmental mosaics of sunlit patches, they can reduce the metabolic costs of thermoregulation, a capacity that was demonstrated by the pioneer studies listed above. Birds should therefore select sunlit patches whenever ambient temperatures are below their thermoneutral zone, even if food resources are not limiting or particularly scarce.

The expected effects of this form of behavioural thermoregulation on habitat selection are straightforward: the winter abundance of small bird species should be positively related to the amount of solar radiation received by different habitat sectors. The influence of the thermal environment on the distribution of birds has been approached on a broader, continental scale (Weathers 1979; Root 1988; Repasky 1991) or, alternatively, from a microhabitat-based, behaviourally oriented perspective (Wachob 1996), but not from the intermediate viewpoint of the regional distribution of avian population densities (but see Shields and Grubb 1974; Dolby and Grubb 1999). In fact, the relationship between sunlight and bird abundance, despite being intuitive and perhaps obvious, has surprisingly little or no evidence to support it.

We tested this hypothesis in a montane forest in the centre of the Iberian Peninsula, where the predominant anticyclonic conditions produce a relatively high frequency of cold, sunny days. The goals of our study were twofold: first, to examine whether the relative abundance of insectivorous birds increases with solar radiation level when the effects of vegetation structure and food availability are controlled for; and second, to examine whether the effects of solar radiation on abundance vary among species that differ in body size and diet. Smaller birds are expected to derive greater benefit from exposure to sunlight, owing to their higher surface/volume ratio. Insectivorous birds might be more prone to save energy by selecting sunlit sites than seed-eating species, owing to the lower energy content of arthropods relative to lipid-rich seeds (Bell 1990; Díaz 1996). However, it should be noted that our bird assemblage included only one strictly insectivorous species (see Methods), hence any conclusions that we can draw here apply only to this species (Carrascal et al. 2001).

Material and methods

Study area

Fieldwork was carried out in January 1998 in a montane coniferous forest of Scots pine, *Pinus sylvestris* (Valsaín forest, Sierra de Guadarrama, central Spain; 40°47′N, 04°00′W). The altitude of the surveyed area (covering ca. 1800 ha) extends from 1500 to 2000 m asl. The landscape contains a wide variety of slopes, hence there is considerable variation in the amount of solar radiation received by different forest tracts. The average winter photoperiod (December–February) is 9.9 h light : 14.1 h dark. During the winter season the area has a cold continental Mediterranean climate. At Navacerrada Pass (1.850 m asl), which is located within the study area, the average maximum and minimum temperatures in January 1998 were 2.0 and –2.5°C. Although severe snowstorms may have a strong local effect, anticyclonic conditions are predominant during many weeks of the winter season. During the winter of 1997–1998, 42% of days were cloudless, and snow occurred on 39% of days.

Study species

The short-toed treecreeper (*Certhia brachydactyla*; relative abundance = 5.4 ± 0.8 birds/10 ha (mean ± 1 SE)), nuthatch (*Sitta europaea*; 3.8 ± 0.7 birds/10 ha), coal tit (*Parus ater*; 18.6 ± 1.2 birds/10 ha), crested tit (*Parus cristatus*; 12.6 ± 1.4 birds/10 ha), and great spotted woodpecker (*Dendrocopos major*; 3.0 ± 0.7 birds/10 ha) are the main species composing the bird assemblage inhabiting this forest during winter. These winter residents forage almost exclusively on trees (Carrascal 1984). In addition, they show variation in body mass (ranging between 8 and 90 g) and diet. Most species include plant material in their winter diet, especially seeds, nuts, and fruits, but treecreepers are strictly insectivorous (Cramp 1985; Cramp and Perrins 1993). Therefore, this assemblage is suitable for analyzing whether the effects of solar radiation on winter abundance vary among species that differ in body size and diet.

Field methods

Bird abundance was estimated along 20 different transects by counting all birds detected within a 1 km long × 50 m wide survey belt. The distance between transects varied between 0.5 and 14 km, with an average of ca. 3.5 km. Two or three transects per day were censused between 08:00 and 12:00 GMT, always on calm, clear days. All species were censused by ear, which eliminates the spurious effect of sunlight in increasing visual detectability. The distribution of transects was selected to represent the variability of the independent variables within the study area (especially altitude and slope, and therefore radiation level; see Results).

The incidence of solar radiation on each survey belt was quantified using (*i*) the duration, in hours per day, of direct sun exposure, estimated by noting the times of the beginning and end of sun incidence (by monitoring the transect slopes from an elevated location on 2 consecutive days); (*ii*) the negative cosine of the cardinal orientation of the transect slope, which gives higher values to more southerly orientations; and (*iii*) the number of tree trunks with at least half of their base surface (below approximately 5 m) exposed to the sun, counted along a 20 m wide belt surrounding the transect line.

We also measured several structural variables that might affect bird abundance: mean cover of lichens (which are important as a foraging substrate for many of the species considered; Carbonell 1995),[2] mean trunk diameter, mean tree height, and mean height of the lower part of the trunk (the upper part of Scots pines, which is covered by thin, scale-like plates, is avoided by trunk foragers; Carrascal 1988). The values of these variables were averaged over the five nearest trees every 100 m along the transects ($n = 50$ measurements per transect). Likewise, we estimated tree density by counting all trunks within a 25-m radius every 100 m along the transects ($n = 10$ counts per transect).

The availability of potential prey for trunk foragers was estimated by conducting arthropod counts on the nearest tree every 100 m along the transects ($n = 10$ trees per transect). We searched at breast height on the selected trunks for arthropods ≥1 mm long for a 2-min period (see Cooper and Whitmore 1990 and references therein). Food availability for foliage foragers was estimated indirectly using mean values for vegetation structure. Previous data

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[2] R. Carbonell. 1995. El papel de los líquenes como sustrato de alimentación de las aves insectívoras forestales. Graduate thesis, Universidad Complutense, Madrid, Spain.

(Carbonell 1995)[2] had shown that although arthropods are relatively more abundant near the trunk than in the outer canopy (1.7 per 2 min of searching on the trunk and lichens on large branches vs. 0.3 on needles and lichens on small branches), their absolute number, and hence their overall availability for insectivorous birds, is much higher in the canopy (97% of total estimated prey) because of its much larger contribution to the total foraging surface. Thus, we assume that our structural variables related to tree volume (mean trunk diameter and mean tree height) allow for appropriate estimates of food availability to foliage foragers.

Statistical procedures

We used principal component analyses (PCAs) to reduce the original set of structural and radiative variables and to detect structure in the relationships between them. Only PCs with eigenvalues ≥1 were retained, and when necessary the Varimax rotation was performed to facilitate the interpretation of PCs. The relative ability of the different types of variables (radiation PC, vegetation structure PCs, altitude above sea level, and arthropod counts) to predict the abundance of the species studied was assessed by means of stepwise multiple regressions. A similar procedure was used to examine the effects of the same independent variables (PCs, height above sea level, etc.) on overall abundance (number of birds/10 ha) and species richness (number of species) of bird assemblages. To check the stability of the results obtained, all regressions were performed both forward and backward. When regression models included more than one independent variable, we used the equation

$$\%\mathrm{var} = 100 \times \beta \times r$$

where β is a standardized partial regression coefficient and r is Pearson's correlation coefficient, to estimate the independent contributions of each of them to the prediction of the dependent variable.

We used analysis of covariance (ANCOVA) to test the hypothesis that selection of sunlit areas should be more pronounced in species with a smaller body size and a strictly insectivorous diet. The dependent variable was the percentage of variance in abundance explained uniquely by radiation levels (R^2, calculated as explained above). The covariate was body mass and the factor was type of diet, insectivorous for *C. brachydactyla* and mixed (insects and seeds) for *S. europaea*, *P. ater*, *P. cristatus*, and *D. major* (Cramp 1985; Cramp and Perrins 1993). Thus, we hypothesized that R^2 decreases with increasing body mass and has a larger positive residual for *C. brachydactyla* than for the other species.

When necessary, variables were log- or square-root-transformed to meet the requirements of parametric tests. The level of statistical significance was set at $\alpha = 0.05$ in all analyses.

Results

A PCA with the structural variables produced two PCs (SPC1 and SPC2) that accounted for 66.9% of the variance contained in the original matrix (Table 1). The first PC defined a tendency towards forest development, giving higher scores to transects with taller and denser trees. Thus, SPC1 should also provide an estimate of food availability for foliage foragers. The second PC was negatively correlated with tree density and positively correlated with lichen cover.

A second PCA incorporated the three variables related to solar radiation into a single factor (90.6% of variance explained) that gave high scores to south-facing transects, with many trunks that were sunlit at midday and received direct sunlight for a long period daily (Table 1). The high factor loadings of all variables in the radiation principal component (RPC) suggest that topography (i.e., the direction in which the transect slope faced) was the main factor determining both the incidence of sunlight inside the forest (number of sunlit trunks) and the temporal availability of sunlit patches (length of the daily insolation period).

Table 1. Principal component analysis using the structural and radiative variables describing the transects censused in this study.

	SPC1	SPC2	RPC
Vegetation structure			
Mean trunk diameter	**0.759**	0.090	
Mean number of trees	0.238	**–0.818**	
Mean exploitable height	**0.898**	0.118	
Mean total height	**0.855**	–0.172	
Mean lichen cover	0.348	**0.583**	
Solar-radiation level			
Daily insolation period			**0.954**
Number of sunlit trunks			**0.971**
– cosine (transect orientation)			**0.931**
Eigenvalue	2.292	1.057	2.719
% variance	45.8	21.1	90.6
% accumulated variance	45.8	66.9	90.6

Note: Significant correlations between original variables and components (all $P < 0.01$) are shown in boldface type.

Once we had reduced the original structural and radiative variables to a few PCs, we examined the matrix of correlations among them and with altitude and food availability (Table 2). The first structural component (SPC1) was significantly correlated with RPC and altitude, showing that plots with higher radiation levels, or located at higher altitudes, had taller and denser trees, and hence more canopy available for foliage-exploiting birds. However, the total amount of solar radiation had no effect on arthropod abundance on tree trunks. Prey abundance on trunks decreased, though not significantly, at higher elevations (Table 2). Overall, redundancy levels were below 0.5 for all variables except SPC1.

Bird abundance increased with forest development. Simple correlations between abundance and SPC1 were significant for *C. brachydactyla* and *D. major*, and the combined probability for the five species was $P < 0.001$ ($\chi^2 = 2\Sigma \ln P_i = 29.61$, df = 10; Sokal and Rohlf 1981). However, the most important factor explaining the distribution of bird abundances was not vegetation structure but solar radiation (RPC). Thus, the abundance of all bird species was positively related to RPC scores when the effects of vegetation structure (SPC1 and SPC2), estimates of prey availability, and altitude were controlled for (Table 3). Stepwise multiple regressions with the whole set of independent variables retained RPC within the final model for all species (both forward and backward; see Table 3). The amount of variance in bird abundance explained uniquely by solar radiation ranged from 19.4% for *D. major* to 84.8% for *C. brachydactyla* (an average of 42.4% for the five species).

Solar radiation was also the main predictor of the overall abundance and species richness of the bird assemblages. Species richness was negatively related to prey counts on tree trunks, when the effects of RPC were controlled for, because of a single case that had both the highest residual with

Table 2. Correlations and redundancies (R^2; percentage of variance explained by all other variables in the matrix) of the variables employed to model the distribution of bird abundances.

	SPC1		SPC2		ALT		ART		
Variable	r	P	r	P	r	P	r	P	R^2
RPC	0.586	0.007	–0.221	0.350	0.099	0.679	0.278	0.235	47.6
SPC1			0.000	1.000	0.509	0.022	0.031	0.897	56.6
SPC2					0.031	0.898	0.058	0.807	9.9
ALT							–0.430	0.058	47.0
ART									31.9

Note: The interpretation of principal components (SPC1, SPC2, and RPC) is shown in Table 1. ALT, altitude above sea level; ART, mean number of arthropods on trunks.

Table 3. Results of (forward) stepwise multiple regressions for the abundances of the species studied and the number of species on each transect censused as a function of the corresponding independent variables (for an explanation of abbreviations see Tables 1 and 2).

Dependent variable	Independent variable	r	P	%var	Σ %var
Certhia brachydactyla	RPC	0.961	<0.001	84.8	
	ALT	0.532	0.023	3.9	
	SPC2	–0.493	0.037	5.0	93.7[a]
Sitta europaea	RPC	0.507	0.022	25.7	
Parus ater	RPC	0.691	<0.001	47.7	
Parus cristatus	RPC	0.585	0.007	34.2	
Dendrocopos major	ALT	0.548	0.015	25.8	
	RPC	0.488	0.034	19.4	45.2[b]
Overall abundance	RPC	0.828	<0.001	68.6	
Number of species	RPC	0.753	<0.001	52.5	
	ART	–0.467	0.044	5.0	57.5[c]

Note: r, Pearson's correlation coefficient (partial correlation when the model includes more than one independent variable); % var, the independent contribution of each of the independent variables to the prediction of the dependent variable (equal to $100 \cdot \beta \cdot r$, where β is a standardized partial regression coefficient and r is a simple correlation coefficient); Σ % var, percentage of accumulated variance explained. The sample size is 20 in all cases. Backward regressions yielded identical results for all variables except number of species, for which RPC was the only variable retained in the final backward model ($r = 0.676$, $P = 0.001$).

[a] $F_{[3,16]} = 78.72$, $P < 0.001$.

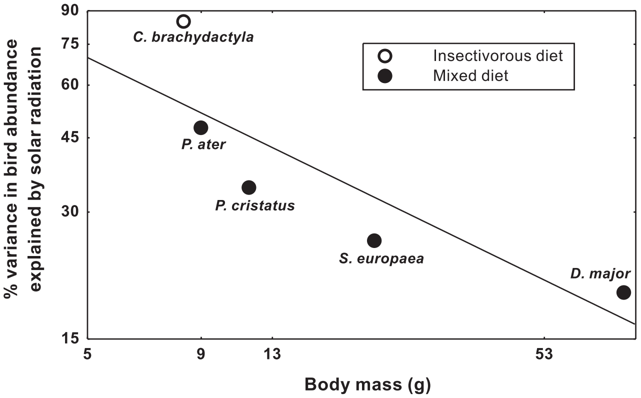
[b] $F_{[2,17]} = 6.99$, $P = 0.006$.

[c] $F_{[2,17]} = 11.52$, $P < 0.001$.

respect to solar radiation (Studentized residual, $t_{[18]} = -2.69$, $P = 0.015$) and the maximum number of arthropods on trunks (2.7/2 min of searching; z score on log-transformed data = 2.02 SDs). In fact, the backward stepwise regression retained solar radiation as the only variable related to species richness (Table 3).

Body mass and diet explained 96.0% of interspecific variation in the independent contribution of radiation levels to the prediction of bird abundance (Fig. 1; $F_{[2,2]} = 23.71$, $P = 0.04$; ANCOVA implemented as a general linear model with diet coded as a dummy variable). Moreover, partial correlations would have been significant had they been judged by means of one-tailed tests based on directional hypotheses (diet, with "insectivorous" coded as 0 and "mixed" coded as 1: $r = -0.924$, $P_{\text{one-tailed}} = 0.038$; body mass: $r = -0.939$, $P_{\text{one-tailed}} = 0.03$).

Fig. 1. Influence of body mass and diet on the relationship between solar radiation and bird abundance (R^2, measuring the independent contribution of radiation level to the prediction of each species' abundance) for the five species studied.



Discussion

Our results indicate that solar radiation is a relevant factor in the habitat-selection patterns of the bird assemblage wintering in the Sierra de Guadarrama. Thus, RPC, a synthetic measure of the availability of sunlit sites, was a significant predictor of relative abundance for all species. In addition, its role in habitat selection was less important for those species that had lower energy requirements because of their larger body size but more important, after the effects of body size were removed, for the strictly insectivorous *C. brachydactyla* than for the remaining species that include seeds in their winter diet.

Although we found a significant relationship between solar-radiation levels and avian population densities, a possible criticism of our interpretation is that such a relationship might emerge as a casual correlate of other factors potentially related to solar radiation. Solar radiation, for instance, could affect vegetation structure by promoting the vegetative growth of trees, as is suggested by the significant correlation between RPC and SPC1. In that case, vegetation structure might be the ultimate factor affecting the distribution of bird abundances between plots. However, the correlation between bird abundance and RPC was higher than that between bird abundance and SPC1 for all species except *D. major*, and structural variables were not selected in any of the final regression models. Thus, we conclude that the effect of exposure to sunlight is predominant over that attributable to vegetation structure, although the latter factor might also influence the distribution of the avian populations studied.

Food availability might be another important confounding factor because arthropods are ectothermic organisms. The selection of sunlit forest tracts by birds could therefore be based not on the metabolic benefits of increased temperature but on higher food availability (Brush and Styles 1986). For trunk foragers, solar radiation had a small and nonsignificant effect on the relative abundance of arthropods on trunks (less than 10% of variance explained; see Table 2), and prey counts in a nearby area showed that the variance in arthropod numbers due to differences between sunlit and shaded trunks was smaller than that attributable to differences in individual trees (unpublished data). With respect to assessing prey availability for foliage foragers, a reasonable approach is to use the means of the variables that measure forest development (i.e., SPC1 scores), so the above discussion concerning the secondary role of vegetation structure as a factor determining bird abundances can also be applied to food availability for these species.

We can therefore conclude that the habitat-selection patterns of the bird populations studied seem to reflect thermoregulatory concerns. Selecting forest sectors with a higher availability of sunlit patches could reduce metabolic costs, and this would allow birds to maintain good body condition at the beginning of the night period (Blem 1990; Bednekoff and Houston 1994; Bednekoff et al. 1994) and (or) to accumulate less fat during the day, which may increase manoeuvrability and thus reduce predation risk (Gosler et al. 1995). However, the benefits of this behaviour would only emerge when anticyclonic conditions producing sunny weather occur simultaneously with low winter temperatures. Such a combination of atmospheric factors is unexpected at northern latitudes, where most studies on the winter biology of forest passerines have been conducted (Suhonen et al. 1994 and references therein). The mean proportion of sunny hours out of total daylight time in January–February is only 0.29 at European latitudes above 52°N compared with 0.50 in our study area (W. Cramer, personal communication), and this difference is magnified by the decrease in daylight time as latitude increases. It is therefore not surprising that the relationship between solar radiation and the winter distribution of Palaearctic forest birds has received little attention in the literature, despite being clear-cut and perhaps common in southern, Mediterranean areas. On the other hand, birds may develop alternative solutions for improving their energy balance, such as behavioural shifts in foraging tactics (Grubb 1975, 1978; Alatalo 1982), which are more frequent at northern latitudes but have also been reported in Mediterranean mountains during severe snowstorms (Carrascal 1988; Brotons 1997).

It is worth noting that exposure to sunlight was also a good predictor of the overall abundance and species richness of bird assemblages (see also Carrascal 1988). Although we do not exclude the possibility that this effect merely represents the sum of responses of individual species, or that the distribution of each species is affected by the distribution of the others in mixed-species flocks, we emphasize the utility of this result for assessing the habitat quality of different forest sectors. The fact that avian communities were more abundant and diverse on south-facing, highly insolated slopes could be a simple cue to guide management or conservation strategies.

The importance of body size and diet for shaping the relationship between avian abundance and availability of sunlit sites is consistent with the high energy requirements of small insectivorous birds. However, although energy expenditure per unit mass increases as body size decreases, overall food requirements increase with body size (McNab 1971; Calder 1974). Therefore, many authors have proposed that the relative advantage of a large body size should rather be ascribed to a better fasting capacity (Lindstedt and Boyce 1985), owing to larger fat deposits and lower mass-specific metabolic rates. In that case, a mixed diet that includes lipid-rich seeds (with greater availability and a more predictable distribution than arthropods during winter) should facilitate energy saving more than the strictly insectivorous diet of *C. brachydactyla*, the species that was more sensitive to solar radiation (the largest positive residual in Fig. 1; Carrascal et al. 2001).

Finally, we should emphasize that the applicability of our conclusions is not necessarily restricted to these species when subjected to particularly adverse climatic conditions. Rather, they should benefit from selecting sunlit forest sectors whenever ambient temperatures are below their lower critical temperature (ca. 15°C; Kendeigh et al. 1977), that is to say, during a large proportion of their activity time during the winter. Such a thermal benefit would be greater for the smaller species, whose high surface/volume ratio should favour a higher rate of radiation absorption. This form of behavioural thermoregulation could also allow birds to save energy and (or) reduce their detectability by predators by decreasing their movement rates and increasing the time spent motionless in safe locations.

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