Woodland Mediterranean birds can resist a dry extreme cold wave

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Abstract   The ecological consequences of climate extreme events are still poorly understood, especially those related to cold episodes. Winter cold spells might imperil the energy balance of small passerines, thus compromising their survivorship. Here we analyze how the abundance and habitat use of three tree-gleaning passerine species wintering in a montane oakwood of central Spain at ca. 1,300 m a.s.l. was influenced by the cold wave that hit Europe in February 2012. We monitored temperature, wind and the relative abundance of great tit *Parus major,* blue tit *Cyanistes caeruleus* and long-tailed tit *Aegithalos caudatus* in 15 plots throughout three periods: before, during and after the cold wave. Our results clearly rule out widespread mortality and temporal migration of the studied passerine populations, as the abundance of these species did not diminish during the cold wave. Moreover, the species usually foraging higher in the tree canopy -and thus more exposed to wind- moved to the less windy woodland plots (long-tailed tit) and reduced their foraging height above ground during the cold wave (long-tailed tit and blue tit), probably to mitigate the deleterious effects of wind chill. Therefore, these forest birds were able to cope with a dry cold wave that was statistically extreme in terms of temperature and wind chill, according to the historic climate records of the region. It seems that, at least when foraging substrates are not heavily covered by snow or ice, Mediterranean birds can resist an extreme cold wave [*Current Zoology* 60 (4): 429–437, 2014].

Keywords   Cold wave, Harsh weather, Mediterranean oakwoods, Temperature, Tree-gleaning birds, Wind chill

Assessing the ecological effects of extreme climate events poses a major challenge because of the nature of such events: they are short, rare, not very predictable, and highly dependent on the context. The extremeness of a climatic event must be defined based on the historic climate record, because the ecological response of species may depend on what the population has experienced in the past (Jentsch, 2006; Jentsch et al., 2007; Gutschick et al., 2010; Smith, 2011a, b). The ecological responses to statistically extreme climatic conditions have been approached through both experiments and opportunistic observational studies. A number of experiments show a surprising lack of strong ecological responses (Smith, 2011a and references therein), but sadly negative results are less often reported in observational studies (but see Jiguet et al., 2011). This may reflect a biased motivation of scientists for episodes with obvious ecological responses (e.g., widespread mortality of a species; Smith, 2011a) or difficulties publishing negative results (Fanelli, 2012). However, this research discipline may benefit from combining the results obtained from both extreme events and "normal" natural situations to disentangle the triggers of the responses in each system.

Ecological responses to climate extremes may range from temporal migration of individuals, to population crashes, to long-term changes in community structure or ecosystem function (see reviews of Jiguet et al., 2011 and Smith, 2011b, and references therein). In a global warming scenario, the emphasis is rarely put on extreme cold events (e.g., Jentsch and Beierkuhnlein, 2008; Cattiaux et al., 2013). Nevertheless, severe cold weather might imperil the energy balance of wintering small passerines beyond normal thresholds. At temperate latitudes, birds have to cope with winter temperatures well below their thermoneutral zone (Calder and King, 1974; Kendeigh et al., 1977), and their metabolic costs of thermoregulation increase with decreasing temperatures and increasing wind speeds (eg. Wood and Lustick, 1989; Wolf and Walsberg, 1996; Wolf et al., 2000). Accordingly, these species may select the warmest areas at the landscape scale to overwinter in order to minimize thermoregulation costs (e.g., Canterbury, 2002; Meehan et al., 2004; Evans et al., 2006; La Sorte et al., 2009;


Carrascal et al., 2001; 2012).

Here we analyze the resistance of three resident woodland passerines, with a broad distribution in Europe, facing a cold wave that hit Europe in February 2012, by measuring their changes in abundance, local distribution and habitat use. The studied species do not store food during winter and belong to a tree-gleaning guild of the montane areas of the Iberian Peninsula. We postulate three possible scenarios of population response to this dry extreme cold wave (Fig. 1). First, the cold wave may not negatively affect local abundance of species, because birds present adaptations to cope with severe weather at a local scale (e.g., changes in foraging behavior and habitat use), and these conditions may not be extreme for these species in the context of their total geographic distribution (i.e., similar low winter temperatures in central and northern Europe). In this case, the relative abundance of species may not diminish with the arrival of the cold wave. Second, the cold wave should impose a temporal migration of part of or the whole wintering populations, which would return after the end of the cold wave to their winter territories and restore normal abundance levels. And third, the cold wave could provoke widespread population mortality, so local abundance would decrease during the cold wave but would not recover to reach previous levels afterwards.
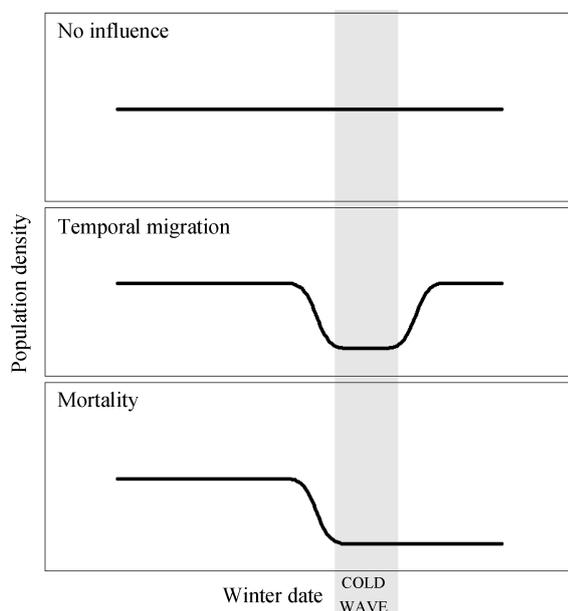
Fig. 1   Three possible scenarios of response of bird populations to the studied cold wave (grey area)
From top to bottom: (1) the cold wave did not affect species abundance at all, (2) it promoted a temporal downslope migration of individuals, or (3) it provoked a widespread mortality of the population. Winter dates go from 1st January to 28th February.

The two last predictions assume that Mediterranean populations present a reduction in the level of adaptation to extreme cold compared with more northern and central Europe populations. To test these hypotheses, we monitored local abundance of birds before, during and after the dry cold wave, measuring the local environmental conditions in terms of temperature, wind speed and wind chill. We also analyzed the environmental determinants of the spatial variation in abundance within the study area during the cold wave, to detect if birds move to the warmer and less windy forest patches to mitigate the deleterious effects of wind chill. Finally, we analyzed whether these species vary their height above ground as a way to behaviorally minimize the effects of wind chill *in situ*.

1   Materials and Methods

1.1   Study area

Field work was conducted in an oakwood located in Navacerrada (40.725°N, 4.033°W; Sierra de Guadarrama, Central Spain). The study area is a ca. 3 km² mosaic of open and dense patches of a monospecific forest of *Quercus pyrenaica* (a marcescent species typical of southwestern Mediterranean mountains), mainly dominated by young trees of 6–14 m. The rugged terrain comprises a high heterogeneity of cardinal orientations, which means a broad variation in sun radiation incidence and in the protection from dominant winds, and thus in microclimate conditions. Altitude ranges between 1,200 and 1,360 m a.s.l. Landscape surrounding the study area within a radius of 20 km is mainly dominated by pine forests of *Pinus sylvestris* and shrublands of *Cistus ladanifer* above 1,300 m a.s.l., and by parklands of holm oak *Quercus rotundifolia* and ash *Fraxinus angustifolia*, pastures and urban areas below 1,200 m a.s.l. The nearest oakwood larger than 1 km² is located 20 km downslope at 960–1100 m a.s.l. Nest boxes have not been available in the whole study area since 2004 (i.e., birds could not make use of artificial roosting places).

The climate is continental cold Mediterranean, with dry and hot summers and abundant snowfall and frost in winter. For more details on vegetation structure, temperature and bird communities of these forests in Central Spain see Seoane et al. (2013).

1.2   Study period

Three study periods were defined: mild-weather period prior to the cold wave (hereafter Before CW; sampled on 3, 9, 10, 11 January 2012), cold wave (CW; 2, 3, 4, 8 February 2012), and mild-weather period after the

cold wave (After CW; 17, 18, 22, 23, 24 February 2012). Our study design ensured that there were no significant differences among plots in average sampling time in the three study periods ($P > 0.96$ in the three one-way ANOVAs).

1.3 Focal species

The focal species were the most abundant of the tree-gleaning guild of the mountainous oakwoods of Central Spain (Carrascal et al., 1987): *Parus major major* (great tit), *Cyanistes caeruleus oligastrae* (blue tit) and *Aegithalos caudatus irbii* (long-tailed tit). They are residents and relatively abundant throughout the winter in the oak forests of the Guadarrama mountains (Carrascal and Díaz, 2006). These small-sized species mainly forage on the twigs and small branches of trees, although they can also use the forest floor for foraging (especially the great tit; Carrascal et al., 1987). The study was centered in these species because passerines foraging in small branches are more severely affected by low temperatures and high wind speed than those foraging on the ground or on the trunks of trees (Grubb, 1975). Moreover, they do not store food, so they rely only on body reserves to overcome severe periods of inclement weather (Perrins, 1979). Other small tree-gleaning species were present in the study area, but were too scarce to obtain a large and representative sample to measure abundance changes among study periods of different weather (lesser spotted woodpecker, *Dendrocopos minor*, nuthatch, *Sitta europaea*, short-toed treecreeper, *Certhia brachydactyla*).

Although these species can experience latitudinal and local altitudinal movements to avoid harsh weather in winter (Perrins, 1979; Cramp, 1998), they are highly sedentary during winter in central Spain according to data obtained from the Spanish Centro de Migración de Aves (http://www.anillamientoseo.org) using ring recoveries obtained during the last 30 years (data for 640 *P. major*, 640 *C. caeruleus* and 247 *A. caudatus* birds recaptured in Madrid province). Only 0.5% of great tits and 1.2% of blue tits were recaptured in different ringing stations located farther than 1 km during the same autumn-winter (December to February), moving a maximum of 22 km and an average of 7.5 km for blue tits ($n=8$) and 10.7 km for great tits ($n=3$). No recoveries of long-tailed tits were made outside the ringing stations within the same autumn-winter period. These data for the three study species in Central Spain are very similar to those recorded in northeastern Iberian Peninsula (Herrando et al., 2011). We think that there is a very remote probability of birds belonging to the three focal species coming to the study area from higher altitudes during the cold spell, considering that (1) these species are almost absent from the nearby *Pinus sylvestris* pine forests found upslope (Carrascal et al., 1987), and (2) there are no deciduous forests at higher altitudes close to our study area (the nearest large oakwood located at higher altitude is 21 km away crossing several ridges of higher altitude).

1.4 Statistical characterization of the cold wave in February 2012

The meteorological characteristics of the cold wave studied here were compared with the daily historical record from the period 1946–2012 (data from the nearby meteorological station in Navacerrada Pass, located at 7 km from the study area, 1894m, AEMET; $n = 24193$ days for temperature data; $n = 18843$ days for wind data). Cold days were defined as those with minimum temperatures below the long-term 5th percentile of daily minimum temperatures, or wind chill temperatures below the long-term 5th percentile of daily wind chill temperatures (analogous to Della-Marta et al. [2007] criterion to define hot days).

The month of February 2012 was the coldest February in Spain since 1956 (i.e., the one with the lowest daily averages of minimum temperatures in 56 years). We focus on a cold wave of 12 days, which included three 'sub-waves' of three consecutive cold days each (with daily minimum temperatures below the long-term 5th percentile of daily minimum temperatures). Three cold days in a row cannot be considered a statistically extreme event in the study area (where the upper 5th percentile of number of consecutive cold days is five). However, temperatures were very low during the whole cold wave and, during this 12-day period, the mean of the minimum (-11.6°C at Navacerrada Pass, 1894 m a.s.l.), average (-8.3°C), and maximum (-5°C) temperatures were all within the lower 5th percentile of historical records (-10°C, -8°C and -5°C, respectively).

During the 12 days, average wind speed was 4.9 m/s (data for 10 days with wind records), which is above the upper quartile of historically-recorded average wind speeds (4.7 m/s). The extreme low temperatures coupled with these relatively strong winds resulted in an average wind chill temperature (WCT; following Osczevski and Bluestein, 2005) of -15.3°C, which is well below the lower historical 5th percentile (-11.7°C). During the cold wave there were at least four cold days in a row considering the WCT (days with WCT below the lower historical 5th percentile). Four cold days considering WCT is a statistical extreme event in the study area

(where the upper 5th percentile of number of consecutive cold days is four). In addition, we sampled during the windiest days of the cold wave, with an average wind speed of 6.4 m/s and an average WCT of -19.7°C. The cold wave in the area was not accompanied by heavy precipitation (average of 5 mm for the 12 days; 1.5 mm for sampling days in Navacerrada Pass). Sun was shining 28% of the time, it was snowing lightly 42% of time, and snow cover and depth on the ground was, on average, 55% and 2.5 cm (measurements obtained during the sampling of woodland plots). Therefore, we consider that it was a relatively dry period.

1.5   Bird censuses, habitat structure and temperature and wind measurements

We measured local bird abundance using point count stations lasting 5 min, recording all birds heard or seen within a 25 m radius (0.19 ha). The census began upon arrival at the center of each plot, and continued following the same protocol in all samples: we walked very slowly within the area of the census plot over an imaginary circumference of radius 12.5 m. By means of this approach we aimed to maximize the detection probability of the birds within the census plot even under windy or snowy circumstances. Thus, our census method does not intend to measure exact bird densities (i.e., birds / ha), but to obtain a measure of habitat use in different woodland plots under different weather conditions. Upon detection of each bird, we also estimated its height above ground as a measure of habitat use. After the census, we walked at a brisk pace in order to reach the following sampling point as soon as possible so as to minimize the probability of sampling the same birds in two consecutive plots (i.e., we moved faster than the study species usually do while moving in the forest).

The two authors carried out the censuses. Fifteen woodland plots of 25 m radius were established within the study area. Plots were separated by at least 250 m. We followed an a priori planned protocol of sequential sampling in order to obtain a completely overlapping distribution of the time of the day when the 15 plots were sampled. To accomplish this goal, we began each sampling day with a different sequence of contiguous plots (e.g., 1, 2, …14, 15; 5, 6, … 15, 1, … 4; etc). Sampling began at 9:00 h and ended at 17:00 h GMT. Four censuses per plot were carried out before the cold wave (Before CW), seven during the cold wave (COLD WAVE) and ten after it (After CW).

Within each census plot, we sampled two vegetation structure variables related to maturity and density of the oakwood plot: average height of trees and number of trunks with a diameter larger than 10 cm at breast level. Average oak height was 10.2 m (range: 6–14; $SD = 2.7$) while average oak density was 146 trees / 0.19 ha (range: 62–303; $SD = 68.9$). All vegetation structure measurements were obtained by the same person within the same sampling day (LMC).

To describe local fine-grained variation in winter air temperatures, one temperature logger (Onset HOBO Pendant, accuracy 0.47°C) was set in each oakwood plot. Loggers were placed on trunks, oriented to the north and at approximately 1.5 m above ground. Data loggers recorded air temperature every 5 min from 01 January to 29 February 2012. Thus, we could link the moment of the census of each woodland plot to the prevailing temperature while sampling (using the nearest temperature record to the time when the census began). Wind speed during the census was measured as the average of two wind measurements obtained with a portable handheld meter during 30 seconds (Ventix Thermo-Anemometer 8908); one 30 seconds before the beginning of the census, and another immediately after the end of the 5 min census. For each 30-sec sampling period we obtained the maximum registered wind speed.

1.6   Data analyses

Due to logistic limitations we could not mark the study population for individual identification. However, we estimate that our study area of ca. 3 km² may host several hundred individuals of each species, considering that the average abundance of the studied species ranges from 8.3 to 14.5 birds/ 10 ha^{-1} in the oakwoods of Central Spain (Carrascal and Díaz, 2006). This high number of birds reduces, although it does not eliminate, the risk of pseudo-replication, and thus type I error inflation. Therefore, we built null statistical distributions using Monte Carlo analyses to estimate proper significance levels in data analyses (Davison and Hinkley, 2007).

To test the hypotheses in Fig. 1, local abundance of birds before the cold wave (B-CW), during the cold wave (CW) and after it (A-CW) were compared using t-tests. First, we obtained the t-test statistics for each species comparing the averages of the 15 woodland plots in B-CW vs. CW, and in CW vs. A-CW. Second, a randomization process was carried out maintaining the data within each plot (i.e., the values of the average number of birds recorded in [B-CW / CW] and [CW / A-CW]). The aim of this randomization procedure was to preserve the spatial structure of the data, accounting for the spatial autocorrelation of the data and for the possible pseudoreplication derived from the fact that the same individual bird may be present in more than one

woodland plot on different days. Third, the *t*-tests were carried out considering the randomized data for each species in the B-CW *vs*. CW, and CW *vs*. A-CW comparisons, thus obtaining a null t statistic; this process was repeated 9,999 times. And fourth, the actual figures of the *t* statistic testing B-CW *vs*. CW, and CW *vs*. A-CW were compared with 9,999 null t values obtained. Significance of *t*-tests was estimated considering the position of these true t statistics within the null distribution of *t* figures, by means of the percentiles using a two-tailed approach.

We also analyzed the environmental determinants of the spatial variation in abundance within the study area during the cold wave to detect if individuals move to the warmer and less windy forest patches to mitigate the deleterious effects of the cold wave. The influence of temperature, maximum wind speed and habitat variables on bird habitat use during the cold weather period was analyzed by means of multiple regression. Average number of birds per woodland plot was the response variable, while average temperature, maximum wind speed, oak height and oak density were the predictors. A multiple regression was carried out with the data for each species separately. The significance of partial regression coefficients was estimated by means of Monte Carlo analyses. A randomization process was carried out bootstrapping the data on bird abundance for each plot. With the bootstrapped data, the same multiple regression analyses (one per species) were carried out, obtaining null partial regression coefficients; this process was repeated 9,999 times. The actual figures of the partial regression coefficients were compared with the 9,999 null values obtained. Significance of partial regression coefficients were estimated considering the position of the true coefficients within the null distribution by means of the percentiles using a two-tailed approach. Analyses were carried out using the Resampling and Monte Carlo functions of «Pop Tools 3.0» (http://www.cse.csiro.au/poptools/) within MicroSoft-Excel 2010.

2   Results

2.1   Temperature and wind at sampling plots

Temperature measured locally during sampling at the 15 woodland plots fell an average of 12.9°C (from 9.1°C to -3.8°C) from the previous mild-weather to the cold wave period (Fig. 2). After the cold wave it raised 14.2°C to reach an average of 10.4°C. Wind speed increased an average of 4.21 m s^{-1} (from 0.83 m s^{-1} to 5.04 m s^{-1}) from the previous mild-weather period to the cold

wave period, and decreased a similar amount after the cold wave to an average of 1.13 m s^{-1}.

The cold wave reduced the spatial variation in the average temperatures among woodland plots (i.e., difference between the warmest and the coldest plots), from a range of 5.6°C in the previous mild-weather sampling period to 2.7°C during the cold wave. Nevertheless, the variation in average wind speed among plots was higher during the cold wave: the range between the windiest and the least windy plot increased from 0.96 m s^{-1} in the previous mild-weather sampling period to 4.46 m s^{-1} during the cold wave. Nearly identical results are obtained comparing the spatial heterogeneity in temperature and wind speed between the cold wave period and the posterior "normal" period (not presented for the sake of brevity).
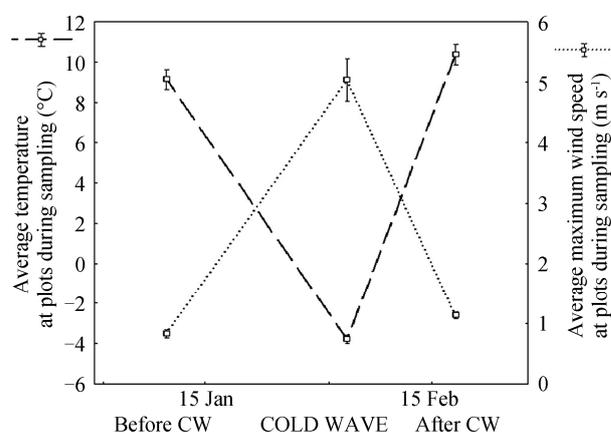
Fig. 2   Changes in temperature and wind speed during the cold wave, compared with previous and post-sampling periods (average ± one standard error)
Temperature (°C) and maximum wind speed (m·s^{-1}) were registered on several occasions during sampling and averaged per plot and sampling period (see Methods). Sample size is 15 plots. X-axis shows the average sampling date of each period.

2.2   Temporal and spatial variation in relative abundance of birds regarding the cold wave

The relative abundance of the three species during the cold wave did not change with respect to previous mild conditions. However, bird abundance increased after the cold wave for all species, reaching statistical significance for blue and great tits (Fig. 3 and Table 1).

Habitat use by *A. caudatus* and *C. caeruleus* changed significantly during the cold wave (Table 2). Both species forage at lower positions in the vertical axis of the forest, by reducing by one half the average height above ground during the normal periods. The height above ground of *P. major* during mild winter conditions was

much lower than that of the other species, and did not significantly change during the cold wave.

The spatial variation of abundance within the forest during the cold wave was not tightly related to local temperature or wind speed, after controlling for habitat structure regarding oak height and density (Table 3). Only the relative abundance of the long-tailed tit was significantly and negatively affected by wind speed; i.e., the long-tailed tit preferred woodland areas with lower
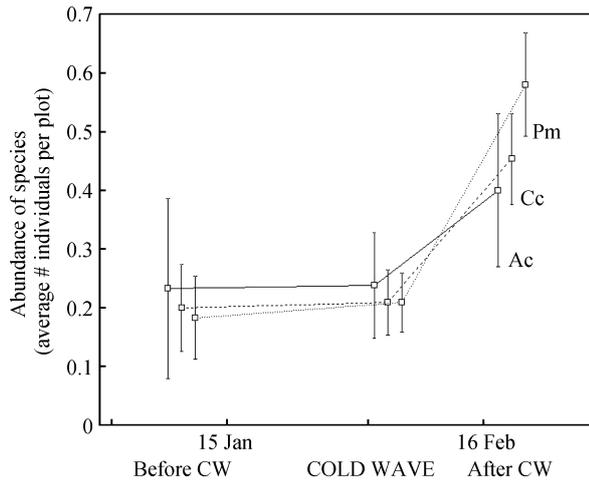
Fig. 3 Abundance of birds during the cold wave, compared with previous and post-sampling periods
Abundance measures the average number of individuals (± one SE) of *Aegithalos caudatus* (Ac), *Cyanistes caeruleus* (Cc) and *Parus major* (Pm) found in censuses of 5 min in 15 plots of 0.19 ha. Sample size is 15 plots. X-axis shows the average sampling date of each period.

wind speed. Vegetation structure had no significant partial effects on bird abundance, probably due to the low maturity of the studied oakwood (see Methods) and the relatively low heterogeneity of oak height (coefficient of variation, CV = 26.5%) and oak density (CV = 47.2%).

Table 1 Average changes in the abundance of the three species between periods

	Before CW - CW		CW - After CW	
	Difference	*P*	Difference	*P*
Aegithalos caudatus	0.00	0.929	0.16	0.173
Cyanistes caeruleus	0.01	0.947	0.24	0.003
Parus major	0.03	0.660	0.37	<0.001

Positive figures are increases in abundance. Before CW: Mild-weather period prior to the cold wave; CW: Cold wave; After CW: Mild-weather period after the cold wave. P-values correspond to two-tailed *t* tests. See also Fig. 3.

3 Discussion

Woodland Mediterranean birds were able to cope with a winter dry cold spell that was statistically extreme in terms of the historical climate records of the region according to measurements of temperature, wind speed or wind chill. Our results clearly rule out widespread mortality and temporal migration of the studied passerine populations and emphasize the winter residency of blue, great and long-tailed tits in Mediterranean oakwoods (Tellería et al., 1999).

Table 2 Bird height above ground (m) during the cold wave and during the normal winter periods (i.e., "Before CW" plus "After CW")

	COLD WAVE			MILD WINTER			Z	P
	n	mean	SD	*n*	mean	SD		
Aegithalos caudatus	12	3.5	2.7	25	6.4	3.8	2.450	0.014
Cyanistes caeruleus	24	4.0	2.6	46	7.5	4.3	3.613	<0.001
Parus major	31	2.6	2.5	50	2.9	2.6	0.763	0.445

Sample sizes (*n*) refer to different foraging birds (one sample per bird and per plot). Z and P: results from Mann-Whitney *U* tests.

Table 3 Regression model on the influence of environmental factors on the abundance of *Aegithalos caudatus*, *Cyanistes caeruleus* and *Parus major* during the cold wave

	A. caudatus		*C. caeruleus*		*P. major*	
	b	*P*	*b*	*R*	*b*	*P*
Tree height	0.004	0.916	0.020	0.429	0.017	0.432
# trees > 10 cm dbh	0.001	0.666	0.001	0.137	0.001	0.144
Average temperature (°C)	-0.013	0.934	-0.076	0.448	0.065	0.478
imum wind speed (m s⁻¹)	-0.176	0.045	-0.048	0.398	-0.009	0.854

Figures are partial regression coefficients (*b*) of tree height, density of trees with dbh > 10 cm, average temperature and maximum wind speed. *P*-values are two-tailed tests; significant tests are in bold type.

Populations may have a high ability to surpass periodic extreme events of cold weather, especially in habitats subjected to very high seasonal climatic fluctuations like the Mediterranean (average temperatures from 22°C in summer to -5°C in winter in Iberian oakwoods of *Quercus pyrenaica*; Costa et al., 1998). Moreover, cold spells might be less damaging in the southern part of the distribution range of these Palearctic species, where the extended day length, the milder average temperatures and the higher food availability may facilitate survivorship with respect to higher latitudes (Root, 1988, 2000).

Certain combinations of climate extremes might be necessary to evoke more extreme ecological responses than those found here (Smith, 2011b). In this study, a dry cold spell characterized by extreme low temperatures and strong wind speeds on a regional basis, and a low amount of precipitation, was not enough to trigger a decrease in species abundance derived from temporal migration or mortality. Snow cover and ice impede access to ground resources, and, under freezing temperatures, water from mist, rain or snow adhere to branches impeding access to food (Brotons, 1997; Nakamura and Shindo, 2001). Robinson et al. (2007) found that the consecutive number of snow days and cold-wet days were the variables most affecting survival of British Great and Blue tits, respectively. Moreover, Carrascal (1988) found that a winter snow storm provoked a significant decrease in the abundance and species richness of the avian community of a subalpine pinewood located in the same region, where a very broad altitudinal gradient of continuous pinewoods let the birds migrate to lower altitudes. Although environmental temperatures in the Carrascal (1988) study were considerably higher than those registered in this study (average of -0.5°C vs -3.8°C, in the cold wave period of our study), there was a complete coverage of snow and ice on the ground, bushes and trees, which may have triggered the temporal migration of most branch- and foliage-gleaning birds along the altitudinal gradient of the mountain range. Nevertheless, snow cover and thickness was low in our study and ice crust did not affect the branches of the oaks in a generalized and widespread way. The comparison of these two studies (very cold, windy and relatively dry weather vs. widespread cover of a thick layer of snow and ice-crust with less cold temperatures) points out that the role of temperature will be of lower importance considering that birds can withstand severe cold periods if enough food is available and its access is not completely limited (Newton, 1980; Jenni, 1987).

The significant increase in abundance shown from the cold wave to the following milder period is an unexpected result impossible to explain according to the highly improbable migration of the studied species from the mountain scrublands and pineforests located at higher altitudes where these species are very scarce or absent (Carrascal et al., 1987, 2002). The increase in abundance of the three focal species immediately after the cold spell may reflect the steady increase in population abundance usually registered in these forests towards the following breeding season. At these latitudes, an important proportion of resident woodland birds inhabiting mountain areas move to lower areas at the beginning of the autumn to spend the winter under milder winter conditions, and move back upslope to their breeding grounds at the end of winter (Cramp, 1998). This pattern of local movements from higher altitudes to lower altitudes in mountain areas at the beginning of the autumn, and from woodlands in valleys to high altitude forests, is probably responsible for the seasonal changes in bird abundance in Central Spain (e.g., Sánchez 1991), and is the most parsimonious explanation for the steady increase in the abundance of tits in the study region from midwinter as spring approaches (O. Gordo, J. J. Sanz and L. M. Carrascal pers. obs.). Early residence in future breeding grounds may promote an early laying date, which is usually related to reproductive success (Norris, 1993), as later clutches tend to be smaller, and earlier-fledged young tend to be heavier and have higher recruitment probabilities (e.g., Verboven and Visser, 1998; Potti, 2009). In this context, the cold wave could have meant a temporal slowdown of this steady increase in abundance, because bird numbers remained unchanged between the cold spell and the prior normal periods (see Table 1).

The harshness of a cold spell can be lessened by a temporal migration towards lower altitudes with ameliorated weather conditions (Perrins 1979). In this case, birds could have moved to small deciduous forest patches, parklands and villages found 100–300 m below. However, we found no evidence of such altitudinal migration. Escaping to unknown areas implies a high risk considering the energy investment on small-scale migration, and the uncertainty related to weather conditions, the availability of food resources and competition with resident birds at the new areas (Senar and Borrás, 2004). These disadvantages may have prevented resident birds from moving away from their regular foraging areas. Future studies with marked individuals would help to further understand to what extent resident woodland birds move when facing unexpected short

periods of inclement weather.

Alternatively, the three study species may have resisted the cold wave by ameliorating the negative consequences of the harsh weather *in situ* through various behavioral strategies. First, birds may selectively move locally within the forest area, searching for woodland patches where the topography and the vegetation offer higher temperatures and a greater shelter from wind (Grubb, 1977; Petit, 1989; Dolby and Grubb, 1999). We indeed found that the long-tailed tit, the species that mainly forages in the most pliable substrates of deciduous trees (Carrascal et al., 1987), avoided the windiest plots during the cold wave (Table 3), although this search for locally milder weather conditions was not shown by the other two tit species (that make an intense use of the inner parts of the oaks and even forage on the ground). One explanation for the very low importance of local movements seeking better thermal conditions is that temperature and wind conditions were much homogenized throughout the study area during the cold wave, limiting the potential benefit of spatial redistribution. This, together with the uncertainties of displacements to other locations where competition with other resident birds may increase, might prevent the role of local movements in escaping from severe weather conditions. On the other hand, birds may have buffered the deleterious effects of wind chill locally by changing their foraging behavior, shifting to more sheltered, lower and inner parts of trees (Grubb, 1975; 1977; see Carrascal, 1987 for forests in Central Spain). Indeed we found that the two species that mainly forage at higher parts within trees, and thus are more exposed to wind (i.e., *A. caudatus* and *C. caeruleus*), reduced their average height above ground during the cold wave to almost half the height under normal circumstances (Table 2).

In summary, birds wintering in a montane forest of cold Mediterranean climate were able to resist an extreme dry cold wave, and showed no evidence of migration or widespread local mortality. They probably buffered the deleterious effect of wind chill by moving to the most protected forest patches and by reducing their foraging height within the tree canopy.

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