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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 °C 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 .

1 **Preferred temperature and thermal breadth of birds wintering in peninsular**
2 **Spain – the limited effect of temperature on species distribution.**

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

11 Abstract

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

18 **Methods.** We model the influence of minimum winter temperature on the relative abundance of
19 106 terrestrial bird species wintering in peninsular Spain, at 10x10 Km² resolution, using
20 95%-quantile regressions. We analyze general trends across species on the shape of the
21 response curves, the environmental preferred temperature (at which the species abundance is
22 maximized), the mean temperature in the area of distribution and the thermal breadth (area
23 under the abundance-temperature curve).

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

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

36

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

39 INTRODUCTION

40 The distribution of overwintering animals is assumed to be strongly influenced by
41 environmental energy availability, notably in regions with a marked year-round seasonality such
42 as temperate ecosystems. Peninsular Spain is an important target for many avian populations of
43 the southwestern Palearctic during the winter (Moreau, 1972), when there are massive migrations
44 of northern populations towards circum-Mediterranean countries. Even though conditions are
45 milder than in the north, it is an energy-limiting period in which food resources are scarce and/or
46 difficult to locate and the low temperatures impose a high metabolic cost to maintain a constant
47 body temperature for homeothermic animals (Calder & King, 1974). Specifically, winter
48 temperature in peninsular Spain (average 2.55°C) is well below the lower critical temperature for
49 a broad variety of bird species (ca. 18-22 °C, Calder & King, 1974; Kendeigh et al., 1977). Thus,
50 winter survival depends primarily on a positive energy balance, obtaining enough food for self-
51 maintenance and reducing metabolic costs of thermoregulation (e.g. Newton, 1998). In this
52 ecological scenario, species abundances are expected to reach their maxima in warmer areas,
53 through the direct effects of reduced thermoregulation costs and reduced mortality by
54 hypothermia, or indirectly via the improvement of the winter foraging environment (e.g., Gosler,
55 1996; Doherty & Grubb, 2002; Rogers & Reed, 2003; Robinson et al., 2007; Cresswell et al.,
56 2009; Carrascal et al., 2012a). However, the availability of “optimal environments”, combining
57 preferred temperatures together with other habitat or trophic requirements, may be restricted. As a
58 consequence, the environments in which the individuals of a species end up wintering may show
59 a mean temperature different from the thermal preferences of the species. On the other hand,
60 although general patterns are expected in relation to thermal optima, there might be notable
61 interspecific differences on the thermal tolerance of species. Thermal breadth of species may
62 define how individuals utilize the thermal space and ultimately the geographical area occupied by
63 species (Slatyer et al. 2013).

64 Moreover, while the abundance of species may be limited by temperature at some points,
65 it might be further limited by other environmental factors related to species-specific habitat or
66 trophic preferences at other locations (Herrando et al. 2011, SEO/BirdLife 2012). Thus, the
67 correlation between species abundance and temperature may often display a solid distribution as
68 that shown in Figure 1a. The upper limit of this distribution is defined by locations in which
69 temperature is the factor actually limiting abundance, while the points below this limit
70 correspond to locations in which other environmental factors are limiting abundance further than
71 temperature. The upper limit of these distributions would represent the maximum potential
72 abundance of species attainable at each environmental temperature, which in theory is
73 independent of other environmental factors (Cade & Noon 2003, Fig 1a).

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

86 We modeled the influence of minimum winter temperature on the abundance of 103
87 species of terrestrial birds wintering in the Iberian Peninsula using quadratic 95%-quantile

88 regression models (Figure 1a). To analyze macroecological patterns in the abundance-
89 temperature relationship across species, we use the standardized regression coefficients and two
90 parameters derived from quantile regression models: the ‘environmental preferred temperature’ of
91 species, calculated as the temperature at which its abundance is maximal within the thermal span
92 of the study region, and the ‘thermal breadth’ of species, calculated as the area under the response
93 curve relative to the maximum abundance of the species (Figure 1b). These measures are able to
94 detect higher inter-specific variability in both thermal preferences and thermal breadth of species
95 than other classical approaches (Villén-Pérez and Carrascal, 2015).

96

97 **MATERIALS AND METHODS**

98 *Bird abundance and temperature data*

99 Field data were obtained from the national-scale project conducted by SEO/BirdLife for
100 the first Spanish Atlas of Wintering Birds (SEO/BirdLife, 2012). See Figure 2b for the
101 geographical location of the study area within the Western Palearctic. ‘Relative abundance’ of
102 each species at 1,689 UTM 10x10 km² cells was calculated as the frequency of occurrence in
103 sixty 15-min transects sampled throughout three consecutive winters (see a summary of the
104 methods in the Spanish Atlas of Wintering Birds in Text S1). We selected 103 bird species for the
105 analyses, excluding nocturnal and aquatic birds, species that were detected in less than 50 UTM
106 10x10 km cells, and those that were rare or very difficult to detect (i.e., those with a maximum
107 recorded frequency of occurrence lower than 0.05, or three 15-min transects per 60 transects
108 censused).

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

111 (www.aemet.es) and calculated as the daily averages during the period of study (mid-November
112 to mid-February 2007-2010).

113 **Data analyses**

114 We analyze the influence of minimum winter temperature (T) on the relative abundance
115 (A) of each species using quantile regressions models at percentiles 50th, 75th, 90th and 95th (i.e., τ
116 = 0.50, 0.75, 0.90, 0.95; see Cade & Noon, 2003 and references therein, Figure 1a). To account for
117 non-linear effects of temperature, we define the linear and quadratic terms of the relationship (A
118 = $a + bT + cT^2$). In order to obtain standardized regression coefficients and to avoid the
119 undesirable relationship between the linear and quadratic terms in the estimation of partial
120 regression coefficients, the original temperature variable is standardized to mean = 0 and sd = 1
121 prior to the calculus of squared and cubic predictors and data analyses (Schielzeth, 2010). We
122 estimate pseudo- R^2 for each quantile regression model as a goodness-of-fit measure (Konker and
123 Machado 1999), analogous but not exactly homologous to R^2 in least square models (i.e., how
124 well the quantile regression represents the variability observed in the response variable; a higher
125 pseudo- R^2 indicates a better fit). In addition, we calculate the increase in AIC of these models
126 with respect to the null model as a measure of the likelihood of the model (Burham & Anderson
127 2002).

128 The environmental preferred temperature (T_{PREF}) is calculated by solving the equation dA
129 $\cdot dT^{-1} = 0$ in quadratic 95%-quantile regression models. The mean temperature in the area of
130 distribution (T_{MEAN}) is calculated as the weighted average of the winter minimum temperature of
131 the UTM cells where the species were present, using the relative occurrence of species in the
132 sixty 15-min transects. Finally, the thermal breadth of species (T_{BREADTH}) is an index varying from
133 0 to 1 obtained by integrating $A \cdot dT$ in quadratic 95%-quantile regression models between -2
134 and 10°C, standardizing the maximal abundances of all species to 1 (Figure 1b).

135 All data analyses were carried out using the R packages “quantreg” and “Hmisc” (version
136 1.8-10; R Core Team 2014; Harrell 2015; Konker 2015). See Figure 2 for three example species

137 showing different patterns of relationship relative abundance – temperature. The script employed
138 in analyses is found in Code and Data S2.
139

140 RESULTS

141 Minimum winter temperature explains an average of 2.7% (se=0.534), 4.8% (0.773),
142 7.1% (0.924) and 8.7% (0.964) of species abundances using quantile regression models at
143 percentiles 50%, 75%, 90% and 95%, respectively (see pseudo-R² for quantile regression models
144 of all species in Table S3). Only in ten out of 103 species, 95%-quantile regression models attain
145 figures of pseudo-R² higher than 25%, while it is lower than 5% in 50 species. There is a
146 significant increase in pseudo-R² from the percentile 50% to 95% (repeated measure ANOVA
147 testing for the linear contrast of increase from 50% to 95%: $F_{1,102}=64.49$, $p<<0.001$).

148 In 93 out of 103 species, the 95%-quantile regression models including the linear and
149 quadratic terms of temperature attain AIC figures that are 13.82 units lower than those AIC
150 figures obtained for 95%-quantile null regression models (i.e., the temperature models are 1,000
151 times better in explaining the variation in relative abundance of the species than the null models;
152 $1,000 = \exp[-0.5*13.816]$; Burham & Anderson 2002). In other ten species the ΔAIC is higher
153 than -6 (see Table S3).

154 Standardized lineal regression coefficients **b** in the 93 species with “significant” 95%-
155 quantile regression models are on average positive, and significantly different from zero (t test =
156 4.994, df = 92, $p<<0.001$; Table 1, Table S3). Standardized quadratic regression coefficients **c**
157 show predominantly negative values, on average significantly different from zero (t test = -3.144,
158 df = 92, $p=0.002$), defining a hump-shaped relationship between temperature and the relative
159 abundance of bird species. Linear terms **b** have larger absolute values than the quadratic terms **c**
160 (average of absolute figures of **b** and **c**: 4.97 and 3.05, respectively; paired t test: $t = 5.51$, df = 92,

161 $p \ll 0.001$). Therefore, the linear increase of relative abundance with winter temperature is, on
162 average, positive and more important than the curvilinear pattern defining maxima.

163 The average T_{PREF} is 4.36 °C for 93 species with “significant” 95%-quantile regression
164 models (range: -2 °C to 10 °C; Table 1, Table S3), and this average is significantly higher than the
165 average environmental temperature available during winter in peninsular Spain (2.55 °C; t-test: t
166 = 3.70, $df = 92$, $p < 0.001$). T_{PREF} is lower than 0°C in 24 out of 93 species (i.e., preferences for
167 colder areas; e.g., *Dryocopus martius*, *Cinclus cinclus*, *Turdus pilaris*, *Serinus citrinella*,
168 *Fringilla montifringilla*, *Emberiza cia*), while it is higher than 5°C in 40 species (i.e., preferences
169 for warmer areas; e.g., *Elanus caeruleus*, *Upupa epops*, *Alcedo atthis*, *Burhinus oedicephalus*,
170 *Ptyonoprogne rupestris*, *Phylloscopus collybita*, *Troglodytes troglodytes*, *Cisticola juncidis*, *Sylvia*
171 *undata*, see Table S3).

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

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

183 T_{BREADTH} is on average 0.64 for all studied species (range: 0.26 to 1.00, $n=103$ species; see
184 Table 1, Table S3). It is low (i.e., thermal specialists, <0.33) in species such as *Dryocopus*
185 *martius*, *Oenanthe leucura*, *Turdus pilaris*, *Remiz pendulinus*, *Serinus citrinella*) and high (i.e.,

186 thermal generalists, >0.90) in species such as *Accipiter nisus*, *Turdus merula*, *Parus major*,
187 *Corvus monedula*, *Carduelis cannabina*, *Fringilla coelebs* (see Appendix 2). In those ten species
188 in which 95%-quantile regression models are “non-significant” the average thermal breadth is
189 0.93, both facts indicating the independence of the distribution of these species with respect to
190 temperature.

191

192 **DISCUSSION**

193 The maximum abundance of birds wintering in the Iberian Peninsula is influenced by
194 minimum winter temperature in 90% of the studied species. Nevertheless, the importance of
195 temperature defining the maximum abundance depends on the species: the thermal breadth of the
196 studied species varies from 0.26 to 1.00, reflecting a broad spectrum from thermal specialists to
197 thermal generalists (Table S3; Moussus et al., 2011). As a general trend, the relative abundance of
198 species increases with minimum winter temperature and, on average, species reach their
199 maximum abundances at temperatures 1.9 °C warmer than the average temperature available in
200 the study region. In a winter scenario with temperatures well below the thermoneutral zone, this
201 general preference for warmer environments may significantly reduce bird metabolic costs and
202 improve the foraging environment, overall reducing winter mortality rates (Calder & King, 1974;
203 Kendeigh et al., 1977; Root 1988; Canterbury 2002; Meehan et al. 2004; Cresswell et al. 2009;
204 Zuckerber et al. 2011). Nevertheless, 33% of species show statistical significant preferences for
205 environments colder than average conditions (see T_{PREF} in Table S3). Contrary to the general
206 positive relationships between winter temperature and bird abundance, which are easy to explain
207 according to thermoregulatory costs and food accessibility, these negative relationships are hardly
208 explainable using metabolic arguments for endotherms in wintertime. There might exist other
209 important aspects of bird natural history, such as specialized food preferences or selection for

210 particular habitats with a restricted spatial distribution that are the responsible for the emergence
211 of those negative relationships between temperature and animal abundance. This may be the case
212 of resident species with restricted habitat preferences, such as for example very mature and
213 extensive forests (e.g., *Dryocopus martius*), mountain streams (*Cinclus cinclus*), montane
214 coniferous forests dominated by pine species with small cones (*Serinus citrinella*), or alpine rock
215 outcrops (*Prunella collaris*), and species with a very specialized diet such as the fruits of the
216 Spanish juniper (*Juniperus thurifera*) that grow in highlands of continental cold climate (*Turdus*
217 *torquatus*, *T. pilaris*, *T. viscivorus*). If these habitats and food types are unequivocally linked with
218 areas of cold climate, then the negative relationship with temperature may be the casual
219 consequence of those functional responses to habitats and food resources. Summing up, our
220 results show that the relationships between bird abundance and temperature are variable and
221 idiosyncratic (see also Reif et al. 2010; La Sorte & Jetz 2012; Fraixedas et al. 2015), even under
222 the energetically restricted conditions imposed by the winter at temperate latitudes (e.g., long
223 winter nights, low temperatures, high probability of extreme cold events, and generalized low or
224 restricted food availability).

225 Our results also suggest that temperature has little importance in limiting winter bird
226 distribution, as the pseudo- R^2 figures obtained were low (average of 8.7% for the 95%-quantile
227 regression models, and only ten species with pseudo- $R^2 > 25\%$). The steady increase of pseudo- R^2
228 from the median (50% quantile) to the maximum response (95% quantile) shows that the
229 influence of temperature on bird distribution is more clearly revealed at the upper edge of the
230 wedge-shaped pattern of covariation abundance – temperature, where the limiting effect of
231 temperature surpasses that of other factors affecting bird abundance (see Figure 1a). The detected
232 meager influence of temperature on the spatial variation of winter bird abundance is consistent
233 with results obtained in other European areas (Reif et al. 2010; Dalby et al. 2013; Fraixedas et al.

234 2015), suggesting that other factors such as feeding ecology, habitat preferences or human-
235 induced land-use changes are more important governing winter bird distribution in this region of
236 the southwestern Palearctic (see also Carrascal et al. 2012a, 2012b for the competing effects of
237 food, vegetation and temperature on the winter abundance of small passerines at smaller spatial
238 scales in the Iberian Peninsula).

239 Quantile regression is a method of analyzing the unequal variation in a variable of interest
240 along a set of predictor of variables when there are multiple rates of change (or slopes) from the
241 minimum to the maximum response (Cade et al. 1999; Cade and Noon 2003). This approach
242 allows the identification of limiting factors, paying more attention to the slopes near the
243 maximum response (e.g., maximum abundance attained at each temperature), which provides a
244 thorough picture of the patterns of covariation between the animal abundance and temperature.
245 Thus, the estimation of the response of a high quantile of population density to a measured
246 predictor variable is generally considered to be a better estimate of the effect of that variable as a
247 limiting factor than the estimate of the response to the mean calculated with least squares. This is
248 because other unmeasured variables may be the active limiting constraint in the dependent
249 variable of interest, through their correlations with the measured predictor (Borsuk 2008). For
250 example, if a UTM cell has a winter temperature that approaches the thermal preference of a
251 species but lacks the habitat with the vegetation structure characteristics and food availability that
252 configure the spatial-trophic niche of the species, the species should be probably very scarce in
253 that UTM cell (e.g., *Sylvia melanocephala* may be scarce in a warm cell with minimum winter
254 temperature 9 °C but lacking Mediterranean maquis with high abundance of ripe fruits). That
255 sample unit will occupy a low position in the wedge-shaped pattern depicted by Figure 1a.
256 Therefore, estimating the upper edge of the wedge-shaped pattern of covariation abundance -
257 temperature allows for the identification of the limiting effect of temperature on bird abundance,

258 disregarding the probable interactions between temperature and other limiting predictors
259 (measured or unmeasured). This is a sound concern, as the influence of temperature on bird
260 distribution and abundance is probably mediated through surrogate effects of spatial variables,
261 habitat preferences or resource availability (see Aragón et al. 2010 for direct and indirect effects
262 of climatic and non-climatic factors on distribution of ectothermic and endothermic vertebrates in
263 the Iberian Peninsula). For example, Repasky (1991) found little evidence to support that the
264 northern distributions of North American wintering birds are governed principally by
265 temperature, suggesting that temperature probably plays a role through interactions with biotic
266 factors such as food, habitat structure and competition. The importance of these interactions on
267 bird abundance distribution, is clearly reflected by the differences between the mean winter
268 minimum temperature in those UTM cells where the species were present (T_{MEAN}) and the
269 preferred temperature (T_{PREF}) derived from quadratic 95%-quantile regression models (Figure 3).
270 Although both parameters are highly correlated, most individuals end-up overwintering in
271 locations that are colder than the species thermal preferences, which may reflect a limitation of
272 sites combining thermal and other environmental optima. For instance, insectivorous small
273 passerines, such as *Cettia cetti*, *Sylvia undata*, *Motacilla alba* or *Saxicola rubicola*, occupy areas
274 of peninsular Spain that are ca. 6°C colder than their preferred temperatures (see Table S3),
275 probably because they lack their preferred habitats in those warm areas. Considering this
276 evidence, the low use of quantile regressions in the study of animal distribution patterns in
277 relation to climate is highly surprising, a fact that may be a constraint in ecologists' ability to
278 analyze the influence of climatic variables for elucidating the underlying patterns (Austin 2007,
279 Vaz et al. 2008).

280 The general preference for warmer environments that we found suggest that winters will
281 be less restrictive for most birds wintering in the Iberian peninsula under future climate warming

282 scenarios (IPCC, 2007; Brunet et al., 2009; Stocker et al. 2013), though the impact of changes
283 will depend on species-specific thermal preferences and plasticity. Zuckerberg et al. (2011)
284 showed for birds wintering in North America that average minimum temperature is an important
285 factor limiting bird distributions, and that local within-winter extinction probabilities are lower,
286 and colonization probabilities higher, at warmer sites, supporting the role of climate-mediated
287 range shifts. Climate warming may be especially beneficial for those species with narrow thermal
288 breadths that prefer higher winter temperatures and that mainly rely on arthropods and fruits as
289 winter food (e.g., *Upupa epops*, *Ptyonoprogne rupestris*, *Troglodytes troglodytes*, *Luscinia*
290 *svecica*, *Cisticola juncidis*, *Phylloscopus collybita*, *Sylvia melanocephala*, *S. atricapilla*). In the
291 same vein, Tellería et al. (2016) found that according to temperature increase projections for
292 2050–2070, two insectivorous passerines wintering in the Western Mediterranean basin (*Anthus*
293 *pratensis* and *Phylloscopus collybita*) will broaden their distribution ranges into the cold highland
294 expanses typical of the western Mediterranean (but see La Sorte et al. 2009 for ‘space-for-time’
295 substitution when forecasting temporal trends from spatial climatic gradients). These forecasts on
296 bird distributions are supported by the analyses of recent avian populations and winter minimum
297 temperature changes in North America, where shifting winter climate has provided an
298 opportunity for smaller, southerly distributed species to colonize new regions (Prince and
299 Zuckerberg 2015). Future studies in the Iberian Peninsula -one of the most important wintering
300 quarters of the western Palearctic- should explore the biological traits associated and interacting
301 with interspecific differences in winter thermal preferences, considering the phylogenetic
302 relatedness and differences among species in body mass, habitat selection, diet, metabolic
303 characteristics and biogeographic origins.

304 CONCLUSIONS

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

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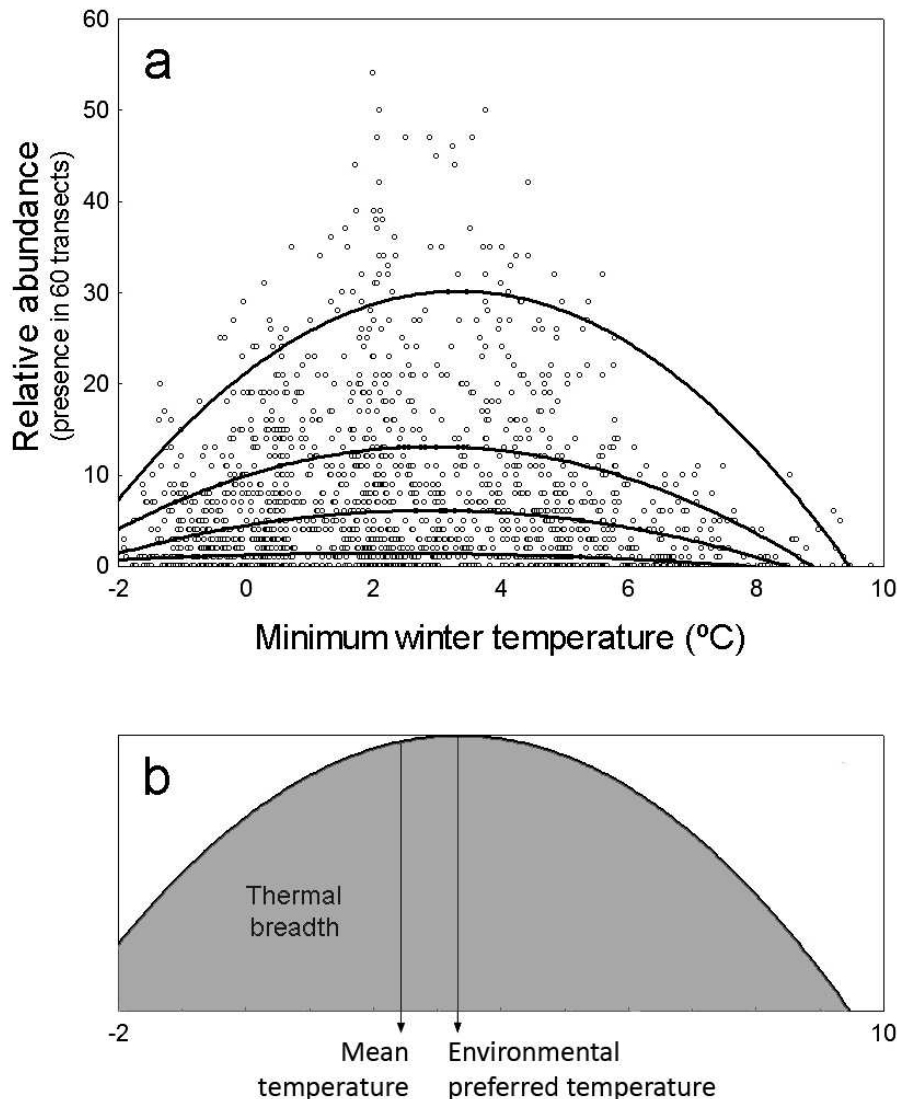
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423 **Table 1. Parameters of the response of species abundance to winter temperature.** Figures are
 424 mean, standard deviation and range of parameters derived from 95%-quantile regression models
 425 describing the influence of minimum winter temperature on abundance of bird species wintering
 426 in peninsular Spain, sampled at 1689 UTM 10x10 km² cells in three consecutive winters (2008-
 427 2011). Sample size is 93 species when considering only significant models with a reduction in
 428 AIC figures (Δ AIC) lower than -13.82 units, and 103 species when significance of models is not
 429 relevant and therefore all species are considered. Detailed data for all species are shown in Table
 430 S3.

	mean	sd	range	n
Standardized linear coefficient, b	3.22	6.22	-9.38 / 18.94	93
Standardized curvilinear coefficient, c	-1.43	4.39	-18.12 / 7.54	93
Environmental preferred temperature (°C), T_{PREF}	4.36	4.72	-2 / 10	93
Mean temperature on distribution areas (°C), T_{MEAN}	2.75	1.10	-0.2 / 5.5	103
Thermal breadth, T_{BREADTH}	0.64	0.20	0.26 / 1	103

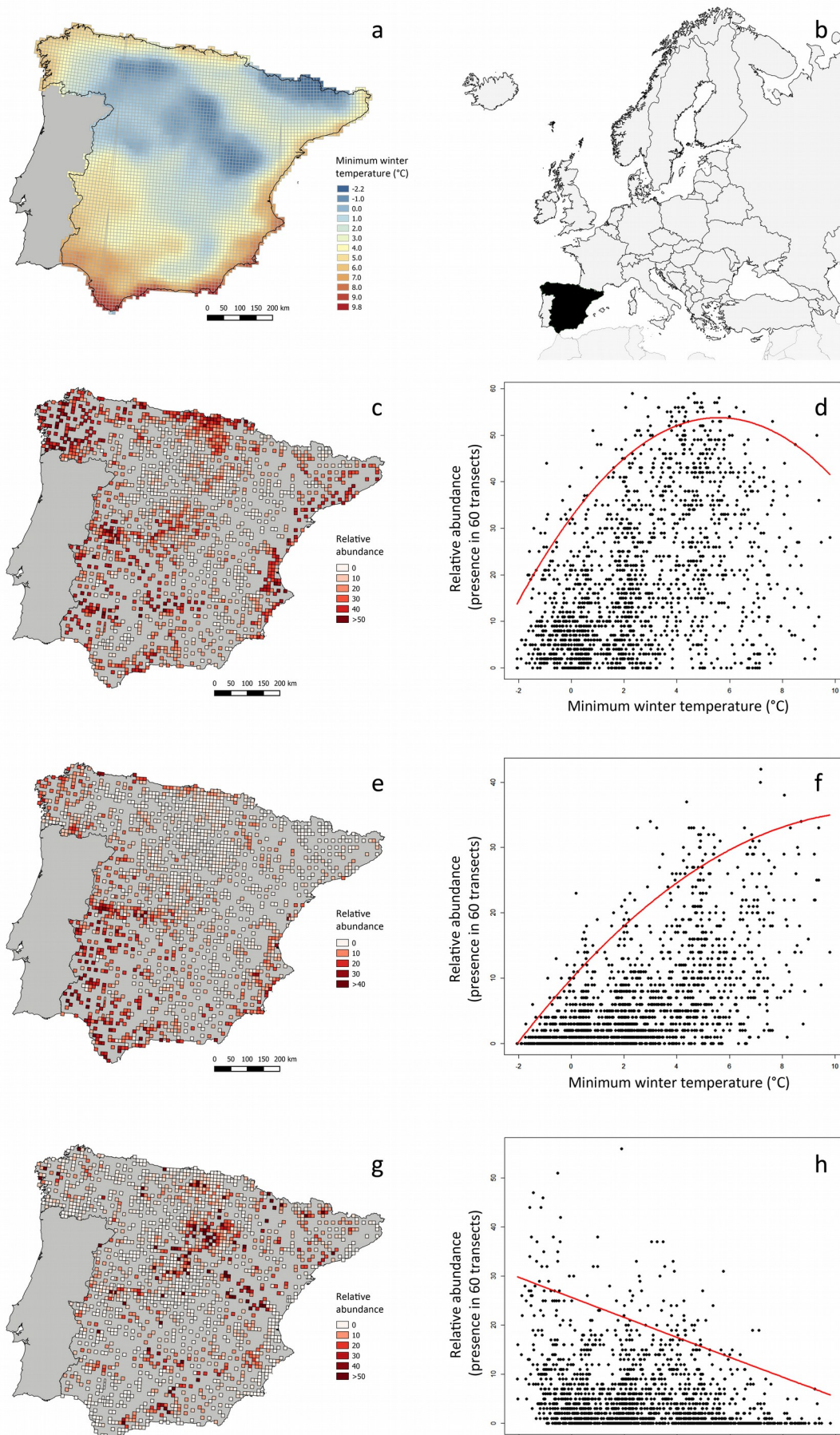
431 **b, c:** linear and quadratic regression coefficients obtained from 95%-quantile regression models on the effect of
 432 minimum winter temperature on the relative abundance of species; **T_{PREF}**: winter minimum temperature at which the
 433 relative abundance of the species is maximized; **T_{MEAN}**: mean of average winter minimum temperature in those UTM
 434 cells where the species were present, weighed by the relative abundance of the specie at the cell; **T_{BREADTH}**: area
 435 under the curve defined by the second order polynomial equation that relates the relative abundance of species to the
 436 temperature using the coefficients of the 95%-quantile regression models. n: number of species considered.
 437

438 **Figure 1. Representation of environmental preferred temperature (T_{PREF}), mean**
 439 **temperature (T_{MEAN}) and thermal breadth (T_{BREATH}) of an example specie. (a) Abundance of**
 440 *Columba palumbus* in relation to minimum winter temperature along 1689 UTM cells, and fitting
 441 curves for quantile regression models (from top to bottom: models on 95th, 75th, 50th and 25th
 442 percentiles). Relative abundance is the number of 15 min transects over 60 in which the species is
 443 detected at each UTM 10x10Km cell. (b) T_{PREF} , T_{MEAN} and T_{BREATH} of *Columba palumbus*.
 444 Environmental preferred temperature (T_{PREF}) is the temperature at which the maximum
 445 abundance of the species is predicted by the quantile regression model for percentile 95th in (a).
 446 Mean temperature (T_{MEAN}) is the mean winter minimum temperature in those UTM cells where
 447 the species was present, weighed by the relative abundance of the species at each cell. Thermal
 448 breadth (T_{BREATH}) is the standardized area under the curve of quantile regression model for
 449 percentile 95th in (a), from -2 to 10°C (shaded area in b).

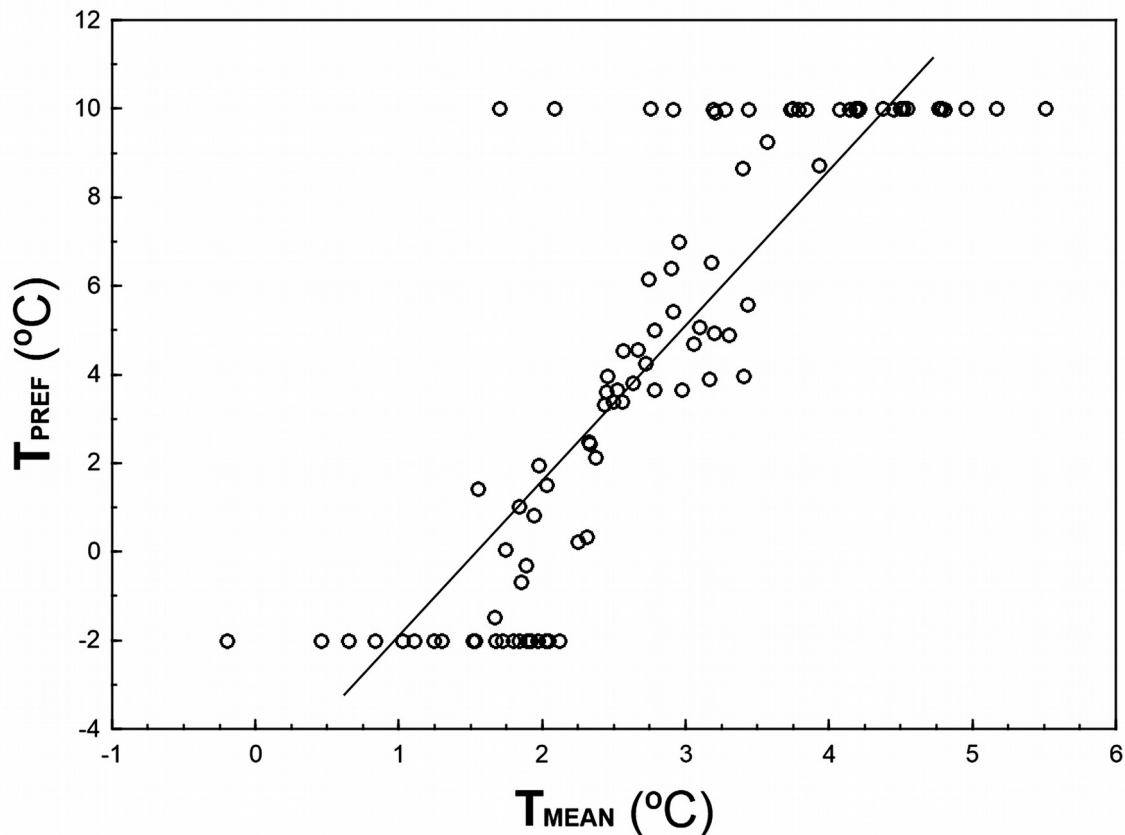


450

451 **Figure 2. Minimum winter temperature (°C) and relative abundance of three example bird**
452 **species in peninsular Spain, and relationship between these variables.** (a) Minimum winter
453 temperatures in the study area (peninsular Spain). (b) Location of the study area within the
454 western Palearctic. (c, e, g) Winter relative abundance of three sample species (*Saxicola rubicola*,
455 *Erithacus rubecula* and *Turdus viscivorus*, respectively), at 1689 UTM 10x10 km² cells within
456 the study area, sampled in three consecutive winters (2008-2011). Relative abundance is the
457 frequency of occurrence in sixty 15-min linear transects carried out in each UTM cell. (d, f, h)
458 Relationship between the relative abundance of these species and minimum winter temperature,
459 as modeled by quadratic 95%-quantile regression models.



461 **Figure 3. Relationship between T_{PREF} and T_{MEAN} for 93 bird species wintering in peninsular**
462 **Spain.** The graph shows 93 species for which the 95%-quantile regression models including the
463 linear and quadratic terms of temperature attained AIC figures that were 13.82 units lower than
464 those AIC figures obtained for 95%-quantile null regression models. Solid line represents the
465 linear regression between T_{PREF} and T_{MEAN} .



466

467 **Supplemental Information**

468 **Supplemental Text S1.** Description of the Spanish Bird Atlas of Winter Birds.

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

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