A peer-reviewed version of this preprint was published in PeerJ on 19 July 2016.

View the peer-reviewed version (peerj.com/articles/2156), which is the preferred citable publication unless you specifically need to cite this preprint.

https://doi.org/10.7717/peerj.2156
Preferred temperature and thermal breadth of birds wintering in peninsular Spain – the limited effect of temperature on species distribution

Luis M. Carrascal, Sara Villén-Pérez, David Palomino

**Background.** Availability of environmental energy, as measured by temperature, is expected to limit the abundance and distribution of endotherms wintering at temperate latitudes. A prediction of this hypothesis is that birds should attain their highest abundances in warmer areas. However, there may be a spatial mismatch between species preferred habitats and species preferred temperatures, so some species might end-up wintering in sub-optimal thermal environments. **Methods.** We model the influence of minimum winter temperature on the relative abundance of 106 terrestrial bird species wintering in peninsular Spain, at 10x10 Km² resolution, using 95%-quantile regressions. We analyze general trends across species on the shape of the response curves, the environmental preferred temperature (at which the species abundance is maximized), the mean temperature in the area of distribution and the thermal breadth (area under the abundance-temperature curve). **Results.** There is a large interspecific variability on the thermal preferences and specialization of species. Despite this large variability, there is a preponderance of positive relationships between species abundance and temperature, and on average species attain their maximum abundances in areas 1.9 ºC warmer than the average temperature available in peninsular Spain. The mean temperature in the area of distribution is lower than the thermal preferences of the species, although both parameters are highly correlated. **Discussion.** Most species prefer the warmest environments to overwinter, which suggests that temperature imposes important restrictions to birds wintering in the Iberian Peninsula. However, most individuals overwinter in locations colder than the species thermal preferences, probably reflecting a limitation of environments combining habitat and thermal preferences. Beyond these general trends, there is a high inter-specific variation in the versatility of species using the available thermal space.
Preferred temperature and thermal breadth of birds wintering in peninsular Spain – the limited effect of temperature on species distribution.

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**Short title:** Temperature effects on bird distribution
Abstract

**Background.** Availability of environmental energy, as measured by temperature, is expected to limit the abundance and distribution of endotherms wintering at temperate latitudes. A prediction of this hypothesis is that birds should attain their highest abundances in warmer areas. However, there may be a spatial mismatch between species preferred habitats and species preferred temperatures, so some species might end-up wintering in sub-optimal thermal environments.

**Methods.** We model the influence of minimum winter temperature on the relative abundance of 106 terrestrial bird species wintering in peninsular Spain, at 10x10 Km² resolution, using 95%-quantile regressions. We analyze general trends across species on the shape of the response curves, the environmental preferred temperature (at which the species abundance is maximized), the mean temperature in the area of distribution and the thermal breadth (area under the abundance-temperature curve).

**Results.** There is a large interspecific variability on the thermal preferences and specialization of species. Despite this large variability, there is a preponderance of positive relationships between species abundance and temperature, and on average species attain their maximum abundances in areas 1.9 ºC warmer than the average temperature available in peninsular Spain. The mean temperature in the area of distribution is lower than the thermal preferences of the species, although both parameters are highly correlated.

**Discussion.** Most species prefer the warmest environments to overwinter, which suggests that temperature imposes important restrictions to birds wintering in the Iberian Peninsula. However, most individuals overwinter in locations colder than the species thermal preferences, probably reflecting a limitation of environments combining habitat and thermal preferences. Beyond these general trends, there is a high inter-specific variation in the versatility of species using the available thermal space.

**Keywords:** bird abundance, preferred temperature, quantile regression, species distribution, thermal breadth, winter.
INTRODUCTION

The distribution of overwintering animals is assumed to be strongly influenced by environmental energy availability, notably in regions with a marked year-round seasonality such as temperate ecosystems. Peninsular Spain is an important target for many avian populations of the southwestern Palearctic during the winter (Moreau, 1972), when there are massive migrations of northern populations towards circum-Mediterranean countries. Even though conditions are milder than in the north, it is an energy-limiting period in which food resources are scarce and/or difficult to locate and the low temperatures impose a high metabolic cost to maintain a constant body temperature for homeothermic animals (Calder & King, 1974). Specifically, winter temperature in peninsular Spain (average 2.55°C) is well below the lower critical temperature for a broad variety of bird species (ca. 18-22 °C, Calder & King, 1974; Kendeigh et al., 1977). Thus, winter survival depends primarily on a positive energy balance, obtaining enough food for self-maintenance and reducing metabolic costs of thermoregulation (e.g. Newton, 1998). In this ecological scenario, species abundances are expected to reach their maxima in warmer areas, through the direct effects of reduced thermoregulation costs and reduced mortality by hypothermia, or indirectly via the improvement of the winter foraging environment (e.g., Gosler, 1996; Doherty & Grubb, 2002; Rogers & Reed, 2003; Robinson et al., 2007; Cresswell et al., 2009; Carrascal et al., 2012a). However, the availability of “optimal environments”, combining preferred temperatures together with other habitat or trophic requirements, may be restricted. As a consequence, the environments in which the individuals of a species end up wintering may show a mean temperature different from the thermal preferences of the species. On the other hand, although general patterns are expected in relation to thermal optima, there might be notable interspecific differences on the thermal tolerance of species. Thermal breadth of species may define how individuals utilize the thermal space and ultimately the geographical area occupied by species (Slatyer et al. 2013).
Moreover, while the abundance of species may be limited by temperature at some points, it might be further limited by other environmental factors related to species-specific habitat or trophic preferences at other locations (Herrando et al. 2011, SEO/BirdLife 2012). Thus, the correlation between species abundance and temperature may often display a solid distribution as that shown in Figure 1a. The upper limit of this distribution is defined by locations in which temperature is the factor actually limiting abundance, while the points below this limit correspond to locations in which other environmental factors are limiting abundance further than temperature. The upper limit of these distributions would represent the maximum potential abundance of species attainable at each environmental temperature, which in theory is independent of other environmental factors (Cade & Noon 2003, Fig 1a).

The first goal of this study is to test the hypothesis that minimum winter temperature – as a surrogate of environmental energy availability – limits the maximum potential abundance of terrestrial birds wintering in the Iberian Peninsula, so that warmer environments will have the potential to maintain a higher number of individuals. Specifically, we test two predictions of this hypothesis: (1) that the maximum abundance of species will correlate positively with minimum winter temperature, (2) that, on average, species will prefer temperatures above the mean environmental temperature available in the region. The second goal is to test the hypothesis that as a consequence of species being limited by other factors (e.g., habitat preferences, food availability), mean temperatures at which species are found ($T_{\text{MEAN}}$) do not coincide with the preferred temperature at which the species abundance is maximized ($T_{\text{PREF}}$). Finally, we analyze the interspecific variation on the level of specialization to use the available thermal space (i.e., the thermal breadth of species, $T_{\text{BREADTH}}$; Figure 1b).

We modeled the influence of minimum winter temperature on the abundance of 103 species of terrestrial birds wintering in the Iberian Peninsula using quadratic 95%-quantile
regression models (Figure 1a). To analyze macroecological patterns in the abundance-temperature relationship across species, we use the standardized regression coefficients and two parameters derived from quantile regression models: the ‘environmental preferred temperature’ of species, calculated as the temperature at which its abundance is maximal within the thermal span of the study region, and the ‘thermal breadth’ of species, calculated as the area under the response curve relative to the maximum abundance of the species (Figure 1b). These measures are able to detect higher inter-specific variability in both thermal preferences and thermal breadth of species than other classical approaches (Villén-Pérez and Carrascal, 2015).

MATERIALS AND METHODS

Bird abundance and temperature data

Field data were obtained from the national-scale project conducted by SEO/BirdLife for the first Spanish Atlas of Wintering Birds (SEO/BirdLife, 2012). See Figure 2b for the geographical location of the study area within the Western Palearctic. ‘Relative abundance’ of each species at 1,689 UTM 10x10 km² cells was calculated as the frequency of occurrence in sixty 15-min transects sampled throughout three consecutive winters (see a summary of the methods in the Spanish Atlas of Wintering Birds in Text S1). We selected 103 bird species for the analyses, excluding nocturnal and aquatic birds, species that were detected in less than 50 UTM 10x10 km cells, and those that were rare or very difficult to detect (i.e., those with a maximum recorded frequency of occurrence lower than 0.05, or three 15-min transects per 60 transects censused).

The average minimum winter temperature of each UTM cell was obtained from updated GIS data covering the whole Iberian Peninsula, provided by the Meteorological Spanish agency.
Data analyses

We analyze the influence of minimum winter temperature (T) on the relative abundance (A) of each species using quantile regressions models at percentiles 50th, 75th, 90th and 95th (i.e., τ =0.50, 0.75, 0.90, 0.95; see Cade & Noon, 2003 and references therein, Figure 1a). To account for non-linear effects of temperature, we define the linear and quadratic terms of the relationship (A = a + bT + cT^2). In order to obtain standardized regression coefficients and to avoid the undesirable relationship between the linear and quadratic terms in the estimation of partial regression coefficients, the original temperature variable is standardized to mean = 0 and sd = 1 prior to the calculus of squared and cubic predictors and data analyses (Schielzeth, 2010). We estimate pseudo-R^2 for each quantile regression model as a goodness-of-fit measure (Konker and Machado 1999), analogous but not exactly homologous to R^2 in least square models (i.e., how well the quantile regression represents the variability observed in the response variable; a higher pseudo-R^2 indicates a better fit). In addition, we calculate the increase in AIC of these models with respect to the null model as a measure of the likelihood of the model (Burham & Anderson 2002).

The environmental preferred temperature (T_{PREF}) is calculated by solving the equation dA · dT^{-1} = 0 in quadratic 95%-quantile regression models. The mean temperature in the area of distribution (T_{MEAN}) is calculated as the weighted average of the winter minimum temperature of the UTM cells where the species were present, using the relative occurrence of species in the sixty 15-min transects. Finally, the thermal breadth of species (T_{BREADTH}) is an index varying from 0 to 1 obtained by integrating A · dT in quadratic 95%-quantile regression models between -2 and 10°C, standardizing the maximal abundances of all species to 1 (Figure 1b).

All data analyses were carried out using the R packages “quantreg” and “Hmisc” (version 1.8-10; R Core Team 2014; Harrell 2015; Konker 2015). See Figure 2 for three example species
showing different patterns of relationship relative abundance – temperature. The script employed in analyses is found in Code and Data S2.

RESULTS

Minimum winter temperature explains an average of 2.7% (se=0.534), 4.8% (0.773), 7.1% (0.924) and 8.7% (0.964) of species abundances using quantile regression models at percentiles 50%, 75%, 90% and 95%, respectively (see pseudo-R² for quantile regression models of all species in Table S3). Only in ten out of 103 species, 95%-quantile regression models attain figures of pseudo-R² higher than 25%, while it is lower than 5% in 50 species. There is a significant increase in pseudo-R² from the percentile 50% to 95% (repeated measure ANOVA testing for the linear contrast of increase from 50% to 95%: F₁,₁₀₂=64.49, p<<0.001).

In 93 out of 103 species, the 95%-quantile regression models including the linear and quadratic terms of temperature attain AIC figures that are 13.82 units lower than those AIC figures obtained for 95%-quantile null regression models (i.e., the temperature models are 1,000 times better in explaining the variation in relative abundance of the species than the null models; 1,000 = exp[-0.5*13.816]; Burnham & Anderson 2002). In other ten species the ΔAIC is higher than -6 (see Table S3).

Standardized lineal regression coefficients \( b \) in the 93 species with “significant” 95%-quantile regression models are on average positive, and significantly different from zero (t test = 4.994, df = 92, p<<0.001; Table 1, Table S3). Standardized quadratic regression coefficients \( c \) show predominantly negative values, on average significantly different from zero (t test = -3.144, df = 92, p=0.002), defining a hump-shaped relationship between temperature and the relative abundance of bird species. Linear terms \( b \) have larger absolute values than the quadratic terms \( c \) (average of absolute figures of \( b \) and \( c \): 4.97 and 3.05, respectively; paired t test: t = 5.51, df = 92,
p << 0.001). Therefore, the linear increase of relative abundance with winter temperature is, on average, positive and more important than the curvilinear pattern defining maxima.

The average $T_{\text{PREF}}$ is 4.36 °C for 93 species with “significant” 95%-quantile regression models (range: -2 °C to 10 °C; Table 1, Table S3), and this average is significantly higher than the average environmental temperature available during winter in peninsular Spain (2.55 °C; t-test: $t = 3.70$, df = 92, $p < 0.001$). $T_{\text{PREF}}$ is lower than 0°C in 24 out of 93 species (i.e., preferences for colder areas; e.g., *Dryocopus martius*, *Cinclus cinclus*, *Turdus pilaris*, *Serinus citrinella*, *Fringilla montifringilla*, *Emberiza cia*), while it is higher than 5°C in 40 species (i.e., preferences for warmer areas; e.g., *Elaneus caeruleus*, *Upupa epops*, *Alcedo atthis*, *Burhinus oedicnemus*, *Ptyonoprogne rupestris*, *Phylloscopus collybita*, *Troglydytes troglodytes*, *Cisticola juncidis*, *Sylvia undata*, see Table S3).

Mean temperature in the area of distribution ($T_{\text{MEAN}}$) is 2.75 °C for the 103 studied species (range: -0.20 °C to 5.51 °C; Table 1, Table S3). In 77 out of 103 species $T_{\text{MEAN}}$ is significantly different from the average minimum temperature available in winter in peninsular Spain (2.55 °C; significant t-tests after the sequential Bonferroni correction), with 35 bird species whose distribution correspond to colder conditions than average, and 42 species inhabiting warmer areas than average. Other 26 species do not show any clear, significant, preference for warmer or colder areas in peninsular Spain.

$T_{\text{PREF}}$ and $T_{\text{MEAN}}$ are highly correlated ($r = 0.856$, $n = 93$, $p << 0.001$; Figure 3), although $T_{\text{PREF}}$ has, on average, higher values than $T_{\text{MEAN}}$ (paired t-test: $t = 3.83$, df = 92, $p << 0.001$). In fact, there are 32 species with $T_{\text{PREF}} > 8^\circ$C that show a $T_{\text{MEAN}}$ 4.5 to 8.3 °C colder. Conversely, there are 21 species with $T_{\text{PREF}} = -2^\circ$C and a $T_{\text{MEAN}}$ 1.8 to 4.1 °C higher.

$T_{\text{BREADTH}}$ is on average 0.64 for all studied species (range: 0.26 to 1.00, $n=103$ species; see Table 1, Table S3). It is low (i.e., thermal specialists, <0.33) in species such as *Dryocopus martius*, *Oenanthe leucura*, *Turdus pilaris*, *Remiz pendulinus*, *Serinus citrinella*) and high (i.e.,
thermal generalists, >0.90) in species such as Accipiter nisus, Turdus merula, Parus major, Corvus monedula, Carduelis cannabina, Fringilla coelebs (see Appendix 2). In those ten species in which 95%-quantile regression models are “non-significant” the average thermal breadth is 0.93, both facts indicating the independence of the distribution of these species with respect to temperature.

**DISCUSSION**

The maximum abundance of birds wintering in the Iberian Peninsula is influenced by minimum winter temperature in 90% of the studied species. Nevertheless, the importance of temperature defining the maximum abundance depends on the species: the thermal breadth of the studied species varies from 0.26 to 1.00, reflecting a broad spectrum from thermal specialists to thermal generalists (Table S3; Moussus et al., 2011). As a general trend, the relative abundance of species increases with minimum winter temperature and, on average, species reach their maximum abundances at temperatures 1.9 ºC warmer than the average temperature available in the study region. In a winter scenario with temperatures well below the thermoneutral zone, this general preference for warmer environments may significantly reduce bird metabolic costs and improve the foraging environment, overall reducing winter mortality rates (Calder & King, 1974; Kendeigh et al., 1977; Root 1988; Canterbury 2002; Meehan et al. 2004; Cresswell et al. 2009; Zuckerber et al. 2011). Nevertheless, 33% of species show statistical significant preferences for environments colder than average conditions (see $T_{\text{PREF}}$ in Table S3). Contrary to the general positive relationships between winter temperature and bird abundance, which are easy to explain according to thermoregulatory costs and food accessibility, these negative relationships are hardly explainable using metabolic arguments for endotherms in wintertime. There might exist other important aspects of bird natural history, such as specialized food preferences or selection for
particular habitats with a restricted spatial distribution that are the responsible for the emergence of those negative relationships between temperature and animal abundance. This may be the case of resident species with restricted habitat preferences, such as for example very mature and extensive forests (e.g., *Dryocopus martius*), mountain streams (*Cinclus cinclus*), montane coniferous forests dominated by pine species with small cones (*Serinus citrinella*), or alpine rock outcrops (*Prunella collaris*), and species with a very specialized diet such as the fruits of the Spanish juniper (*Juniperus thurifera*) that grow in highlands of continental cold climate (*Turdus torquatus*, *T. pilaris*, *T. viscivorus*). If these habitats and food types are unequivocally linked with areas of cold climate, then the negative relationship with temperature may be the casual consequence of those functional responses to habitats and food resources. Summing up, our results show that the relationships between bird abundance and temperature are variable and idiosyncratic (see also Reif et al. 2010; La Sorte & Jetz 2012; Fraixedas et al. 2015), even under the energetically restricted conditions imposed by the winter at temperate latitudes (e.g., long winter nights, low temperatures, high probability of extreme cold events, and generalized low or restricted food availability).

Our results also suggest that temperature has little importance in limiting winter bird distribution, as the pseudo-$R^2$ figures obtained were low (average of 8.7% for the 95%-quantile regression models, and only ten species with pseudo-$R^2$>25%). The steady increase of pseudo-$R^2$ from the median (50% quantile) to the maximum response (95% quantile) shows that the influence of temperature on bird distribution is more clearly revealed at the upper edge of the wedge-shaped pattern of covariation abundance – temperature, where the limiting effect of temperature surpasses that of other factors affecting bird abundance (see Figure 1a). The detected meager influence of temperature on the spatial variation of winter bird abundance is consistent with results obtained in other European areas (Reif et al. 2010; Dalby et al. 2013; Fraixedas et al.
2015), suggesting that other factors such as feeding ecology, habitat preferences or human-
induced land-use changes are more important governing winter bird distribution in this region of
the southwestern Palearctic (see also Carrascal et al. 2012a, 2012b for the competing effects of
food, vegetation and temperature on the winter abundance of small passerines at smaller spatial
scales in the Iberian Peninsula).

Quantile regression is a method of analyzing the unequal variation in a variable of interest
along a set of predictor of variables when there are multiple rates of change (or slopes) from the
minimum to the maximum response (Cade et al. 1999; Cade and Noon 2003). This approach
allows the identification of limiting factors, paying more attention to the slopes near the
maximum response (e.g., maximum abundance attained at each temperature), which provides a
thorough picture of the patterns of covariation between the animal abundance and temperature.
Thus, the estimation of the response of a high quantile of population density to a measured
predictor variable is generally considered to be a better estimate of the effect of that variable as a
limiting factor than the estimate of the response to the mean calculated with least squares. This is
because other unmeasured variables may be the active limiting constraint in the dependent
variable of interest, through their correlations with the measured predictor (Borsuk 2008). For
example, if a UTM cell has a winter temperature that approaches the thermal preference of a
species but lacks the habitat with the vegetation structure characteristics and food availability that
configure the spatial-trophic niche of the species, the species should be probably very scarce in
that UTM cell (e.g., Sylvia melanocephala may be scarce in a warm cell with minimum winter
temperature 9 ºC but lacking Mediterranean maquis with high abundance of ripe fruits). That
sample unit will occupy a low position in the wedge-shaped pattern depicted by Figure 1a.
Therefore, estimating the upper edge of the wedge-shaped pattern of covariation abundance -
temperature allows for the identification of the limiting effect of temperature on bird abundance,
disregarding the probable interactions between temperature and other limiting predictors (measured or unmeasured). This is a sound concern, as the influence of temperature on bird distribution and abundance is probably mediated through surrogate effects of spatial variables, habitat preferences or resource availability (see Aragón et al. 2010 for direct and indirect effects of climatic and non-climatic factors on distribution of ectothermic and endothermic vertebrates in the Iberian Peninsula). For example, Repasky (1991) found little evidence to support that the northern distributions of North American wintering birds are governed principally by temperature, suggesting that temperature probably plays a role through interactions with biotic factors such as food, habitat structure and competition. The importance of these interactions on bird abundance distribution, is clearly reflected by the differences between the mean winter minimum temperature in those UTM cells where the species were present ($T_{\text{MEAN}}$) and the preferred temperature ($T_{\text{PREF}}$) derived from quadratic 95%-quantile regression models (Figure 3). Although both parameters are highly correlated, most individuals end-up overwintering in locations that are colder than the species thermal preferences, which may reflect a limitation of sites combining thermal and other environmental optima. For instance, insectivorous small passerines, such as *Cettia cetti*, *Sylvia undata*, *Motacilla alba* or *Saxicola rubicola*, occupy areas of peninsular Spain that are ca. 6°C colder than their preferred temperatures (see Table S3), probably because they lack their preferred habitats in those warm areas. Considering this evidence, the low use of quantile regressions in the study of animal distribution patterns in relation to climate is highly surprising, a fact that may be a constraint in ecologists’ ability to analyze the influence of climatic variables for elucidating the underlying patterns (Austin 2007, Vaz et al. 2008).

The general preference for warmer environments that we found suggest that winters will be less restrictive for most birds wintering in the Iberian peninsula under future climate warming
scenarios (IPCC, 2007; Brunet et al., 2009; Stocker et al. 2013), though the impact of changes will depend on species-specific thermal preferences and plasticity. Zuckerberg et al. (2011) showed for birds wintering in North America that average minimum temperature is an important factor limiting bird distributions, and that local within-winter extinction probabilities are lower, and colonization probabilities higher, at warmer sites, supporting the role of climate-mediated range shifts. Climate warming may be especially beneficial for those species with narrow thermal breadths that prefer higher winter temperatures and that mainly rely on arthropods and fruits as winter food (e.g., Upupa epops, Ptyonoprogne rupestris, Trogloxytes troglodytes, Luscinia svecica, Cisticola junci, Phylloscopus collybita, Sylvia melanocephala, S. atricapilla). In the same vein, Tellería et al. (2016) found that according to temperature increase projections for 2050–2070, two insectivorous passerines wintering in the Western Mediterranean basin (Anthus pratensis and Phylloscopus collybita) will broaden their distribution ranges into the cold highland expanses typical of the western Mediterranean (but see La Sorte et al. 2009 for ‘space-for-time’ substitution when forecasting temporal trends from spatial climatic gradients). These forecasts on bird distributions are supported by the analyses of recent avian populations and winter minimum temperature changes in North America, where shifting winter climate has provided an opportunity for smaller, southerly distributed species to colonize new regions (Prince and Zuckerberg 2015). Future studies in the Iberian Peninsula -one of the most important wintering quarters of the western Palearctic- should explore the biological traits associated and interacting with interspecific differences in winter thermal preferences, considering the phylogenetic relatedness and differences among species in body mass, habitat selection, diet, metabolic characteristics and biogeographic origins.

CONCLUSIONS
This study highlights the high interspecific variability on the response to temperature and on the tolerance of species to different thermal spaces. Bird species wintering in peninsular Spain range from the coldest to the warmest thermal preferences and from thermal specialists to generalists. Nevertheless, the general trend is to select the warmest environments, so that abundance of most species increases with temperature and is predicted to reach its maximum at temperatures higher than the average available temperatures in the study area. Even though species generally prefer warm environments, a large proportion of the populations end-up overwintering in colder locations, probably reflecting a limitation of locations combining thermal optima with other environmental preferences of species. The biogeographical patterns found here may reflect the ecological, large-scale, consequences of reducing thermoregulation costs in these endotherms during winter.

### Acknowledgements

Juan Carlos del Moral (SEO / BirdLife) provided the raw data from the Winter Spanish Bird Atlas. We also thank Jorge M. Lobo for helpful comments on a first draft of the paper and C. Jasinski for improving the English of the manuscript.

### Funding Statement

This paper is a contribution to projects CGL2008-02211/BOS and CGL2011-28177/BOS of the Spanish Ministry of Education and Science. During the development of this work, Sara Villén-Pérez was supported by a ‘Formacion de Personal Investigador’ predoctoral fellowship (BES-2009-029386) of the Spanish Ministry of Education and Science and by a ‘Young Talent Attraction’ fellowship (300274/2015-7) of the Nacional Council of Scientific and Technological Development of Brazil. David Palomino was contracted by SEO / BirdLife to organize, design, analyze and develop the Winter Spanish Bird Atlas.

### REFERENCES


Table 1. Parameters of the response of species abundance to winter temperature. Figures are mean, standard deviation and range of parameters derived from 95%-quantile regression models describing the influence of minimum winter temperature on abundance of bird species wintering in peninsular Spain, sampled at 1689 UTM 10x10 km² cells in three consecutive winters (2008-2011). Sample size is 93 species when considering only significant models with a reduction in AIC figures (ΔAIC) lower than -13.82 units, and 103 species when significance of models is not relevant and therefore all species are considered. Detailed data for all species are shown in Table S3.

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<td>Environmental preferred temperature (ºC), ( T_{\text{PREF}} )</td>
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<td>Mean temperature on distribution areas (ºC), ( T_{\text{MEAN}} )</td>
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<td>1.10</td>
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<td>Thermal breadth, ( T_{\text{BREADTH}} )</td>
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<td>0.20</td>
<td>0.26 / 1</td>
<td>103</td>
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</table>

\( b, c \): linear and quadratic regression coefficients obtained from 95%-quantile regression models on the effect of minimum winter temperature on the relative abundance of species; \( T_{\text{PREF}} \): winter minimum temperature at which the relative abundance of the species is maximized; \( T_{\text{MEAN}} \): mean of average winter minimum temperature in those UTM cells where the species were present, weighed by the relative abundance of the specie at the cell; \( T_{\text{BREADTH}} \): area under the curve defined by the second order polynomial equation that relates the relative abundance of species to the temperature using the coefficients of the 95%-quantile regression models. n: number of species considered.
Figure 1. Representation of environmental preferred temperature ($T_{\text{PREF}}$), mean temperature ($T_{\text{MEAN}}$) and thermal breadth ($T_{\text{BREATH}}$) of an example species. (a) Abundance of *Columba palumbus* in relation to minimum winter temperature along 1689 UTM cells, and fitting curves for quantile regression models (from top to bottom: models on 95th, 75th, 50th and 25th percentiles). Relative abundance is the number of 15 min transects over 60 in which the species is detected at each UTM 10x10Km cell. (b) $T_{\text{PREF}}$, $T_{\text{MEAN}}$ and $T_{\text{BREATH}}$ of *Columba palumbus*. Environmental preferred temperature ($T_{\text{PREF}}$) is the temperature at which the maximum abundance of the species is predicted by the quantile regression model for percentile 95th in (a). Mean temperature ($T_{\text{MEAN}}$) is the mean winter minimum temperature in those UTM cells where the species was present, weighed by the relative abundance of the species at each cell. Thermal breadth ($T_{\text{BREATH}}$) is the standardized area under the curve of quantile regression model for percentile 95th in (a), from -2 to 10°C (shaded area in b).
Figure 2. Minimum winter temperature (°C) and relative abundance of three example bird species in peninsular Spain, and relationship between these variables. (a) Minimum winter temperatures in the study area (peninsular Spain). (b) Location of the study area within the western Palearctic. (c, e, g) Winter relative abundance of three sample species (*Saxicola rubicola*, *Erithacus rubecula* and *Turdus viscivorus*, respectively), at 1689 UTM 10x10 km² cells within the study area, sampled in three consecutive winters (2008-2011). Relative abundance is the frequency of occurrence in sixty 15-min linear transects carried out in each UTM cell. (d, f, h) Relationship between the relative abundance of these species and minimum winter temperature, as modeled by quadratic 95%-quantile regression models.
Figure 3. Relationship between $T_{\text{PREF}}$ and $T_{\text{MEAN}}$ for 93 bird species wintering in peninsular Spain. The graph shows 93 species for which the 95%-quantile regression models including the linear and quadratic terms of temperature attained AIC figures that were 13.82 units lower than those AIC figures obtained for 95%-quantile null regression models. Solid line represents the linear regression between $T_{\text{PREF}}$ and $T_{\text{MEAN}}$. 
Supplemental Information


Supplemental Code and Data S2. Script for R environment employed in analyses and dataset including four example species.

Supplemental Table S3. Parameters for all 103 species included in the study.