

L. M. Carrascal · S. Villén-Pérez · J. Seoane

## Thermal, food and vegetation effects on winter bird species richness of Mediterranean oakwoods

Received: 12 May 2011 / Accepted: 24 October 2011 / Published online: 18 November 2011  
© The Ecological Society of Japan 2011

**Abstract** A better understanding of species–energy relationships needs to be developed using fine-grained approaches that involve the use of small geographical scales of known characteristics, such as habitat heterogeneity, food availability, direct measures of temperature, and functional groups of species. We carried out a 2-year study to analyze the effects of the thermal environment and food availability, while controlling for the influence of habitat structure, on winter species richness of birds living in oakwoods of a mountainous region of Central Spain of Mediterranean continental climate. The guild of ground-foraging birds was selected as model organisms considering its susceptibility to winter conditions associated with unpredictable snowfalls. The spatial variation in species richness of this guild was determined by food availability, but only for those stable and predictable resources not affected by frequent snowfall (shrubs producing fruits; a complete lack of association was found with arthropod abundance on the ground). Thermal effects associated directly with air temperature, and mediated indirectly by vegetation structure providing a mosaic of sun-shade patches, were also very influential. These patterns were highly repeatable across years. Daytime temperature had no influence on determining spatial variation in species richness, but night (minimum) temperature was a very important predictor (explained considering the lower temperatures at night, the longer duration of night, and the inability of diurnal birds to develop active behavioral thermoregulation during nighttime). This result highlights the need to consider physiological processes mediating

species–environment relationships when analyzing the relationship between climatic variables and biodiversity phenomena.

**Keywords** Ground-foraging bird · Habitat structure · Mountain forest · Resource availability · Temperature

### Introduction

Global biodiversity gradients are constrained by climate through the influence of solar energy and water availability on trophic cascades, and the metabolic requirements of organisms (Hawkins et al. 2003; Brown et al. 2004; Qian 2010 and references therein). Nevertheless, the relationship between richness and temperature is dependent on taxonomic groups and geographic areas, and temperature is a poor predictor of observed diversity gradients in most terrestrial systems; there is no evidence for a universal response of diversity to temperature on a broad-scale basis (Hawkins et al. 2007; Whittaker et al. 2007). A good mechanistic understanding of species–energy relationships needs to be developed, on small geographical scales, as opposed to exploring relationships between diversity and environment with grid data cells of hundreds or thousands of square kilometers. For example, species–energy relationships may arise because high-energy areas support more individuals, and these larger populations may buffer species from extinction, although abundant species contribute more to species–energy relationships than rare ones (Evans et al. 2005). This fine-grained approach involves using spatial units of known characteristics, such as habitat heterogeneity, food availability or direct measures of temperature, as well as differentiating among functional groups of species (i.e., guilds; see for example, Evans et al. 2006; Carnicer and Díaz-Delgado 2008; Honkanen et al. 2010).

Winter bird ranges and abundance are associated strongly with temperature (Root 1988a, b; Canterbury 2002; La Sorte et al. 2009). The bases for these

L. M. Carrascal (✉) · S. Villén-Pérez  
Dept. Biodiversidad y Biología Evolutiva, Museo Nacional de Ciencias Naturales, MNCN-CSIC, C/José Gutiérrez Abascal 2, 28006 Madrid, Spain  
E-mail: lmcarrascal@mncn.csic.es  
Tel.: +34-91-5668963  
Fax: +34-91-5668960

J. Seoane  
Dept. Interuniversitario de Ecología, Facultad de Ciencias, Universidad Autónoma de Madrid, 28049 Madrid, Spain

relationships are founded on physiological limits and on the influence of temperature on food availability. Physiological temperature limits are correlated strongly with the minimum temperature during winter at the coldest limit of the boundary range, and thus species that can tolerate cold temperatures with small relative increases in resting metabolic rate tend to be found in cold environments (Canterbury 2002). On the other hand, food availability is critical for winter survival of birds (Fretwell 1972; Newton 1980), throughout its influence on the satisfaction of energy demands, on building up body reserves to overcome fasting periods (e.g., the long winter night or during cold spells; Blem 1990; Biebach 1996), and on breeding performance the following spring (Robb et al. 2008). For example, Meehan et al. (2004) found that total abundance of wintering birds increased with environmental productivity and decreases with environmental temperature when individuals are below their thermoneutral zone (usually between 20 and 35°C; Calder and King 1974; Kendeigh et al. 1977). 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 decreasing their body mass), while Rogers and Reed (2003) showed how the ground-feeding finch *Junco hyemalis* maximizes winter survival probability by integrating multiple environmental factors affecting starvation risk including temperature (but also snowfall frequency and food availability).

Ground-foraging birds are a guild susceptible to winter conditions, especially in mountain areas. Unpredictable snowfalls make forest floor foods—such as arthropods, seeds or fruits on bushes—temporally unavailable, and snow cover lasts longer at higher altitudes. On the other hand, fruit productivity and arthropod activity are lower with decreasing temperatures and solar radiation (Honek 1997; Breckle 2002). Under these circumstances, selection of the optimal thermal environment is a basic means of obtaining an energy balance that results from the interaction between food intake and energy expenditure (including basal, activity, digestive and thermoregulation costs). The thermal environment is determined by the interaction of numerous factors, among which temperature, wind and incidence of solar radiation stand out. Altitude is related inversely to temperature and positively with snowfall probability and persistence, although terrain effects can modify the adiabatic lapse rate (e.g., thermal inversion, exposure to sun radiation according to cardinal orientation). Solar radiation modifies the thermal environment patchily as a consequence of its incidence through vegetation screens, offering a fine-grained mosaic of shade and lit areas.

This paper analyzes the effect of the thermal environment and food availability, while controlling for the influence of habitat structure, on species richness of ground-foraging birds living in oakwoods of a mountainous region of Central Spain, using a landscape-scale approach (e.g., Turcotte and Desrochers 2005;

Robb et al. 2008). The winter bird community of these forests has been studied previously (Carrascal and Diaz 2006), but food availability was not measured and the thermal environment was inferred, instead of measured, considering altitude and solar radiation according to cardinal orientation of oakwood plots. We make two important general predictions explaining the spatial variation of species richness of this foraging guild. First, air temperature will be related positively to species richness, although minimum nighttime temperature will be more important than maximum daytime temperature. This contrasting pattern regarding ambient temperature may be understood considering the longer duration of night, the lower values of nighttime temperature, and the limited ability of diurnal birds to cope with thermoregulatory costs during nighttime by means of thermogenesis derived from foraging activity (i.e., heat produced during exercise, Webster and Weathers 1990; Cooper and Sonsthagen 2007). And second, spatial variation in species richness will track food availability; especially for resources whose accessibility is less prone to be constrained by unpredictable snowfalls (i.e., fruit availability in the understory should be more important than arthropods on ground).

---

## Materials and methods

### Study area and period

The study area was situated in the Sierra de Guadarrama (central Spain, 40°44'N, 03°58'W), covering ca. 500 km<sup>2</sup>. The climate of this region is continental cold Mediterranean, with abundant snowfall and a large proportion of days with minimum temperatures below 0°C (25% and 52%, respectively, of the days in December and January of the study period 2008–2010; data from six meteorological stations located in the study region; Spanish Agencia Estatal de Meteorología. Ministerio de Medio Ambiente, y Medio Rural y Marino). We focused on 20 oakwood plots of 75 m in diameter, located in four sectors of dense oakwoods (each sector larger than 3 km<sup>2</sup>: La Herrería, La Golondrina, La Fuente del Cura and south slope of Morcuera Pass and north slope of Morcuera Pass), with altitudes ranging from 1,000 to 1,600 m a.s.l. Though all consisting of monospecific forests of *Quercus pyrenaica* (a marcescent species typical of southwestern Mediterranean mountains), oakwood plots were selected to cover a wide range of variation in forest maturity, steepness and cardinal orientations of slopes and, therefore, in the amount of received solar radiation on the ground. Thermal inversion is a common phenomenon in the study region (deviation from the normal negative decrease of temperature with altitude).

The study was conducted during two consecutive winters, from 1 December 2008 to 31 January 2009 and from 1 December 2009 to 31 January 2010.

## Bird censuses and habitat structure

We assessed bird species richness in 20 oakwood plots using point-count stations (Bibby et al. 2000) lasting 10-min (i.e., the number of different species detected). The settlement period prior to the point count starting was 5 min. All auditory and visual contacts were recorded, but only those within a 75 m (1.77 ha) radius were used in subsequent analyses, because a large proportion (76%) of the contacts were detected within this census belt. Censuses were conducted by the same persons (L.M.C. and J.S.) on nearly windless (wind speed  $< 3 \text{ m s}^{-1}$ ) and rain-free days. We made an effort to improve accuracy in distance estimates, and to reduce inter-observer variability, by training continuously with a laser rangefinder to the cut-off point of 75 m. Plots were separated by at least 300 m to minimize the probability of sampling the same birds more than once, the nearest oakwood plots being separated by steep ridges. The average distance between oakwood plots within the four forest sectors was 1,206 m (range 300–3,693 m), while average distance among the four forest sectors was 26.5 km (range 8.2–41.3 km). Each year, the censuses were repeated on three different days during December and January (wintering season for all species), within the first 3 h of the morning and in the afternoon beginning 2 h before sunset. Thus, each oakwood plot had an accumulated census time of 30 min, which is adequate for bird surveys of woodland birds during the non-breeding season (Shiu and Lee 2003). Species richness was measured as the average number of ground-foraging birds species per 10 min census, and bird abundance was estimated as the average of bird counts across the three censuses (expressed in birds  $10 \text{ min}^{-1} 1.77 \text{ ha}^{-1}$ ).

Two adjacent 25-m-radius plots were placed within each oakwood plot to sample vegetation structure, representing the total environmental heterogeneity within the census plot. Measurements defining vegetation structure were covers of the tree and shrub layers (distinguishing four bush types: oak regrowth  $< 2 \text{ m}$  in height; thorny, fruit producing, shrubs of genus *Crataegus*, *Rubus*, *Prunus* and *Rosa*; *Cistus* spp. macchie shrubs; and *Cytisus* and *Genista* brooms), average height of the shrub and tree layers, mean and number of trunks within two diameter classes: 10–30 cm, and  $> 30 \text{ cm}$  at breast height (see “Appendix” for more details on habitat structure in the 20 study oakwood plots). We assumed that cover of fruiting shrubs (*Crataegus*, *Rubus*, *Prunus* and *Rosa*) was a surrogate for fruit availability (Shochat et al. 2002; Tellería et al. 2008). All vegetation structure variables were estimated visually, after prior training, by L.M.C. and J.S.

## Focal species

The study species belong to a ground-foraging guild whose species spend more than 80% of feeding time on

the ground (L.M.C., unpublished data; Cramp 1998 for general details; Carrascal et al. 1987 for this group of species in forests of Central Spain). The species included are (in decreasing order of abundance): blackbird, *Turdus merula* (average of 0.25 birds per oakwood plot in the two study winters); mistle thrush, *Turdus viscivorus* (0.24); redwing, *Turdus iliacus* (0.22); european robin, *Erithacus rubecula* (0.16); chaffinch, *Fringilla coelebs* (0.14); eurasian wren, *Troglodytes troglodytes* (0.13); song thrush, *Turdus philomelos* (0.09); citril bunting, *Emberiza cirlus* (0.05); rock bunting, *Emberiza cia* (0.04); dunnock, *Prunella modularis* (0.03); black redstart, *Phoenicurus ochruros* (0.02). The majority of these birds are facultative frugivores that also include a large proportion of invertebrates in their diets (*Turdus merula*, *Turdus viscivorus*, *Turdus iliacus*, *Erithacus rubecula* and *Turdus philomelos*; Guitián 1985; Cramp 1998; these five species account for 70% of all detected individual birds in the censuses carried out in the 20 woodland plots). A considerably smaller proportion of birds wintering in these oakwoods rely mainly or exclusively on seeds or vegetal matter (*Fringilla coelebs*, *Emberiza cirlus*, *Emberiza cia* and *Prunella modularis*; 19% of all detected individual birds in the censuses). Finally, only *Troglodytes troglodytes* and *Phoenicurus ochruros* were mainly insectivorous species (11% of all birds counted).

## Air temperatures

To describe winter air temperature we set one temperature logger (Onset HOBO Pendant) in each oakwood plot, placed on thick trunks, oriented to the north, and at approximately 1.5 m above ground. Data loggers recorded air temperature every 10 min from 1 December 2008 to 31 January 2009 and from 1 December 2009 to 31 January 2009. For each recording day (144 measurements) we obtained average temperature, average daytime temperature, average night temperature, maximum daytime temperature and minimum night temperature. Temperatures for the 62 days of the study period were averaged for each oakwood plot. All these five temperature measurements were highly correlated across days and oakwood plots. Thus, and in order to avoid multicollinearity in data analyses, we selected the two least correlated measurements: minimum night and maximum daytime temperature. Moreover, these two temperatures have a clear functional meaning related, respectively, to maximum thermoregulatory costs at night and minimum thermoregulatory costs at daytime.

## Operative temperature and radiation on the ground

As an approximation to the operative temperature experienced by foraging birds on the ground, we used hollow copper cylinders (length 5 cm, diameter 1 cm) closed at both ends except for a small fissure that

allowed us to insert the sensing tip of an electronic digital thermometer (digi-thermo;  $\pm 0.1^\circ\text{C}$  precision). On calm days, this environmental temperature integrates all the exogenous heat sources influencing a foraging bird: radiation from the sun, conduction from the substrate, and the effect of wind on thermal conductance. We assume that these devices indicate the temperature a bird would eventually reach if it did not have metabolic heat production. Previous measurements showed that copper cylinders and taxidermic mounts (copper models covered by passerine skins) eventually reached the same equilibrium temperatures (see Carrascal et al. 2001 and references therein for more details on the application of this technique to small forest bird species).

We selected 30 sampling points centered in the study area (Biological Station of El Ventorrillo) that were sampled within 7 h around the zenith of cloudless and windless days. At each sampling point we set two electronic digital thermometer-hollow copper cylinders 5 cm above the forest floor separated by 25–50 cm, one exposed to direct sun radiation and another in deep shade (e.g., in the shade of a trunk). We distributed the two thermometer-hollow copper cylinders so that they sampled the whole variability in radiation intensity in the study forest on six different days (14 January–10 February). We also sampled air temperature at the same place using another thermometer-hollow copper cylinder (located 1.5 m above ground, in the shade). Environmental temperatures were registered 3 min after hollow copper cylinders were settled 5 cm above the ground, to assure temperature measures were stabilized, and checking for its stability during the next minute. Radiation intensity was also measured at each sampling point with a PAR light sensor (Quantum QSO, measuring radiation from 400 to 700 nm). At the end of the 3-min periods, we took 12 radiation measurements at 5-s intervals in the same position where the thermometer-hollow copper cylinders were placed (incident radiation was estimated as the average of these 12 measurements). Variation in operative temperature was analyzed with a GLM regression model using air temperature and radiation as predictor variables.

#### Arthropod availability on ground

Prey availability for ground-foraging species was estimated by counting all arthropods longer than 1 mm found during visual searches of 2 min on patches of  $50 \times 50 \text{ cm}^2$  (see Cooper and Whitmore 1990, and references therein). Counts were made in winter 2009–2010 from 10:00 a.m. to 5:00 p.m., when temperatures reached higher values for arthropods to be active. Ground patches were composed mainly of oak litter and were dry and clean of snow during sampling. Arthropods were searched for on the surface of the ground because the study species are ground gleaners that do not dig or remove oak litter while foraging for arthropods. Twenty patches were sampled in each oakwood

plot within 50 m from their centers. All prey items were identified to order and estimated to the nearest millimeter in situ without collecting them. Dry body masses were estimated using the allometric equations available in Diaz and Diaz (1991). No arthropods were found in 40.2% of the patches. Average encounter rate with arthropods was 1.29 arthropods/2 min ( $n = 400$  2-min samples). The average length of the encountered arthropods was 3.78 mm ( $n = 515$  individuals), with an average dry mass of 2.02 mg. The main arthropod groups were Hemiptera, which accounted for 47.6% of total individuals, Arachnids 20.6%, Orthoptera 8.7%, Diptera 6.2%, Coleoptera 5.0%, and Hymenoptera 4.9%.

#### Data analyses

The relationships between the response variable (species richness, i.e., average number of ground-foraging birds species per 10 min census in winter 2009–2010) and habitat structure variables, temperatures and arthropod availability (predictors) were analyzed by means of partial least squares regressions (PLSR; Abdi 2007), using oakwood plots as sample units. Results obtained with PLSR are similar to those from conventional multiple regression techniques; however, being extremely robust to the effects of sample size and degree of correlation between predictor variables, PLSR is especially useful in cases of low sample size and severe multicollinearity (Carrascal et al. 2009). Associations with the response variable are established with factors extracted from predictor variables that maximize the explained variance in the dependent variable. These factors are defined as linear combinations of independent variables, so the original multidimensionality is reduced to a lower number of orthogonal factors to detect structure in the relationships between predictor variables and between these factors and the response variable. The extracted factors account for successively lower proportions of original variance. The relative contribution of each variable to the derived factors was calculated by means of the square of predictor weights. Only those components significant after a fivefold validation procedure were retained.

Although the results for average species richness of the study species are presented, very similar results are obtained when analyzing data for the cumulative number of species in the three censuses per oakwood plot, and the three most abundant species. Therefore, and for the sake of brevity, these results are not presented.

Variation in operative temperature 5 cm above ground was analyzed by means of a multiple regression, using solar radiation and air temperature (in the shade) as predictor variables. Other statistical procedures used were paired *t* tests, Pearson correlations, and parallelism test (applying one-way ANCOVA with the two study winters as factor). All the statistical analyses were carried out using Statistica 9.0 (StatSoft, Tulsa, OK).

## Results

### Air temperature

The lowest minimum night temperatures in the 20 oakwood plots ranged between  $-16.7$  and  $-7.5^{\circ}\text{C}$ , while the maximum daytime temperatures ranged between  $12.8$  and  $19.4^{\circ}\text{C}$  (see the “Appendix” for more details on ranges and mean air temperatures in the 20 oakwood plots). Thus, temperature throughout the study period was constantly below the lower critical temperature, outside the thermoneutral range for a small passerine (usually below  $18$ – $22^{\circ}\text{C}$  for many winter acclimated species in temperate areas; Calder and King 1974; Kendeigh et al. 1977). That is, the studied birds faced an environment that probably required regulatory thermogenesis much of the time.

### Variation in operative temperature on the ground

Average operative temperature 5 cm above ground under direct solar radiation was  $23.1^{\circ}\text{C}$  (SD = 6.06,  $n = 30$ ) on cloudless days from 10:00 a.m. to 5:00 p.m., while it decreased to  $12.7^{\circ}\text{C}$  in the shade (SD = 2.16,  $n = 30$ ). These temperatures were recorded under a broad variability in air temperature ( $-0.5$  to  $16^{\circ}\text{C}$ ). The highest recorded operative temperature exposed to full sun at midday was  $34.3^{\circ}\text{C}$  in a warm winter day when air temperature was  $13.9^{\circ}\text{C}$ . The average difference in operative temperatures 5 cm above ground between full sun-shade exposition was  $10.4^{\circ}\text{C}$ , with a relatively low coefficient of variation (43.7%). Therefore, birds foraging on the ground exposed to direct sun radiation, instead of on the ground in deep shade, obtained a considerable thermal benefit during winter in the study oakwoods.

Operative temperature 5 cm above ground was a very deterministic phenomenon ( $R^2 = 89.2\%$ ;  $F = 235.2$ ,  $df = 2, 57$ ,  $P \ll 0.001$ ). Solar radiation was the most important factor explaining variation in operative temperature (standardized regression coefficient,  $\beta = 0.86$ ,  $P \ll 0.001$ ; partial effect: 70.4% of variance). Air temperature (in the shade) was also associated significantly and positively with operative temperature ( $\beta = 0.23$ ,  $P \ll 0.001$ ; partial effect: 4.8% of variance).

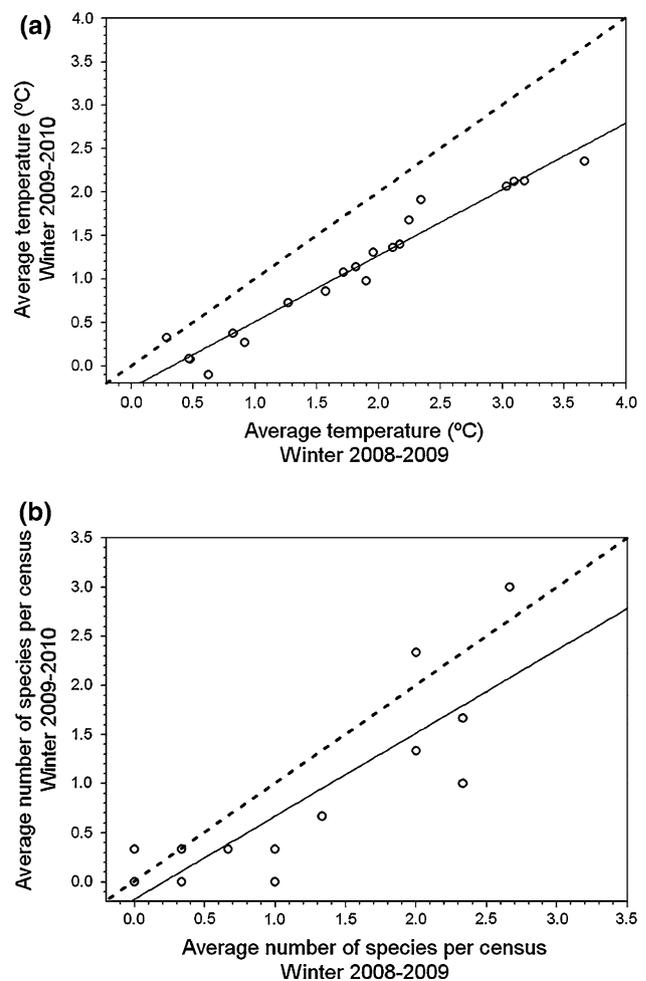
### Variation in species richness and microclimate across woodlands and years

Average air temperature was highly correlated with minimum night temperature across oakwood plots in the two study winters 2008–2009 and 2009–2010 (Pearson correlation coefficients are, respectively, 0.975 and 0.972,  $n = 20$  and  $P \ll 0.001$ ). Average temperature reached significantly lower figures in winter 2009–2010 than in

2008–2009;  $0.68^{\circ}\text{C}$  lower in 2009–2010; 95% confidence interval:  $0.54$ – $0.81^{\circ}\text{C}$  (paired  $t$  test:  $P \ll 0.001$ ; Fig. 1a).

The average number of ground-foraging species per oakwood plot was correlated highly and significantly in the two study winters ( $r = 0.873$ ,  $n = 20$ ,  $P < 0.001$ ). The same result was obtained for the accumulated number of species detected in the three censuses ( $r = 0.793$ ,  $P < 0.001$ ). Species richness was significantly lower in winter 2009–2010 than in 2008–2009 for both average number of species per census (Fig. 1b), and the accumulated number of ground-foraging species ( $P < 0.005$  in the two paired  $t$  tests).

In summary, differences in microclimatic conditions and bird species richness among oakwood plots were repeatable across years. Numbers of ground-foraging species per plot were lower in the colder and cloudier

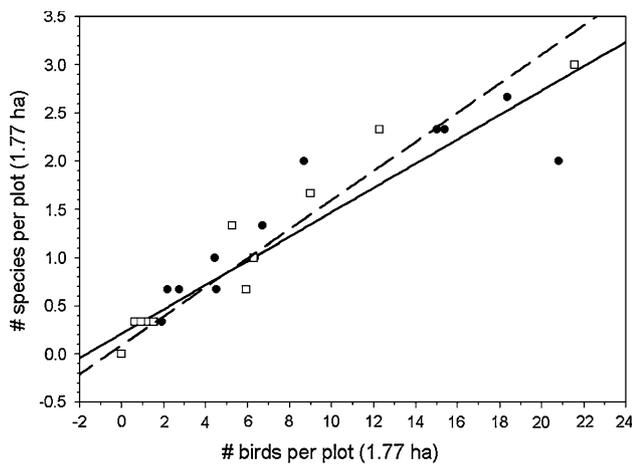


**Fig. 1** Relationship between **a** average temperature and **b** average number of species per census in winters (December–January) 2008–2009 and 2009–2010 in Central Spain. The study species are *Emberiza cirius*, *E. cia*, *Erithacus rubecula*, *Fringilla coelebs*, *Phoenicurus ochruros*, *Prunella modularis*, *Troglodytes troglodytes*, *Turdus iliacus*, *T. merula*, *T. philomelos* and *T. viscivorus*. Sample size is 20 oakwood plots and  $P$  values are  $P < 0.0001$  in both cases. Dashed line Identity between measures in both years; continuous line regression line between data in the two study winters

winter (2009–2010) than in the warmer and sunnier one (2008–2009).

### Spatial variation in species richness of ground-foraging birds

Species richness and abundance of ground-foraging birds were highly correlated in both study winters:  $r = 0.942$  for winter 2008–2009 and  $r = 0.974$  for winter 2009–2010 ( $n = 20$  woodland plots and  $P < 0.001$  for both correlations; Fig. 2). The regression slopes did not differ significantly between winters 2008–2009 and 2009–2010 (parallelism test:  $F_{1,36} = 3.14$ ,  $P = 0.09$ ). Therefore, species richness increases



**Fig. 2** Relationship between species richness and bird abundance of ground-foraging birds per woodland plot of 1.77 ha in two consecutive winters in Central Spain. Dots and continuous line: winter (December–January) 2008–2009. Box and dashed line 2009–2010. Data refers to the average of three censuses in 20 woodland plots. Several data points overlap completely

just because there are more individuals, and this pattern did not change between consecutive winters.

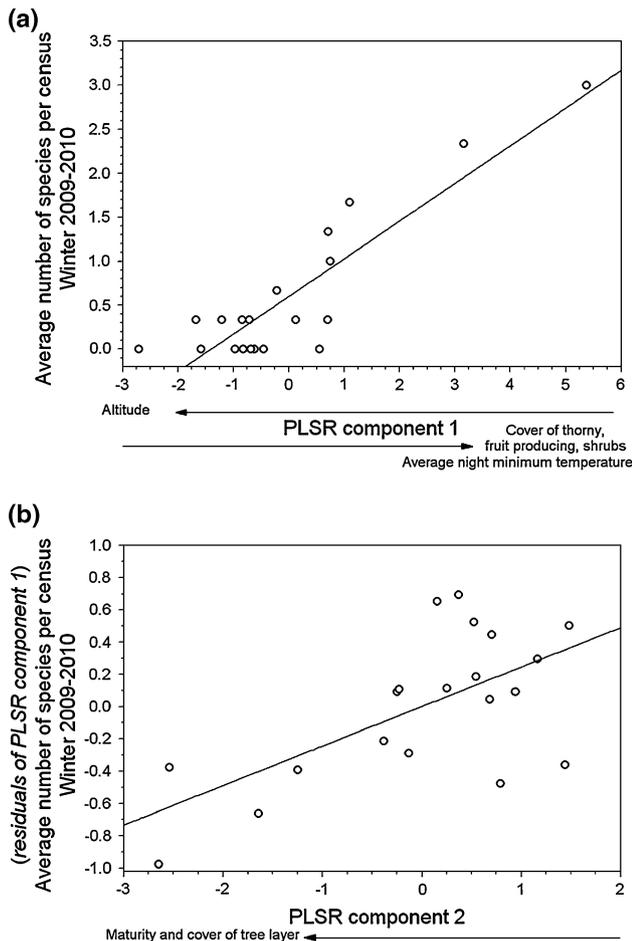
Two significant components, accounting for 87.5% of total variance in species richness, were obtained in the PLSR analysis with the 20 oakwood plots in winter 2009–2010, when arthropod availability was sampled (Table 1). Residuals of this PLSR model did not differ among the four forest sectors ( $F_{3,16} = 2.47$ ,  $P = 0.1$ ). The most influential variables in this PLSR model were cover of thorny, fruit producing, shrubs, average night minimum temperature, altitude, density of large and medium-sized oaks (trunk diameter at breast height  $> 30$  and  $10$ – $30$  cm, respectively), and oak average height (i.e., they summarized 90.6% of the information content of predictor variables explaining ground-foraging species richness; percentage obtained adding the squares of variable importances in Table 1). Conversely, diurnal maximum temperature and arthropod availability on ground had no influence explaining inter-plot differences in species richness (see variable importances in Table 1).

The first PLSR component (79.1% of variance,  $P \leq 0.001$ ) was associated positively with cover of thorny shrubs producing fruits and minimum night temperature, while it was related negatively to altitude (these three variables were responsible of 75.2% of the information content of this component). Thus, oakwood plots located at lower altitudes, with a dense cover of thorny shrubs producing fruits, and with higher minimum night temperatures had higher number of species foraging on the ground (Fig. 3). The second PLSR component, although quantitatively of lower importance (8.5% of variance,  $P = 0.003$ ), was related mainly (negatively) to oak cover (both tree and regrowth layers), average tree height, and density of large sized oaks. Thus, species richness of ground-foraging birds decreased with maturity and development of the tree layer and cover of oak regrowth: mature and dense oakwood plots maintained a lower number of species of this foraging guild.

**Table 1** Results of the partial least squares regression (PLSR) model explaining species richness of ground-foraging birds in 20 oakwood plots in Central Spain in winter 2009–2010

|  | VarImp | PLSR-1 <sup>a</sup> | PLSR-2 <sup>a</sup> |
|--|--------|---------------------|---------------------|
| Cover of thorny, fruit producing, shrubs                 | 0.513  | 0.53                |                     |
| Average minimum night temperature                        | 0.465  | 0.48                |                     |
| Altitude   | 0.463  | -0.49               |                     |
| Density of large sized oaks (trunks $> 30$ cm dbh)       | 0.312  |                     | -0.45               |
| Density of medium sized oaks (trunks $10$ – $30$ cm dbh) | 0.248  |                     |                     |
| Average oak height                                       | 0.231  |                     | -0.46               |
| Tree layer cover   | 0.170  |                     | -0.34               |
| Cover of <i>Cytisus</i> and <i>Genista</i> shrubs        | 0.169  |                     |                     |
| Average shrub layer height                               | 0.116  |                     |                     |
| Cover of oak regrowth ( $< 2$ m in height)               | 0.096  |                     | -0.30               |
| Average maximum diurnal temperature                      | 0.085  |                     |                     |
| Cover of <i>Cistus</i> spp. shrubs                       | 0.075  |                     |                     |
| Arthropod biomass on ground                              | 0.028  |                     |                     |
| $R^2$ by PLSR components                                 |        | 0.791               | 0.085               |

<sup>a</sup>VarImp Variable importance in the PLSR model with two components, dbh diameter at breast height  
<sup>a</sup>Figures under PLSR-1 and PLSR-2 are the predictor weights of each variable in each component; only relationships between individual variables and PLSR components with  $|\text{weights}| > 0.3$  are shown



**Fig. 3** Relationship between ground-foraging species richness and the two first components of a partial least squares regression analysis (PLSR; see Table 1). **a**, **b** The second PLSR component (**b**) analyzes the residuals of the relationship depicted by the first PLSR component (**a**), according to the sequential variance extraction carried out by PLSR models. Sample size is 20 oakwood plots located in Central Spain in winter 2009–2010 and  $P$  values are  $P = 0.0026$  and  $0.0000$ , respectively

## Discussion

### Abiotic effects of temperature and altitude

Our results show that temperature plays an important role in determining the spatial variation in species richness of this guild of ground-foragers during winter. Moreover, this within-year pattern is also observed in the between-year analysis: the number of ground-foraging species per oakwood plot is lower in the colder winter despite the between-years difference in average air temperature being as low as  $0.68^{\circ}\text{C}$ . The mechanistic link between species richness and temperature can be understood as a deterministic outcome of physiological processes, because temperature affects the metabolism of individuals, and species richness increases just because there are more individuals per woodland plot (see Fig. 2). Low temperatures and long nights of winter are

associated with an increased risk of starvation through body reserves regulation (e.g., Cresswell 1998; Gosler 2002; Macleod et al. 2005; Krams et al. 2010). Temperature determines metabolic expenditure of birds below the thermoneutral zone, the lower limit being around  $20^{\circ}\text{C}$  for many winter acclimated species in temperate areas (Calder and King 1974; Kendeigh et al. 1977). The temperature in our study area is considerably lower than the lower critical temperature, ranging from  $4.5$  to  $8.9^{\circ}\text{C}$  for average maximum diurnal temperature, and  $-3.2$  to  $1.2^{\circ}\text{C}$  for average minimum nocturnal temperature. Thus, overwintering in these continental Mediterranean oakwoods is energetically demanding in terms of thermoregulatory metabolic costs.

Nevertheless, winter temperature has a different meaning for this group of birds depending upon what temperature is considered. Daytime (maximum) temperature has no influence explaining spatial variation in species richness, but night (minimum) temperature is a very important predictor according to its variable importance in the PLSR analysis. This contrasting pattern of covariation with species richness may be explained easily considering the low temperatures attained during night and the considerably longer duration of night (average duration of night: day during the study period =  $14.4$  h:  $9.6$  h). Whenever not sleeping, heat production resulting from locomotor muscles during foraging activity and from food assimilation, can account for part of thermoregulatory requirements in the cold for diving, glean-and-hang foraging species, as well as in ground-foraging birds (Webster and Weathers 1990; Dawson and O'Connor 1996; Kaseloo and Lovvorn 2006; Cooper and Sonsthagen 2007). On the other hand, small passerines are able to compensate for low air temperatures behaviorally, by spending more time in sunlit patches while foraging (Carrascal et al. 2001). The contrasting effects of temperature on bird species richness suggest the need to consider with caution any attempt to relate climatic variables to biological phenomena simplistically, with disregard to the autoecological and physiological processes mediating the species–environment relationships.

Finally, the large negative influence of altitude determining the observed pattern of species richness is probably a combination of temperature (discussed above) and snow-mediated effects. Snow cover forces birds to shift their foraging behavior or migrate (Brotons 1997; Nakamura and Shindo 2001); thus, snowfall frequency and persistence may be considered as a surrogate measure of resource deterioration. At higher altitudes, snowfall probability increases while snow cover lasts longer, constraining food searching on the ground, and thus determining the observed reduction in species richness with altitude.

### Biotic effects of vegetation structure and food resources

Food availability has been proposed to drive winter distribution in small birds (see review in Newton 1980;

Wiens 1989), although its effect depends on the ability of birds to track its spatio-temporal distribution efficiently (Shochat et al. 2002). A greater abundance of food resources would reduce the amount of time required for searching during the few light hours of winter days, and increase the rate of food intake in order not to starve. Therefore, food abundance should be an important factor determining population density and habitat selection through foraging efficiency. Nevertheless, previous research with both frugivorous and insectivorous birds have reported a mixed bag of results, as in some studies food abundance has been found to be important whereas in other studies its effect was negligible (see examples for the Iberian Peninsula in Herrera 1998; Carrascal et al. 2001; García and Ortiz-Pulido 2004; Tellería and Pérez-Tris 2003, 2007; Tellería et al. 2008).

Resources like arthropods or seeds on the forest floor of Pyrenean oakwoods are scarce and highly unpredictable for ground-foraging birds living in mountainous areas, where snowfalls severely constrain its accessibility. In winter, the grass layer is nearly absent in these forests, and the seed bank produced during summer is completely covered by a dense layer of leaves fallen during autumn. This is the reason why granivorous birds are so scarce in dense deciduous forests during winter in the Mediterranean region (Tellería et al. 1988). On the other hand, arthropods are very scarce according to a very low encountering rate with them (1.29 arthropods/2 min) and their average low body masses (dry mass of 2.02 mg). These facts, together with the impossibility of having a sure access to this resource throughout the winter due to snowfall unpredictability, could explain the almost null effect of arthropod biomass on species richness found in this study.

Conversely, cover of fruit producing shrubs (as a surrogate of fruit availability) is the best predictor of species richness of ground-foraging bird in the Pyrenean oakwoods, indicating that this group of species (dominated mainly by facultative frugivorous species) is food-limited during winter time and that they track the spatial patterning of fruit-producing shrubs (see also Guitián and Munilla 2008 and Tellería et al. 2008 for bird and fruit abundance in scrublands and woodlands of northern and southern Spain). Shrub cover of other plant species does not exert any influence on species richness of ground-foraging birds. Snow cover scarcely affects availability of fruits in shrubs, which could in turn be a highly predictable food resource. On the other hand, as these fruit-producing shrubs (*Rosa*, *Prunus*, *Crataegus*, *Rubus* species) are thorny and grow in dense patches, they may play an additional role providing protection against predators while foraging on the ground.

Another habitat structure variable related to bird species richness is tree maturity (tree thickness, cover and height), explaining a considerably lower amount of variance. Nevertheless, and in contrast with other bird guilds for which positive relationships have been found

(e.g., Turcotte and Desrochers 2005; Carrascal and Diaz 2006; Godinho et al. 2010; Honkanen et al. 2010), species richness of ground-foraging birds decreases with maturity and development of the tree layer. The unexpected negative influence of forest maturity on bird species richness of this foraging guild may be explained by considering the detrimental effect of shadow projection on thermoregulation during normal foraging activities on forest floor: mature forests have a well developed tree crown projecting more shadows where operative temperatures are considerably lower than in patches with incident sun radiation (see Carrascal et al. 2001 for empirical evidence on behavioral patch selection with *Certhia brachydactyla*). Operative temperature on ground is very predictable, and the received sun radiation explains 70% of its variation. Thus, the thermal benefit obtained by a bird staying on ground exposed to sun instead of in the shade is, on average, 10.4°C. Complementing this effect, this increased temperature could have a positive, indirect, effect on foraging efficiency through the activation of arthropods at higher temperatures (Avery and Krebs 1984; Carrascal et al. 2001), which would lead birds in sunlit patches to achieve higher foraging success. Therefore, small-scale effects mediated by the interaction sun radiation-vegetation structure may enhance the role of the thermal state of the environment on bird species richness.

In conclusion, regional variation of small scale (~1–2 ha) species richness of the ground-foraging guild of birds wintering in oakwoods of mountainous areas in Central Spain is determined mainly by cover of fruit producing shrubs followed by thermal effects, associated directly with minimum temperature during long winter nights. Thus, food availability is very influential, but only for those stable and predictable resources (shrubs producing fruits), not affected by frequent snowfalls (i.e., null influence of arthropods on ground). These patterns are highly repeatable across years, and support the species–energy relationship at small spatial scales, as high-energy areas with higher temperatures and more resources (fruits) support larger bird abundances that buffer species from local disappearance. The marked difference in the influence of diurnal (null) and nocturnal (very positive) temperatures on the regional variation in species richness highlights the need to consider physiological processes mediating species–environment relationships when analyzing relationships between climatic variables and biodiversity phenomena.

**Acknowledgments** This paper was funded by project CGL2008-02211/BOS of the Spanish Ministry of Educación y Ciencia. We also thank Claire Jasinski for improving the English of the manuscript.

---

## Appendix

See Table 2.

**Table 2** Mean and range (min/max) of study variables in 20 oakwood plots in Central Spain during winters 2008–2009 and 2009–2010

|  | Mean  | Range     |
|--|-------|-----------|
| Cumulative number of ground-foraging species (in 3 censuses)                                   | 1.85  | 0/7       |
| Average number of ground-foraging species (in 3 censuses) <sup>a</sup>                         | 1.09  | 0/3       |
| Altitude (m)   | 1,282 | 976/1,597 |
| Light intensity at midday (lux 10 <sup>-3</sup> ); two winters                                 | 12.8  | 4.1/21.9  |
| Average air temperature (°C); two winters  | 1.44  | -0.1/3.7  |
| Average maximum diurnal temperature (°C); two winters  | 7.05  | 4.5/8.9   |
| Average minimum night temperature (°C); two winters  | -0.75 | -3.0/1.2  |
| Arthropod biomass on ground (dry mass, mg, per 2 min)  | 1.33  | 0.2/5.4   |
| Cover of thorny, fruit producing, shrubs ( <i>Crataegus</i> , <i>Rubus</i> , <i>Rosa</i> ) (%) | 4.3   | 0/45      |
| Cover of maquis ( <i>Cistus</i> ) shrubs (%)   | 2.3   | 0/36      |
| Cover of brooms ( <i>Cytisus</i> and <i>Genista</i> shrubs) (%)                                | 9.4   | 0/37      |
| Cover of oak regrowth (<2 m in height) (%)   | 5.0   | 0/19      |
| Average shrub layer height (m)   | 1.0   | 0.33/2.40 |
| Tree layer cover (%)   | 62.6  | 24/90     |
| Average oak height (m)   | 10.8  | 6/16      |
| Density of medium-sized oaks (trunks 10–30 cm dbh in 0.2 ha)                                   | 99    | 28/205    |
| Density of large-sized oaks (trunks >30 cm dbh in 0.2 ha)                                      | 7     | 0/31      |

<sup>a</sup>Number of ground-foraging species refer to census plots 75 m in diameter

## References

- Abdi H (2007) Partial least square regression (PLS regression). In: Salkind NJ (ed) Encyclopedia of measurement and statistics. Sage, Thousand Oaks, pp 740–744
- Avery MI, Krebs JR (1984) Temperature and foraging success of great tits *Parus major* hunting for spiders. *Ibis* 126:33–38
- Bibby CJ, Burgess ND, Hill DA, Mustoe SH (2000) Bird census techniques. Academic, London
- Biebach H (1996) Energetics of winter and migratory fattening. In: Carey C (ed) Avian energetics and nutritional ecology. Chapman & Hall, New York, pp 280–323
- Blem CR (1990) Avian energy storage. *Curr Ornithol* 7:59–113
- Breckle SW (2002) Walter's vegetation of the earth. The ecological systems of the geo-biosphere. Springer, Berlin
- Brotans L (1997) Changes in foraging behaviour of the Coal Tit *Parus ater* due to snow cover. *Ardea* 85:249–257
- Brown JH, Gillooly JF, Allen AP, Savage VM, West GB (2004) Toward a metabolic theory of ecology. *Ecology* 85:1771–1789
- Butler JR, MacMynowski DP, Laurent C, Root TL (2007) Temperature-associated dynamics of songbird winter distributions and abundances. *Ambio* 36:657–660
- Calder WA, King JR (1974) Thermal and caloric relations of birds. In: Farner DS, King JR (eds) Avian biology, vol 4. Academic, New York, pp 259–413
- Canterbury G (2002) Metabolic adaptation and climatic constraints on winter bird distribution. *Ecology* 83:946–957
- Carnicer J, Díaz-Delgado R (2008) Geographic differences between functional groups in patterns of bird species richness in North America. *Acta Oecol* 33:253–264
- Carrascal LM, Alonso CL (2006) Habitat use under latent predation risk. A case study with wintering forest birds. *Oikos* 112:51–62
- Carrascal LM, Díaz JA, Huertas D, Mozetich I (2001) Behavioral thermoregulation by treecreepers: a tradeoff between energy saving and reduced crypsis. *Ecology* 82:1642–1654
- 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, Galván I, Gordo O (2009) Partial least squares regression as an alternative to most currently used regression methods in Ecology. *Oikos* 118:681–690
- Carrascal LM, Potti J, Sánchez-Aguado FJ (1987) Spatio-temporal organization of the bird communities in two Mediterranean montane forests. *Holarctic Ecol* 10:185–192
- Cooper RJ, Whitmore RC (1990) Arthropod sampling methods in ornithology. *Stud Avian Biol Ser* 13:29–37
- Cooper SJ, Sonsthagen S (2007) Heat production from foraging activity contributes to thermoregulation in Black-capped Chickadees. *Condor* 109:446–451
- Cramp S (1998) The complete birds of the Western Palearctic. CD-Rom version 1. Oxford University Press, Oxford
- Cresswell W (1998) Diurnal and seasonal mass variation in blackbirds *Turdus merula*: consequences for mass dependent predation risk. *J Anim Ecol* 67:78–90
- Cresswell W, Clark JA, Macleod R (2009) How climate change might influence the starvation–predation risk trade-off response. *P R Soc London* 276:3553–3560
- Dawson WR, O'Connor TP (1996) Energetic features of avian thermoregulatory responses. In: Carey C (ed) Avian energetics and nutritional ecology. Chapman & Hall, New York, pp 85–124
- Díaz JA, Díaz M (1991) Estimaciones de tamaños y biomasa de artrópodos aplicables al estudio de la alimentación de vertebrados insectívoros. *Doñana Acta Vertebrata* 17:67–74
- Doherty PF, Grubb TC (2000) Habitat and landscape correlates of presence, density, and species richness of birds wintering in forest fragments in Ohio. *Wilson Bull* 112:388–394
- Evans KL, James NA, Gaston KJ (2006) Abundance, species richness and energy availability in the North American avifauna. *Global Ecol Biogeogr* 15:372–385
- Evans KL, Greenwood JJD, Gaston KJ (2005) Relative contribution of abundant and rare species to species–energy relationships. *Biol Lett* 1:87–90
- Fretwell SD (1972) Populations in a seasonal environment. Princeton University Press, Princeton
- García D, Ortiz-Pulido R (2004) Patterns of resource tracking by avian frugivores at multiple spatial scales: two case studies on discordance among scales. *Ecography* 27:187–196
- Godinho C, Rabaca JE, Segurado P (2010) Breeding bird assemblages in riparian galleries of the Guadiana River basin (Portugal): the effect of spatial structure and habitat variables. *Ecol Res* 25:283–294
- Gosler AG (2002) Strategy and constraint in the winter fattening response to temperature in the great tit *Parus major*. *J Anim Ecol* 71:771–779
- Gregory RD, Vorisek P, Strien AV, Meyling AWG, Jiguet F, Fornasari L, Reif J, Chylarecki P, Burfield IJ (2007) Population trends of widespread woodland birds in Europe. *Ibis* 149:s78–s97
- Griesser M, Nystrand M (2009) Vigilance and predation of a forest-living bird species depend on large-scale habitat structure. *Behav Ecol* 20:709–715
- Guitián J (1985) Datos sobre el régimen alimenticio de los Paseriformes de un bosque montano de la Cordillera Cantábrica occidental. *Ardeola* 32:155–172

- Gutián J, Munilla I (2008) Resource tracking by avian frugivores in mountain habitats of northern Spain. *Oikos* 117:265–272
- Hawkins BA, Albuquerque FS, Araujo MB, Beck J, Bini LM, Cabrero-Sanudo FJ, Castro-Parga I, Diniz JAF, Ferrer-Castan D, Field R, Gomez JF, Hortal J, Kerr JT, Kitching IJ, Leon-Cortes JL, Lobo JM, Montoya D, Moreno JC, Olalla-Tarraga MA, Pausas JG, Qian H, Rahbek C, Rodriguez MA, Sanders NJ, Williams P (2007) A global evaluation of metabolic theory as an explanation for terrestrial species richness gradients. *Ecology* 88:1877–1888
- Hawkins BA, Field R, Cornell HV, Currie DJ, Guégan J-F, Kaufman DM, Kerr JT, Mittelbach GG, Oberdorff T, O'Brien EM, Porter EE, Turner JRG (2003) Energy, water, and broad-scale geographic patterns of species richness. *Ecology* 84:3105–3117
- 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
- Herrera CM (1998) Long-term dynamics of Mediterranean frugivorous birds and fleshy fruits: a 12-year study. *Ecol Monogr* 68:511–538
- Hinsley SA, Bellamy PE, Moss D (1995) Sparrowhawk *Accipiter nisus* predation and feeding site selection by tits. *Ibis* 137:418–420
- Honek A (1997) The effect of temperature on the activity of Carabidae (Coleoptera) in a fallow field. *Eur J Entomol* 94:97–104
- Honkanen M, Roberge J-M, Rajasarkka A, Monkkonen M (2010) Disentangling the effects of area, energy and habitat heterogeneity on boreal forest bird species richness in protected areas. *Global Ecol Biogeogr* 19:61–71
- Kaselloo PA, Lovvorn JR (2006) Substitution of heat from exercise and digestion by ducks diving for mussels at varying depths and temperatures. *J Comp Physiol B* 176:265–275
- Kendeigh SC, Dol'nik VR, Gavrilov VM (1977) Avian energetics. In: Pinowski J, Kendeigh SC (eds) *Granivorous birds in ecosystems*. Cambridge University Press, New York, pp 127–204
- Krams I, Cirule D, Suraka V, Krama T, Rantala MJ, Ramey G (2010) Fattening strategies of wintering great tits support the optimal body mass hypothesis under conditions of extremely low ambient temperature. *Funct Ecol* 24:172–177
- La Sorte FA, Lee TM, Wilman H, Jetz W (2009) Disparities between observed and predicted impacts of climate change on winter bird assemblages. *P R Soc B* 276:3167–3174
- Lima SL, Dill LM (1990) Behavioural decisions made under the risk of predation: a review and prospectus. *Can J Zool* 68:619–640
- Macleod R, Gosler AG, Cresswell W (2005) Diurnal mass gain strategies and perceived predation risk in the great tit *Parus major*. *J Anim Ecol* 74:956–964
- Meehan TD, Jetz W, Brown JH (2004) Energetic determinants of abundance in winter landbird communities. *Ecol Lett* 7:532–537
- Nakamura M, Shindo N (2001) Effects of snow cover on the social and foraging behavior of the great tit *Parus major*. *Ecol Res* 16:301–308
- Newton I (1980) The role of food in limiting bird numbers. *Ardea* 68:11–30
- Qian H (2010) Environment–richness relationships for mammals, birds, reptiles, and amphibians at global and regional scales. *Ecol Res* 25:629–637
- Repasky RR (1996) Using vigilance behavior to test whether predation promotes habitat partitioning. *Ecology* 77:1880–1887
- Robb GN, McDonald RA, Chamberlain DE, Reynolds SJ, Harrison THE, Bearhop S (2008) Winter feeding of birds increases productivity in the subsequent breeding season. *Biol Letters* 4:220–223
- Rogers CM, Reed AK (2003) Does avian winter fat storage integrate temperature and resource conditions? A longterm study. *J Avian Biol* 34:112–118
- Root TL (1988a) Energy constraints on avian distributions and abundances. *Ecology* 69:330–339
- Root TL (1988b) Environmental factors associated with avian distributional boundaries. *J Biogeogr* 15:489–505
- Shiu HJ, Lee PF (2003) Assessing avian point-count duration and sample size using species accumulation functions. *Zool Stud* 42:357–367
- Shochat E, Abramsky Z, Pinshow P, Whitehouse MEA (2002) Density dependent habitat selection in migratory passerines during stopover: what causes the deviation from IFD? *Evol Ecol* 16:469–488
- Tellería JL, Santos T, Carrascal LM (1988) La invernada de los passeriformes (*O. Passeriformes*) en la Península Ibérica. In: Tellería JL (ed) *Invernada de Aves en la Península Ibérica*. Sociedad Española de Ornitología, Madrid, pp 153–166
- Tellería JL, Pérez-Tris J (2003) Seasonal distribution of a migratory bird: effects of local and regional resource tracking. *J Biogeogr* 30:1583–1591
- Tellería JL, Pérez-Tris J (2007) Habitat effects on resource tracking ability: do wintering Blackcaps *Sylvia atricapilla* track fruit availability? *Ibis* 149:18–25
- Tellería JL, Ramirez A, Pérez-Tris J (2008) Fruit tracking between sites and years by birds in Mediterranean wintering grounds. *Ecography* 31:381–388
- Turcotte Y, Desrochers A (2005) Landscape-dependent distribution of northern forest birds in winter. *Ecography* 28:129–140
- Walther BA, Gosler AG (2001) The effects of food availability and distance to protective cover on the winter foraging behaviour of tits (*Aves: Parus*). *Oecologia* 129:312–320
- Webster MD, Weathers WW (1990) Heat produced as a by-product of foraging activity contributes to thermoregulation by Verdins, *Auriparus flaviceps*. *Physiol Zool* 63:777–794
- Whittaker RJ, Nogués-Bravo D, Araújo MB (2007) Geographical gradients of species richness: a test of the water energy conjecture of Hawkins et al. (2003) using European data for five taxa. *Global Ecol Biogeogr* 16:76–89
- Wiens JA (1989) *The ecology of bird communities*, vol 2. Cambridge University Press, Cambridge