



Temperature and food constraints in wintering birds - an experimental approach in montane Mediterranean oakwoods

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Abstract: Although energy is a major driver of global patterns of biodiversity and species distribution, the test of species-energy relationships needs further development using fine-grained approaches involving different functional groups of species and small geographical scales of known characteristics (habitat heterogeneity, food availability, direct measures of temperature). We carried out an experiment over a broad range of habitat structure and environmental conditions to disentangle the effects of two different energy measures on the small-scale variation of habitat use in winter: one directly related to food resources (manipulated food availability with artificial feeders), and another related to thermoregulatory costs (night temperature). The spatial variation in abundance of a guild of tree-gleaning birds wintering in montane Mediterranean oakwoods of Central Spain was positively related to both components of energy availability (temperature and food resources), even in these mild Mediterranean montane forest of southern Europe. Spatial variation in consumption of food from artificial feeders was negatively related to spatial variation in temperature. The influence of food availability on bird abundance was mediated by vegetation structure, with a lower influence in maturer oakwoods. This study highlights the important role of the energy-related factors, over habitat structure, in determining winter abundance of the studied tree-gleaning guild.

Nomenclature: Gutiérrez et al. (2012, based on Crochet et al. 2010).

Introduction

A major explanation for current global patterns of biodiversity, and for predictions of its future alterations under climate change, is given by the set of hypotheses based on energy availability (Hawkins et al. 2003, Pimm and Brown 2004). Energy availability is associated with temperature, radiation and food resources, and has been shown to influence patterns of species richness or community structure at a range of spatial and temporal scales across several taxa (e.g., Lennon et al. 2000, Hurlbert 2004, Evans et al. 2006). At northern and high elevation range margins, energy availability is the single best factor to explain species richness (Whittaker et al. 2003), and it is commonly argued that temperature is the single most important abiotic environmental factor that affects the performance of organisms and determines the distribution of species (but see Clarke and Gaston 2006). Thus, climatic conditions influence the dynamics of animal populations (e.g., Newton 1998 for birds). In fact, there is a great deal of evidence of the influence of the recent increase in ambient temperatures on the breeding biology of many bird species, both at local and large spatial scales (e.g., Saether et al. 2003, Sanz 2002, Sanz et al. 2003, Visser 2008). Nevertheless, although temperature is often an important abiotic predictor, its influence may not be necessarily exerted through a direct process, which is particularly true for species with

thermoregulatory abilities like birds (e.g., Suggitt et al. 2011).

Meehan et al. (2004) emphasized the importance of individual energetics for understanding these macroecological patterns with a general theoretical model validated with bird data. They found that total abundance of wintering birds increases with environmental temperature and productivity when individuals are below their thermoneutral zone. Zuckerman et al. (2011) found that average minimum temperature was an important factor limiting winter bird distributions in north-eastern North America, supporting the hypothesis that the occupancy of wintering birds is limited by climatic constraints. These patterns agree with the long-held view that there is a ceiling on metabolic rate that constrains the northern winter distributions of bird species, and that such constraint predominates over other biotic processes that might also influence distributions (Root 1988). Nonetheless, Repasky (1991) found little evidence to support that the northern distributions of wintering birds are governed principally by temperature. He argued that temperature probably plays a role in determining distributions through interactions with biotic factors such as food, habitat structure and competition, reinforcing the importance of considering the interaction between temperature and resource availability; that is, between the costs faced by individuals in cold environments and the capacity to overcome these costs.

In spite of these broad-scale spatial patterns of animal numbers, species richness and distribution limits, there are few studies dealing with smaller scales and under less contrasting scenarios according to habitat type and heterogeneity. Wintering birds are suitable organisms to investigate the relative importance of energy and resource constraints in determining the structure of assemblages at local scales and their response to climate change. Winter is the season that arguably affects bird populations that reside year-round in the northern hemisphere, as they appear to be energy limited in this season (Fretwell 1972). Winter survival depends primarily on obtaining enough food for self-maintenance (e.g., Newton 1998, Macleod et al. 2005, Cresswell 2008, Cresswell et al. 2010). Winter climatic conditions do appear to influence overwinter survival of bird populations that reside year-round at northern latitudes of harsh climate through the direct effects on temperature-related mortality or indirectly via food availability (e.g., Lahti et al. 1998, Doherty and Grubb 2002). Temperature acts as a proximate factor influencing fat reserve levels (e.g., Gosler 1996, Rogers and Reed 2003), even in the short term, as the more immediate temperatures (e.g., < 5 h) may be used to optimize fat reserves (see Gosler 2002 for Great Tit, *Parus major*). As a consequence, higher temperatures may reduce energy demands (Calder and King 1974) and are likely to improve the quality of the winter foraging environment (e.g., Dolby and Grubb 1999, Cresswell et al. 2009). Moreover, climate influences on food availability may provide the mechanism by which populations change under different climatic conditions (Robinson et al. 2007).

Here we set out to disentangle the effects of temperature and food availability on the local abundance of birds wintering in Mediterranean oakwoods of the Iberian Peninsula. Although several studies have dealt with forest bird communities along biotic and abiotic gradients during winter in this region (see review by Senar and Borras 2004, Carrascal and Díaz 2006), the role of food availability structuring bird assemblage has been measured or manipulated in very few occasions, and the influence of the thermal environment has been indirectly inferred considering altitude and incidence of solar radiation. Our fine-grained approach involves spatial units of known characteristics, such as habitat heterogeneity, food availability or direct measures of temperature, using a particular functional group of species: the tree-gleaning guild (see for example, Evans et al. 2006, Carnicer and Díaz-Delgado 2008, Honkanen et al. 2010). We carry out a landscape-scale experiment focusing on a homogeneous guild of tree-gleaning birds wintering in continental Mediterranean oakwoods of Central Spain, using two different energy measures: one related to thermoregulatory costs (night temperature) and the other accounting for resources (experimentally manipulated food availability by large-scale diffuse feeding of populations; e.g., Turcotte and Desrochers 2005, Robb et al. 2008, Zuckerberg et al. 2011). The experimental provisioning with supplemental food and the fine-grained measurements of temperature were carried out at local scale of forest patches, over a broad range of altitudes, cardinal

orientations and habitat structure deliberately obtained by means of random and systematic sampling of oakwood forests of *Quercus pyrenaica*. We test three general predictions: the small-scale variation of bird abundance in winter (a) will be positively associated with temperature and (b) will increase with the experimental addition of supplementary food, because higher food availability and temperatures facilitate keeping a suitable energy balance. And finally, (c) winter consumption of supplemented food will be negatively related to temperature.

Material and methods

Study area and species

The study was conducted during the winter of 2009-2010 in the Sierra de Guadarrama (Madrid province, Central Spain, 40°54'11" – 40°33'45"N, 3°46'08" – 4°10'03"W), spanning over 500 km² at altitudes ranging from 900 to 1600 m a.s.l. The region has a continental cold Mediterranean climate, with abundant snowfalls and a large proportion of days with minimum temperatures below 0°C (respectively 25% and 52% of the days in December and January of the study period 2009-2010; data from 6 meteorological stations located in the study region kindly provided by the Spanish Instituto Nacional de Meteorología). Forty census stations were selected in oakwood forests of *Quercus pyrenaica* (a marcescent species typical of southwestern Mediterranean mountains), within forest tracts larger than 3 km² in order to avoid the probable influence of fragmentation in forest bird assemblages (e.g., Telleria and Santos 1995, Battisti et al. 2009 for the Mediterranean region). They covered a wide range of variation in forest maturity, habitat structure due to their management system, altitude and steepness and cardinal orientations of slopes (to account for the amount of incident solar radiation). They were georeferenced with a GPS, and located at least 400 m apart within the same area (the nearest census plots were separated by steep ridges). Twenty of these census stations were randomly selected and food-supplemented with feeders.

The study species were those belonging to the tree-gleaning guild of the mountainous forests of central Spain (Carrascal and Díaz 2006) that have omnivorous diets (Perrin 1998): *Sitta europaea* (Nuthatch), *Parus major* (Great Tit), and *Cyanistes caeruleus* (Blue Tit). These small-sized species mainly forage in the foliage, twigs and branches of trees, although they can also use the forest floor or trunks for foraging (especially Nuthatch). In addition, they are regular exploiters of artificial feeders in the study region (e.g., Carrascal and Alonso 2006). Frequent opportunistic observations at feeders during the study period (while censusing birds or checking feeders for depletion) showed that these species were using the supplemental food during the winter. Three other species make use of artificial feeders in the forests of the study region (see Carrascal and Alonso 2006), but were either very scarce or not detected in the studied woodlands (coal tit, *Periparus ater*, and crested tit, *Lophophanes cris-*

tatus, two coniferous specialist), or do not regularly exploit these feeders due to its bill size (long-tailed tit, *Aegithalos caudatus*). As for other species potentially attracted to feeders, the garden dormouse (*Eliomys quercinus*) hibernates during winter in this region, and squirrels were never seen in the study oak forests during the sampling period (red squirrel, *Sciurus vulgaris*, is a coniferous specialist in our study area, and no squirrel nest was seen in the surroundings of the census plots).

It was not possible to obtain accurate measures of predation risk in our landscape-scale experiment due to logistic difficulties and the scarcity of the potential predator of the focal species (sparrowhawk, *Accipiter nisus*, Perrins 1998). In fact, no Sparrowhawk was observed during the ca. 110 h of time devoted to fieldwork. Nevertheless, food supplemented and control oakwood plots were interspersed within the same forest tracts, and thus our sampling design is not flawed by potential differences in predation risk among study plots.

Bird censuses and habitat structure

Bird censuses were made by means of 10 min point counts (Bibby et al. 2000), within the first 3 h of the morning and the last 2 h of the afternoon. Censuses were carried out from the 1st of December 2009 to the 31st of January 2010. The settlement period prior to the point count starting was 5 min. All auditory and visual contacts were recorded. Each census plot was surveyed three times throughout the study period. Time elapsed between two consecutive censuses of the same plot was 10–20 days. Average census dates were nearly identical for the 40 woodland plots, and the time span of censuses completely overlapped. Censuses were conducted by the same observers (LMC and JS) on nearly windless (wind speed < 3 m·s⁻¹) and rainless days. We estimated bird densities (i.e., birds / 1 ha) correcting for the detectability of the species, by recording the distances to the birds and using DISTANCE 6.0 software (Thomas et al. 2009; see a detailed description of the DISTANCE sampling approach in Buckland et al. 2001). The detection distances were right truncated, thus the detections over 75 m (from the observer) were excluded from the detection model as recommended by Buckland et al. (2001).

Two adjacent 25-m-radius plots were placed within each census plot to sample vegetation structure (one oriented to the north and the other to the south of the census plot center at distances of 25 m). Measurements defining vegetation structure were average height of oaks, and number of tree trunks within two diameter classes: 10–30 cm and more than 30 cm at breast level. Vegetation structure variables were visually estimated, after a preliminary training, by JS and LMC. Both observers estimated vegetation structure in all plots, and their measurements were averaged for each plot. These habitat variables were selected according to general habitat preferences and foraging substrata (Carrascal and Díaz 2006) of the study species (see Table 1 for average figures and variation of habitat structure variables), and because they are relevant or species dependent on highly transient

vegetation structures associated with the early pre-canopy closure stages of forest growth (Hinsley et al. 2009).

Artificial feeders

Artificial feeders were used to control the effect of food availability experimentally on abundance of oakwood birds. They provided *ad libitum* a highly energetic food resource (peeled raw peanuts). Feeders were metallic cylinders (internal dimensions: 25 × 5 cm) built with a 4.8 mm mesh net allowing birds access to food. Feeders were located in the centre of the census plots at a constant height of 4 m above ground (±0.3 m), hung on branches in contact with the trunk by means of special hooks of the same size (30 cm). There was enough variation in tree height and size within each study plot such as to be able to choose suitable branches according to our design. This homogeneous setup of feeders in study plots was chosen in order to minimize the influence of within habitat location of feeders on perceived predation risk, according to distances to trunk, ground, and to the nearest protective cover or the lower edge of tree canopy (see Carrascal and Alonso 2006 for more details on the relationship between the selection of feeding locations within habitat and predation risk, and Turcotte and Desrochers 2003 for landscape-dependent response to predation risk by forest birds in winter).

Artificial feeders were settled in the 20 study plots from 25th November-2009 to 31st January-2010 (average weight: 368 g, SD = 14.6). Feeders remained in the supplemented plots for the whole study period, being replaced before depletion with filled ones.

In order to obtain an accurate consumption rate of supplemented food by birds, the weight loss of feeders was measured. Feeders were dried (40°C for 48 h) and weighed immediately after (precision 0.01 g) before placing them in the field. At the end of the study periods the final weight of feeders was measured after drying them using the same protocol. The weight loss of each feeder was obtained through the difference between the dry weight of the feeder at the beginning and the end of each period. The amount of peanuts consumed in each period was standardized dividing by the time the feeders had been exposed to birds (expressed in grams of peanuts consumed per daytime hour). Weight loss of artificial feeders should accurately reflect the animal demands on food, as the time the bird community spends using feeders is highly correlated with their consumption rate ($r = 0.92$ in Carrascal and Alonso 2006 using the same protocol and the same species). Weight loss of feeders between 26th December-2009 and 31st January-2010 was considered as a direct measurement of feeder use by the study species, after birds had had one month's experience with artificial feeders in the experimental oakwood plots. Consumption rates in the first baiting period (25th November-2009 to 26th December-2009) and in the final study period were highly correlated ($r = 0.792$, $n = 20$, $P < 0.001$). Nevertheless, consumption rate was considerably higher in the final (average = 0.83 g·h⁻¹) than in the baiting (0.25 g·h⁻¹) period (paired *t*-test, $t = 4.44$, $P < 0.001$).

Table 1. Mean and sd of study variables in 40 oakwood census plots in Central Spain during winter (20 control plots and 20 plots supplemented with peanuts). Temperatures for the 62 days of the study period were averaged for each oakwood plot. Density of individual birds per plot refers to the average of three censuses in plots 75 m in radius (i.e., distances to birds truncated to 75 m).

	range	$n = 40$		CONTROL		SUPPLEMENTED	
	min - max	mean	mean	sd	mean	sd	
Average bird density (birds / 1 ha)	0.0 – 12.8	5.2	3.9	3.0	6.5	3.3	
Nuthatch (<i>Sitta europaea</i>) density	0.0 – 8.1	2.3	1.8	1.9	2.8	2.2	
Great Tit (<i>Parus major</i>) density	0.0 – 4.3	1.2	0.9	1.1	1.5	1.1	
Blue Tit (<i>Cyanistes caeruleus</i>) density	0.0 – 5.4	1.7	1.3	1.3	2.2	1.6	
Altitude (m)	965 - 1589	1260.0	1238.4	146.6	1281.5	167.5	
Average air temperature (°C)	1.0 – 3.6	2.3	2.3	0.8	2.3	0.7	
Average diurnal temperature (°C)	2.4 – 5.5	4.0	4.0	0.8	4.0	0.7	
Average maximum temperature (°C)	4.8 – 8.2	6.8	6.8	0.9	6.9	0.8	
Average night temperature (°C)	-0.1 – 2.5	1.2	1.2	0.8	1.2	0.8	
Absolute minimum temperature (°C)	-17.0 – -7.1	-10.0	-10.1	1.6	-9.8	2.0	
Average tree height (m)	6.2 – 17.0	11.7	12.6	2.8	10.8	3.0	
Density of medium sized oaks (trunks 10-30 cm dbh in 0.2 ha)	28 – 450	134.8	170.1	138.5	99.0	50.9	
Density of large sized oaks (trunks > 30 cm dbh in 0.2 ha)	0 – 31	5.7	5.0	5.2	7.0	7.9	

Air temperatures

To describe local winter air temperatures, one temperature logger (Onset HOBO Pendant, accuracy 0.47°C) was set in each oakwood plot. Loggers were placed on thick trunks, oriented to the north and at approximately 1.5 m above ground. Data loggers recorded air temperature every ten minutes from 1st December to 31st January of winter 2009-2010. For each recording day (144 measurements), average temperature, average daytime temperature and average night temperature were obtained. The absolute maximum temperature registered was 20.1 °C (in only one census plot for less than three hours in one day). Temperatures for the 62 days of the study period were averaged for each oakwood plot (see Table 1). These three temperature measurements were highly correlated across days and oakwood plots ($r > 0.8$). Thus, the average night temperature was selected as a measurement of the thermal state of the environment more probably constraining bird distribution and abundance, considering its clear functional meaning related to maximum thermoregulatory costs at night, and the long duration of winter nights (average duration of night : day during the study period = 14.4 h : 9.6 h). We also considered average daytime temperature less discerning because birds compensate thermoregulatory costs associated with daytime temperature by means of heat production resulting from locomotor muscles during foraging activity (e.g., Cooper and Sonsthagen 2007).

Data analyses

Our study focuses on habitat use and food consumption by a defined guild of species, and not on inter-individual differences in patterns of habitat use, so the proper sample unit is the woodland plot. Relationships between bird density (birds·ha⁻¹) or food consumption rate (g·h⁻¹), and the potential explanatory variables were explored by means of generalized linear regression models (canonical distribution: normal; link function: logarithm), using the information-theoretic model comparison approach (food supplementation

was included as a dummy variable: not-supplemented = 0; supplemented = 1). Several alternative models were compared with Akaike's second-order AIC corrected for small sample sizes (AICc; Burnham and Anderson 2002) to assess their weights of evidence. For the analysis of bird density per oakwood plot, these models included exclusive effects of habitat characteristics (altitude and vegetation structure; HC), night temperature (NT), food supplementation (FS), and the combination of these factors (HC+NT, HC+FS, NT+FS and HC+NT+FS). For the analysis of food consumption rate in supplemented oakwood plots, these models included exclusive effects of habitat characteristics (altitude and vegetation structure; HC), night temperature (NT), bird abundance (BA), and the combination of these factors (HC+NT, HC+BA, NT+BA and HC+NT+BA).

We also carried out AIC multimodel inference using the seven *a priori* models for bird density and food consumption rate. Rather than base inferences on a single, selected best model from an *a priori* set of models, inference is based on the entire set of models using weights (W_i) derived from AICc figures. This approach has both practical and philosophical advantages, as it is based on the Kullback-Leibler information theory. A model-averaged estimator has a more honest measure of precision and reduced bias compared to the estimator from just the selected best model (Burnham and Anderson 2004). Standardized regression coefficients (β), and their standard errors (se), were obtained in regression analyses. Parameter estimates (β and se) were averaged using model weights (W_i) derived from all models in which the predictors occurred (see also Crampton et al. 2011 for a similar approach).

For the sake of brevity we only present the results for the total bird density of the study species; very similar results are obtained when analyzing data singly for the Nuthatch, Great and Blue Tit. Therefore, and for the sake of brevity, we avoid the presentation of results for each species.

Table 2. Alternative models for the relative abundance of tree-gleaning birds using artificial feeders in oakwoods of Central Spain during winter 2009-2010. AICc: AIC corrected for small sample sizes. X: predictor variable included in the model. W_i : model weights. R^2 : proportion of variance explained by each model. K= number of effects + intercept. β : weighted averages of standardized regression coefficients considering model weights W_i . $se \beta$: unconditional weighted average of standardized regression coefficient. $n = 40$ oakwood plots. Food supplementation (FS): experimental addition of artificial feeders. Habitat characteristics: altitude, tree height (HTREE), and tree density of two dbh categories (NT10-30, NT>30: respectively 10-30, >30 cm dbh).

	AICc	Δ AICc	K	W_i	R^2	ALTITUDE	HTREE	NT10-30	NT>30	NIGHT TEMP	SUPPL-FOOD
A PRIORI MODELS											
TEMPERATURE (T)	71.3	7.1	2	0.022	0.160					X	
FOOD SUPPLEMENTATION (FS)	71.1	6.8	2	0.026	0.167						X
T + FS	64.3	0.0	3	0.772	0.335					X	X
HABITAT CHARACTERISTICS (H)	73.9	9.6	5	0.006	0.251	X	X	X	X		
H + T	73.2	8.9	6	0.009	0.310	X	X	X	X	X	
H + FS	69.4	5.1	6	0.059	0.3720	X	X	X	X		X
H + T + FS	68.3	4.0	7	0.105	0.431	X	X	X	X	X	X
MULTIMODEL INFERENCE											
standardized regression coef. (β)						-0.023	0.029	0.166	0.294	0.421	0.422
$se \beta$						0.243	0.229	0.181	0.226	0.141	0.143

Table 3. Alternative models for consumption rate of artificial food in oakwoods of Central Spain during winter 2009-2010. AICc: AIC corrected for small sample sizes. X: predictor variable included in the model. W_i : model weights. R^2 : proportion of variance explained by each model. K= number of effects + intercept. β : weighted averages of standardized regression coefficients considering model weights W_i . $se \beta$: unconditional weighted average of standardized regression coefficient. $n = 20$ oakwood plots with the experimental addition of supplementary food. Bird abundance (BA): average density of tree-gleaning birds per plot. Habitat characteristics: altitude, tree height (HTREE), and tree density of two dbh categories (NT10-30, NT>30: respectively 10-30, >30 cm dbh).

	AICc	Δ AICc	K	W_i	R^2	ALTITUDE	HTREE	NT10-30	NT>30	NIGHT TEMP	BA
A PRIORI MODELS											
TEMPERATURE (T)	32.3	5.1	2	0.030	0.020					X	
BIRD ABUNDANCE (BA)	30.8	3.6	2	0.064	0.092						X
T + BA	33.3	6.1	3	0.018	0.092					X	X
HABITAT CHARACTERISTICS (H)	27.2	0.0	5	0.382	0.502	X	X	X	X		
H + T	27.8	0.6	6	0.282	0.572	X	X	X	X	X	
H + BA	29.6	2.4	6	0.116	0.532	X	X	X	X		X
H + T + BA	29.7	2.5	7	0.109	0.618	X	X	X	X	X	X
MULTIMODEL INFERENCE											
standardized regression coef. (β)						-0.261	-0.924	-0.249	0.556	-0.538	0.256
$se \beta$						0.355	0.274	0.245	0.501	0.456	0.221

The residuals of the two regression models did not show a clear spatial autocorrelation pattern (tested by means of a two-order polynomial of latitude and longitude; Legendre 1993): $P = 0.31$ for number of birds per plot, and $P = 0.59$ for food consumption rate. Thus, there was a lack of influence of the spatial location and proximity of the 40 oakwood plots on the observed patterns of variation in the response variables.

All the statistical analyses were carried out using Statistica 10.0 (StatSoft Inc, Tulsa, Oklahoma).

Results

Relative abundance of consumers

Average bird density of the study species per census plot was $5.2 \text{ birds}\cdot\text{ha}^{-1}$, ranging between 0 and $12.8 \text{ birds}\cdot\text{ha}^{-1}$ (see

Table 1). The Nuthatch and the Blue Tit were the most common and widespread species (more than $1.7 \text{ birds}\cdot\text{ha}^{-1}$).

From the seven *a priori* models exploring the among woodland plot variation in bird abundance (Table 2), the model including night temperature and food supplementation was the one with the highest strength of evidence (model weight, $W_i = 0.772$; $R^2 = 0.335$). Its weight of evidence was considerable higher than that of the model including only habitat characteristics ($W_i = 0.006$). The food-supplemented factor and average night temperature were the predictor variables with the highest magnitude effects (weighted averages of $\beta = 0.42$ for both variables). Density of large trees was also an important predictor variable, although its magnitude effect was considerably lower (weighted average of $\beta = 0.294$). The rest of predictor variables played a minor role determin-

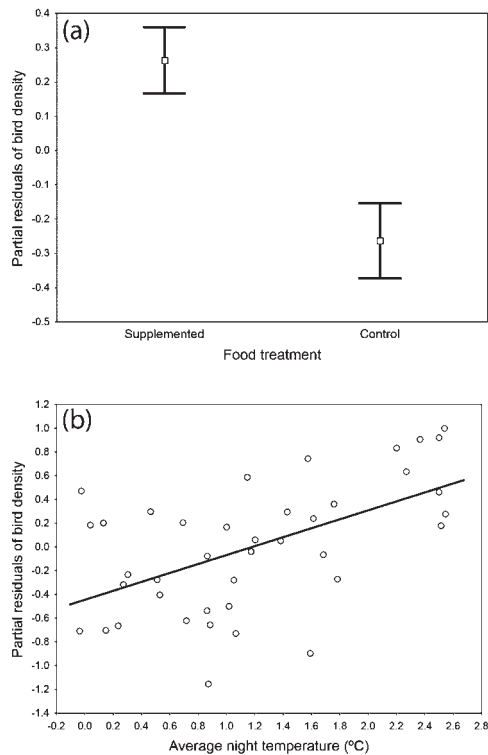


Figure 1. Partial residual plots illustrating the influence of food treatment (a) and average night temperature (b) on the relative abundance of tree-gleaning birds using artificial feeders in oakwoods of Central Spain during winter 2009-2010. $n = 40$ oakwood plots (20 oakwoods with the experimental addition of artificial feeders, and 20 not supplemented). Partial residuals are obtained after controlling for the remaining variables considered in the analysis of Table 2. Vertical bars show mean \pm standard error.

ing bird numbers of small passerines exploiting artificial feeders (absolute values for weighted averages of $b < 0.17$; Table 2). Thus, birds were more abundant in mature oakwoods supplemented with food and with higher average nocturnal temperatures (see Fig. 1 for the partial residual plots of food supplementation and night temperature with the relative abundance of birds after controlling for all other variables).

The interaction between the effects of temperature and resource availability was not significant in determining bird abundance (ANCOVA model testing for the interaction term night temperature \times food supplement: $F_{1,36} = 0.16$, $P = 0.69$).

Variation in feeder consumption

Two models analyzing the variability in feeder consumption in experimental oakwood plots had similarly high strengths of evidence ($\Delta\text{AICc} < 2$; Table 3). They included habitat characteristics and explained more than one half of variance in feeder consumption. The model with the highest strength of evidence ($W_i = 0.382$) explained 50.2% of variance in winter consumption of supplemented food. The most important predictor of feeder consumption was average oak height (with a negative effect), according to the weighted average of standardized regression coefficients (-0.924 ; as well

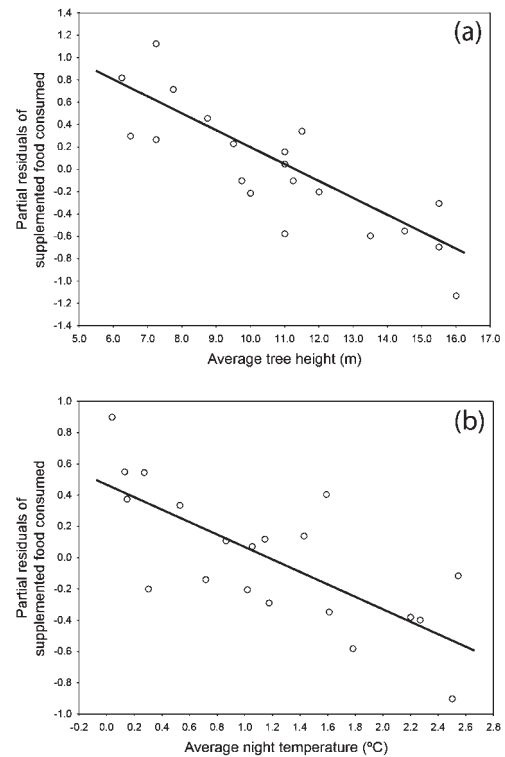


Figure 2. Partial residual plots illustrating the influence of average tree height (a) and average night temperature (b) on the consumption rate of artificial feeders in 20 oakwood plots of Central Spain during winter 2009-2010. Partial residuals are obtained after controlling for the remaining variables considered in the analysis of Table 3.

as density of mature oaks > 30 cm d.b.h.). Average night temperature negatively influenced feeder consumption (weighted averages of $\beta = -0.538$). The remaining variables had considerably lower magnitude effects (weighted averages of $\beta < 0.27$; Table 3). Feeder consumption decreased with the development in height of the tree layer and the increase of night temperature (Fig. 2).

Discussion

Our results show the prominent role of the energy-related factors, over habitat structure, in determining bird occupancy and abundance in woodlands during the non-breeding season (see also Crampton et al. 2011). They also show that both components of energy constraints (metabolic costs of residency and food availability) are involved at local scales in the distribution of this tree-gleaning guild of small passerines wintering in Mediterranean montane forests. The positive relationship between bird abundance and night temperature found in our study suggests that winter temperatures play an important role on the spatial distribution and the relative abundance of small passerines (i.e., winter habitat selection that implies local movements towards suitable habitats) even in the seemingly milder Mediterranean montane forests.

Temperature has shown an increasing trend in Spain in the last 25 years (de Castro et al. 2005), consistent with the

global increase in mean surface air temperatures detected in the mid- and high-latitude continental regions of the northern hemisphere since 1976 (IPCC 2001). This increase has led to important changes in the onset of breeding, clutch size and hatching and fledging success in Mediterranean montane populations of several passerine species (Sanz et al. 2003, Potti 2009). Nevertheless, little is known about the influence of temperature on winter bird biology in this region (Senar and Borrás 2004). If survival of small birds is particularly sensitive to the combination of low temperatures and food shortage in winter (Newton 1998), then an increase in temperature could play a prominent role in those populations inhabiting cold areas-habitats, such as forests in montane areas or northern latitudes (e.g., Butler et al. 2007, Gregory et al. 2007). Our results are consistent with these expectations, as the short term variation of bird abundance is tightly correlated with nocturnal winter temperature. Moreover, there have been marked general increases of these species in the last decade in the same region of cold Mediterranean climate (northern Madrid province; Palomino et al. 2006; significant yearly population growth rates for Nuthatch 11.6%, Great Tit 4.8% and Blue Tit 8.6%). This effect may be acting despite the fact that fewer young usually fledge with warmer temperatures (see Potti 2009 for the study region). Recently, Cresswell et al. (2009) have shown that the increase of 6.5°C from 1995 to 2005 in mean daily winter temperature decreased the starvation risk of Great Tits in England (birds responded to this scenario by decreasing their body mass). Therefore, global warming may exert a positive influence in woodland temperate avifaunas, favouring winter residency and enhancing winter survival, thus translating into positive population trends on a regional basis (Maclean et al. 2008, Seoane and Carrascal 2008).

By means of a food supplementation experiment over a large extension of homogeneous forests, our results demonstrate that bird abundance of the studied tree-gleaning guild was significantly higher in the presence of the artificial feeders, after controlling for local differences in habitat structure and temperature. The great importance of food availability on north European wintering populations has been also found at southern latitudes with less stressful winter conditions (Pérez-Tris and Tellería 2002, Guitián and Munilla 2008, Tellería et al. 2008). Nevertheless, food limitation might not be very stringent in these Mediterranean forests of cold climate. Boutin (1990) reviewed the available literature and found that the typical population response to food supplementation was two- to three-fold increase in density in small-bodied animals in north temperate environments. Local abundance of Black-capped Chickadees (*Poecile atricapilla*) wintering in a cold mixed woodland of North America (Maine, average December-January temperatures of -10.4°C; Wilson 2001) was 55-times higher in supplemented than in unsupplemented plots, compared to a 1.7-times increase in our study area (with an average temperature of 2.3°C; see Table 2). Therefore, supplementary food resources in these Mediterranean montane oakwoods may be a solution when foraging conditions suddenly become worse

(i.e., cold spells), or to overcome short periods of deficient energy budgets (e.g., early in the morning after a very cold night). In such situations, feeders may play an important role as an abundant and predictable food resource to rapidly meet high energy demands (see Carrascal and Polo 1999 for experimental evidence with the coal tit in the same study region).

Our results support a greater consumption of supplementary food in colder conditions at the regional scale (see also Kwit et al. 2004, Chamberlain et al. 2005, Zuckerberg et al. 2011). Nevertheless, and more interestingly, the relative contribution of a fixed amount of supplemented food to its consumption by birds decreased with vertical development of oakwoods (i.e., oak height; see Fig. 2a), which could be explained considering that taller trees provide more structural resources available to foraging and therefore increase absolute natural food availability per unit area. Chamberlain et al. (2007) have also found that the use of artificial food sources by birds is influenced by resources in the surrounding habitat. Therefore, broad variation in habitat structure at regional scale may weaken the subtle effect of the spatial variation in ambient temperature on consumption of supplemented food (e.g., Turcotte and Desrochers 2005).

The relationship between population density and temperature would be dependent on resources, because individuals adjust their foraging activity to meet the energetic demands of the environments they occupy and bird densities often change in relation to varying food supplies (Newton 1998). Therefore, at low resource levels (control plots) we could expect a tighter relationship between abundance and temperature than at high resource levels (supplemented plots). However, we found that temperature affected abundance independently of resource levels. According to species-energy theory this suggests that our study area in winter is, despite food supplementation, a low-energy scenario where the relationship between biodiversity and energy is predicted positive linear (Phillips et al. 2010). Indeed, average minimum night temperatures were low and within the range of 0.05 to 2.54°C (see Fig. 1b), so birds spend a very long proportion of the winter day without foraging and at temperatures approximately 20°C below the thermoneutral zone (average night duration: 14.4 h or 60% of a winter day). Moreover, there must be a limit to acclimatization capacity, even in overabundance of food, mainly because there is a limit to the amount of reserve a bird can carry to survive overnight (McNamara and Houston 1990, Witter and Cuthill 1993). In such conditions, temperature would be limiting even if food resources are abundant. Therefore, even under abundant food, birds may have remained limited by ambient temperature. Their limit of cold tolerance could have improved due to food availability, but not to a point where they can physiologically escape from the effects of temperature.

In conclusion, this study highlights the prominent role of the energy-related factors, over habitat structure, in determining the abundance of birds living under constraining wintering conditions. The positive influence of food availability on bird abundance was mediated by vegetation structure,

with a lower influence in maturer oakwoods. The positive correlation of abundance of the studied species with nocturnal winter temperature, together with the regional population increases of these species recorded during the last decade, show that an increase in winter temperature due to global warming could play a prominent role in these small birds inhabiting cold Mediterranean areas-habitats.

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