Citril finches during the winter: patterns of distribution, the role of pines and implications for the conservation of the species


Abstract
Citril finches during the winter: patterns of distribution, the role of pines and implications for the conservation of the species.—The Citril finch Serinus citrinella is a Palearctic endemic species that breeds in the subalpine mountain zones of western temperate Europe. The species seems to be suffering a serious decline in its northern range, mainly in the Black Forest and the NE of the Alps. Numerous reasons have been provided for this decline, but all of them have been related to breeding habitats. Given that the species undergoes an altitudinal migration and that during winter it may use very different habitats, a sound knowledge of the distribution patterns and habitats used outside the breeding period is needed to conduct adequate conservation policies and management. This information, however, is largely lacking. The aim of this paper was to determine the current habitat used by Citril finches in north–eastern Spain during the winter, to analyse habitat suitability and to study movements, by investigating the origin of birds that overwinter in Catalonia. Citril finch distribution was modelled using both discriminant analysis and maximum entropy modelling, on the basis of species occurrences during winter in Catalonia (data from 1972–2009). Results showed that the presence of two tree species, Black pine (Pinus nigra subsp. salzmannii) and Scots pine (Pinus sylvestris), both as part of mixed open forests, and the presence of abundant farmland and arvensic plants—the two vegetation units located in a typical submediterranean context, where the warm temperatures (sunny days) in late winter permit the cones to open—, were the ecological and bioclimatic variables that explain the distribution model. All these variables in tandem seem to be the key for the current potential distribution of the Citril finch in winter (AUC scores: training data AUC = 0.955; test data AUC = 0.953). We analyzed recoveries (N = 238) of 2,368 birds ringed at wintering grounds and 12,648 birds ringed at subalpine localities in the adjacent Pyrenees from 1977–2004. We found that in the study area, we recovered ringed birds from many different locations from across the distributional range of the species, including trans–Pyrenean birds from the Alps. This stresses the high mobility of Citril finch populations to reach wintering areas. From a conservation point of view, the high importance of pines (mainly Black pine) for the wintering distribution of the species stresses that any threat on pines, especially forest fires, will have acute detrimental effects for Citril finch populations.

Key words: Citril finch, Wintering, Habitat selection, Habitat suitability, Movements, Conservation, Black pine, Scots pine.

Resumen
El verderón serrano en invierno: patrones de distribución, el papel de los pinos e implicaciones para la conservación de la especie.—El verderón serrano (Serinus citrinella) es una especie palearcítica endémica que cría en zonas montañosas subalpinas de la Europa occidental templada. Esta especie parece que está sufriendo un gran declive en su área de distribución septentrional, principalmente en la Selva Negra y en el NE de los Alpes. Se han propuesto muchas razones para dicha disminución, pero todas ellas estaban relacionadas con los hábitats de cría. Dado que esta especie lleva a cabo una migración altitudinal, y que durante el invierno puede utilizar hábitats muy distintos, se precisaría un buen conocimiento de los patrones de distribución y de los hábitats utilizados fuera del período reproductor, para poder establecer unas directrices de conservación y gestión adecuadas. Sin embargo, esta información es muy escasa. El propósito de este estudio es determinar...
el hábitat común utilizado por los verderones serranos en en nordeste de España durante el invierno, para analizar la idoneidad del hábitat, y estudiar los movimientos, investigando el origen de la aves que invernan en Cataluña. La distribución se modelizó utilizando el análisis discriminante y la modelización de entropía máxima con los datos registrados desde 1972 al 2009 sobre la presencia de esta especie durante el invierno en Cataluña. Los resultados evidenciaron que la presencia de bosques abiertos mixtos de pino negral (Pinus nigra subsp. salzmannii) y pino silvestre o albar (Pinus sylvestris), con numerosas tierras de cultivo y plantas arvenses, en áreas submediterráneas típicas en las que las temperaturas templadas de finales de invierno (días soleados) facilitan la apertura de las piñas, fueron las variables ecológicas y bioclimáticas claves responsables de la distribución del verderón serrano en invierno (valores AUC o área bajo la curva: datos de entrenamiento AUC = 0,955; datos del test AUC = 0,953). Análizamos las recuperaciones (N = 238) de 2.368 aves anilladas en las áreas de invernada y 12.648 aves anilladas en localizaciones subalpinas en los Pirineos adyacentes, desde 1977 al 2004. Los resultados de los datos de recuperación de anillas muestran que en el área de estudio se capturaron aves procedentes de muy diversas localizaciones dentro del área de distribución de la especie estudiada, incluyendo aves transpirenaicas procedentes de los Alpes. Ello enfatiza la gran movilidad de las poblaciones del verderón serrano hasta alcanzar las áreas de invernada. Desde el punto de vista de la conservación, la gran importancia de los pinos (principalmente del negral) para la distribución invernal de esta especie pone de manifiesto que cualquier amenaza para los pinos, especialmente los incendios forestales, tendrá grandes efectos adversos sobre las poblaciones del verderón serrano.

Palabras clave: Verderón serrano, Invernada, Selección del hábitat, Idoneidad del hábitat, Desplazamientos, Conservación, Pino negral, Pino silvestre, Pino albar.

(Rebut: 3 V 10; Acceptació condicional: 17 V 10; Acceptacio definitiva: 31 V 10)


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Introduction

The Citril finch *Serinus citrinella* is a Paleartic endemic species that breeds in the subalpine mountain zones of western temperate Europe (Cramp & Perrins, 1994). The status of the species differs considerably throughout its distributional range. While the species seems to be increasing in its southern range (NW and NE of Spain (Borras et al., 2005b; Borras & Senar, 2003), it is suffering a serious decline in the northern range, mainly in the Black Forest (Förschler, 2007) and the NE of the Alps (Bezzel & Brandl, 1988; Mattes & Maurizio, 2005), and predictive models suggest a general decline of the species in the next 100 years (Huntley et al., 2008).

The reasons for this decline are mainly related to changes in land use, basically the loss of pastures due to extensive reforestation and a reduction in cattle transhumance (Förschler, 2007). An additional factor is related to changes in the management of ski areas where typical flower–rich meadows, heavily used as a food source by the species (Borras et al., 2003b), are destroyed to allow a better retention of snow (Bezzel & Brandl, 1988; Rolando et al., 2007).

However, all these factors are related to changes in breeding habitats. It is currently widely recognised that a good understanding of the conservation priorities of a species necessarily needs a good knowledge of the habitat requirements during the winter period and the movements that the species undertakes to reach these areas (Dolman & Sutherland, 1995). This approach has recently been applied to the conservation of long–distance migrants (Martin et al., 2007; Robbins et al., 1989), but it is clear that this should be used in any species in which there is an acute change in habitat use between seasons. This is the case of the Citril finch. The species typically breeds in subalpine coniferous forests (*Pinus uncinata* Ramond ex DC.) from 1,500 m a.s.l. to treeline (Borras & Senar, 2003), foraging on pine and meadow seeds (Borras et al., 2003b). By autumn, snowfalls force birds to undertake a vertical migration to lowlands (300–1200 m a.s.l.). Although the distance of the move is generally short, compared to true migrants, the shift is linked to an important change in habitat use. In autumn and winter Citril finches inhabit farmland and fragmented coniferous forests (*Pinus nigra* J. F. Arnold subsp. *salzmannii* (Dunal) Franco and *Pinus sylvestris* L.) (Borras & Junyent, 1993) and forage on ruderal and arvensic plants, with a shift to pine seeds by the end of winter (Borras et al., 2003b).

Nevertheless, and in spite of the general picture we have presented, the knowledge we have on the wintering habits and habitats of the Citril finch is very sparse. Some information is available on the movements of Citril finches from France, Switzerland and Germany wintering in mountainous areas of southern France (mostly to the east of Cévennes and to the south of Mont Ventoux) (Bezzel & Brandl, 1988; Cramp & Perrins, 1994; Dejonghe, 1991; Märki, 1976; Zink & Bairlein, 1995). However, information on Citril finch movements in other areas during this period is poorly known. This information is even scarcer for the Iberian population, where in fact the species has the highest densities (Baccetti & Märki, 1997). Nearly 90% of the total world population breeds in Spain (Baccetti & Märki, 1997) and seven breeding nuclei can be distinguished herein (fig. 1) (Borras & Senar, 2003).

The aim of this paper was to determine the current habitat used by Citril finches to winter in north–eastern Spain, as well as their habitat suitability, and to analyse the origin of these birds on the basis of capture–recapture data. This information is used to delineate conservation practices to be undertaken to preserve wintering habitats. The Citril finch may be an ideal model species in this respect because of the interaction between annual biological cycles based on two very different habitats which are differently affected by human activity, land use practices and climatic changes.

Material and methods

Study area

The study was carried out in Catalonia, a region of 31,900 km² located in the north–eastern Mediterranean coast of Spain. The relief is highly variable, from sea level to 3,143 m in the Pyrenees, and environmental conditions experiment Mediterranean, Atlantic and even Saharan climatological influences (Ferrer et al., 2006). Rainfall decreases and average temperature increases southwards. A climate gradient is present: on the eastern coast, there is a moist temperate climate, while inland there is a dry continental climate (Ferrer et al., 2006). This high environmental variability of Catalonia climate allows for a better discrimination of variables related to species distribution.

Mapping of Citril finch winter distribution

The location of wintering localities was based on: (1) an exhaustive screening of local publications. References relevant to map Citril finch distribution appear in the appendix; (2) a mailing to ornithologists in Catalonia asking them to report observations about Citril finch wintering; (3) a historical data base (1973–1977) maintained at the Natural History Museum of Barcelona and now managed by Xavier Ferrer; (4) surveys carried out by the authors from 1972 to 2009, focused on the counties of Bages, Bergedà, Solsones, Cerdanya and Alt Urgell. All the data were mapped in standard 10 x 10 km UTM squares. We considered records obtained from October to April attained that the species typically breeds high in the mountains (> 1,800 m a.s.l.) and favorable breeding conditions there are delayed in comparison to other areas, so that the birds remain in lower localities for more extended periods. We considered records as concerning "wintering" birds only when they referred to altitudes < 1,500 m a.s.l.; hence involving only areas outside the typical subalpine breeding areas. Subalpine areas may be occasionally used in winter, but this is highly dependent on favourable meteoro-
 logical conditions, absence of snow and presence of a good pine crop. However, given the irregularity of such presence and the low density of populations in these areas, we decided not to include these data in analyses. We determined that a square showed a consistent wintering appearance when we had more than five records per square over the whole period 1972–2009, denoting a consistent use of the area to winter.

**Discriminant analysis of Citril finch environmental requirements**

We used discriminant analysis (Venables & Ripley, 2002) as a preliminary approach to identify main variables favouring the presence (vs. absence) of wintering Citril finches. As a dependent variable we used the presence/absence of Citril finches in the 10 × 10 km UTM grid of Catalonia, taking as “presence” only squares with more than five observations of the Citril finch over the whole study period (see above). As independent variables, we used data on the relative abundance (ha of occupation) of *Pinus nigra* and *Pinus sylvestris*, mapped in standard 10 × 10 km UTM squares. This was obtained from the cartographic databases of Catalan habitats (E: 1:50,000), Department of Environmental and Housing, Catalan Government. Independent variables concerning geographical position, climate, topography, geology and land-use in Catalonia (i.e., independent variables) were obtained from Ferrer et al. (2006), mapped for the UTM 10 × 10 km grid.

Although discriminant analysis provides a first approach to key variables related to the distribution of a species, the drawback of this analysis is that it assumes a linear response function (Franklin, 2009). Additionally, given the secretive habits of Citril finches and their difficult detection, and as one of our aims was to identify and model overall suitable areas for the wintering of the species, we additionally used the presence-only data model of maximum entropy modelling (Franklin, 2009; Phillips et al., 2006; Phillips & Dudík, 2008) (see below).

**Citril finch distribution model (maximum entropy modelling)**

The species distribution models (SDMs) can be used to predict potential distributional patterns for a given species (Guisan & Thuiller, 2005; Franklin, 2009). An SDM represents an approximation of a species' ecological niche in the environmental dimension being examined, and translated into the geographic space. Based on the environmental conditions of the sites of known occurrence, these models constitute valuable tools for analytical biology (Peterson et al., 1999). Such projections assume that a species is in equilibrium with its environmental requirements—that is, its distribution is determined primarily by the environment, and not by other factors such as competition or dispersal limitation.

In the present study, Citril finch distribution was modelled, first calibrating the model for its current distributions in relation to presence/absence and land cover vegetation mapping (six independent variables), and then adjusting it with the above variables as well as the present topo-climatic Catalonian characteristics (sixteen independent variables).

**Citril finch records**

The spatial resolution of available Citril finch records referred to the UTM 10 × 10 km grid. However this biological information extracted from the database was not directly used for the analyses; instead, we proceeded to perform a resample analysis (nearest neighbour method), so that the original resolution was interpolated to 1 km². This procedure had the advantage of producing data at a resolution relevant to the spatial scale of analysis, especially for Pyrenees where the local climate/vegetation can differ sharply in the corresponding grid box of the models.

A conditional sampling was then used, under the rule of thumb of selecting the closest to the centroid of the UTM cell, in order to locate and select records of *Serinus citrinella* presence in all of the pixels that complied with both an altitude ranging between 500 to 1,200 m, and aspect ranging between W to E, i.e., the two main variables that determine, *a priori*, the winter distribution of the Citril finch. In total, 1,273 records of *Serinus citrinella* were randomly sampled on the raster dataset, ensuring a minimum distance of 2 km between points to avoid sample autocorrelation effects. The dataset was randomly split; 75% was used to calibrate the algorithm MaxEnt (see below), and 25% to evaluate the resulting SDMs.

**Environmental variables**

A total of sixteen variables were used as predictors to calibrate SDMs for the Citril finch, all of which had a spatial correlation degree lower than 0.75 (Pearson coefficient).

The Spanish national forest inventory (IFN2) (1:50,000) was the cartographic base used to estimate the current range of coniferous forests in Catalonia ([http://www.mma.es](http://www.mma.es)). The strata unit was the map information shown (see fig. 1). Based on the mapping information described above, four variables (presence/absence) were derived. The first three variables corresponded to pure forest, with one species constituting up to 70% or more of the total number of trees. These three variables were called: (i) Pnigra; (ii) Psylvestris; and (iii) Puncinata. The fourth variable represented forest that showed varying degrees of presence of trees such as *Pinus nigra*, *P. sylvestris* and even *P. uncinata* or deciduous trees; it was therefore named: (iv) mixed conifer forest.

The land-cover percentages used were obtained from the Moderate-resolution Imaging Spectroradiometer (MODIS) 44B Global 500 m ISIN Grid data set ([http://modis.gsfc.nasa.gov](http://modis.gsfc.nasa.gov/)). In the present study we used the 1 km-resolution; each grid (1 × 1 km) was described as a percent mixture of several vegetation-cover categories, including woody cover percent and herbaceous cover percent. The vari-
ables were called (v) MODIS tree and (vi) MODIS herb, respectively. The MODIS land cover was very successful at mapping extensive cover types (e.g. coniferous forest and grasslands) that typically occur in patches that are smaller than the MODIS pixels, but are reported to be very important to biodiversity conservation.

Apart from the variables related to vegetation, ten topo–climatic predictive variables were used. Five of them represented resource gradients (sensu Austin et al., 1984): (vii) annual precipitation, Pann; (viii) precipitation of the driest month, Pmin; (ix) precipitation of the wettest month, Pmax; (x) maximum annual solar radiation, Rmax; and (xi) minimum annual solar radiation, Rmin. Three other variables refer to direct gradients: (xii) maximum temperature of the hottest month, Tmax; (xiii) minimum temperature of the coldest month, Tmin; and (xiv) annual temperature, Tann. The last two correspond to indirect gradients: (xv) topographic exposure; and (xvi) topographic wetness index, TWI. These latter two variables, derived from the digital elevation model (DEM), are capable of reproducing the physiological role of certain resources (Guisan & Zimmermann, 2000). Climate data (1950–1999) were drawn from the Digital Climatic Atlas of the Iberian peninsula (Ninyerola et al., 2005). The topographic data came from Shuttle Radar Topography Mission (SRTM) [http://srtm.csi.cgiar.org] and were from 90 m to 1 km [1,162 x 899 cells, Universal Transverse Mercator (UTM) projection, European datum 1950 (ED50)]. The GRASS–GIS software (Grass Development Team, 2008) was used to provide the geographical framework.

Modelling algorithm: MaxEnt

MaxEnt (Maximum entropy) modelling of species geographic distributions; (Phillips et al., 2006; Phillips & Dudik, 2008) is an algorithm specifically designed to calculate the potential geographic distribution of a species. It combines artificial intelligence (Machine Learning) and the Principle of Maximum Entropy (Jaynes, 1957), and thus, out of the wide range of possible modelling algorithms, provides one of the most accurate predictions (Elith et al., 2006). MaxEnt estimates the probability of the presence of any species, determining the maximum entropy distribution (the closest to uniformity) from a set of records of the presence of a taxon and from digital cartography of environmental variables, which influence the species distribution (Phillips et al., 2006).

Model calibration and evaluation

A cumulative output format was chosen to determine the potential Citril finch distribution. This output represents habitat suitability with continuous values [0, 100]
Borras et al. (Phillips & Dudik, 2008). The algorithm parameters fixed to calibrate the SDMs were stricter than those recommended by Phillips et al. (2006). The SDMs were evaluated by the area under the ROC curve (AUC) test provided by the MaxEnt software using a random data–splitting approach to establish an evaluation dataset (25% of the entire presence dataset) for Serinus citrinella.

Habitat–suitability maps

The MaxEnt algorithm produced maps of habitat–suitability for the Citril finch. Maps derived from MaxEnt algorithm yield values that vary from 0 (minimum habitat quality) to 100 (maximum). These scores were reclassified into four classes of suitability, based on Chefaoui et al. (2005): very low habitat suitability (0–25); low habitat suitability (26–50); high habitat suitability (51–75); very high habitat suitability (76–100).

Capture–recapture of birds wintering in central Catalonia

Data are based on the analyses of recaptures from a total of 12,648 birds ringed at alpine localities and 2,368 birds ringed at wintering grounds from 1977–2004. However, when analysing long distance recoveries, we additionally used more recent data (up to June of 2010). Birds were trapped using mist nets associated to drinking vessels or natural food resources, and also using live decoys. We routinely trapped birds at subalpine areas in the counties of Solsones, Berguedà, Cerdanya and Alt Urgell from April to November (see (Borras et al., 1998; Borras et al., 2003a; Senar et al., 2002 for details). The main capture localities during the breeding season included Bofia, Vansa and Cap del Rec (fig. 2). Birds at wintering localities were trapped in the counties of Solsonés, Bergueda, Bages, Alt Urgell and Anoia, with a total of 49 localities (fig. 2).

Results

Overall winter distribution

The distribution of Citril finch records during the winter (from October to the end of April) in Catalonia spread over two main areas: a central area located in Solsonès, Alt Urgell, Bages and Berguedà regions, with many observations, and a coastal–prelitoral area, with occasional observations but a consistent pattern, most recorded in October. A few scattered observations were also recorded in western Catalonia (fig. 3).

Modelling Citril finch distribution based on discriminant analyses

Taking localities with a consistent Citril finch winter presence (≥ 5 observations from 1972–2009), the presence of the species was highly related to the presence of Black pine, and to a lesser extent, of Scots pine (table 1, fig. 4). These two variables allowed a correct discrimination on the presence of the species in 93% of cases (Wilks’ Lambda: 0.68001; $F_{2,357} = 83.995; p < 0.0001$). The other variables considered (see table 1) did not add any significant information on the wintering distribution of Citril finches. However, this analysis performed much better in discriminating where the Citril finch should not appear (96% of correct discriminations) than in identifying
where the species should be present (45% of correct discriminations).

Modelling Citril finch distribution based on MaxEnt analysis

The first Citril finch distribution model (Model 1) was modelled only with the vegetation data (see fig. 5). The graphical plot of SDM sensitivity shows that AUC scores were high (Model 1: training data AUC = 0.776; test data AUC = 0.789) (fig. 6). The heuristic estimate of relative contributions of the vegetation variables to the MaxEnt model (table 2) showed that the most important variable to predict occurrence of wintering citril finches was the presence of mixed conifer forests (*Pinus nigra* and *P. sylvestris*) (fig. 7). The contribution of pure conifer forests, consisting of the species mentioned earlier, was also important for the model distribution (fig. 7). However, analyses also stressed the importance of open habitat availability (high scores for woody and herbaceous cover percent variables), so that highly dense forest masses were avoided (table 2, fig. 7). The habitat–suitability map based on this model (Model 1, fig. 8) displays the typical wintering area where the species has been regularly observed, but also areas where the species only appears on a very irregular basis (compare figures 3 and 8).

The second Citril finch distribution model (Model 2) was modelled using topo–climatic variables in addition to vegetation variables. The goodness of fit for this second model was very high (Model 2: training data AUC = 0.955; test data AUC = 0.953) (fig. 9). Annual temperature (Tann) and precipitation during the driest month (Pmin) were the two main variables explaining the distribution of the Citril finch during the winter (table 2). Response curves showed that the species favours a warm temperate climate with occasional (30 mm) rain during the summer (fig. 10). Vegetation variables also had some relative contribution to the model (table 2). The habitat–suitability map based on this model had a high overlap with the observed distribution of the species (Model 2, fig. 11). The only two 10 x 10 km squares where the species has been regularly recorded but the model does not display presence (southeast corner) correspond to areas with largely urbanized landscape or large plains with a high thermic inversion; the species appears here only on the edge of the squares.
Table 1. Results from the discriminant analysis to identify variables that explain the distribution of the Citril finch in winter. Variables are ordered by their contribution to explain Citril finch distribution. The abundance of the different vegetation types and land uses refers to the relative extension of each vegetation and land use within each UTM square. For details on each variable see Ferrer et al. (2006).

<table>
<thead>
<tr>
<th>Variable</th>
<th>r</th>
<th>p</th>
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<tbody>
<tr>
<td>Black pine abundance</td>
<td>0.89</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Scots pine abundance</td>
<td>0.46</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Average temperature January</td>
<td>-0.27</td>
<td>ns</td>
</tr>
<tr>
<td>Urban area presence</td>
<td>-0.21</td>
<td>ns</td>
</tr>
<tr>
<td>Farmland presence</td>
<td>-0.17</td>
<td>ns</td>
</tr>
<tr>
<td>Irrigated land presence</td>
<td>-0.15</td>
<td>ns</td>
</tr>
<tr>
<td>Vineyard presence</td>
<td>-0.11</td>
<td>ns</td>
</tr>
<tr>
<td>Solar radiation</td>
<td>-0.08</td>
<td>ns</td>
</tr>
<tr>
<td>Scrubland presence</td>
<td>0.08</td>
<td>ns</td>
</tr>
<tr>
<td>Deciduous forest presence</td>
<td>0.07</td>
<td>ns</td>
</tr>
<tr>
<td>Average altitude</td>
<td>0.04</td>
<td>ns</td>
</tr>
<tr>
<td>Dryland farming presence</td>
<td>0.03</td>
<td>ns</td>
</tr>
<tr>
<td>Sclerophyll forest presence</td>
<td>0.01</td>
<td>ns</td>
</tr>
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</table>

Origin of birds wintering in central Catalonia

Analysis of captures showed that Citril finches appeared in the wintering grounds from October to May (fig. 12). Analysis of ring recovery data showed that birds wintering in the main wintering area in central Catalonia (Solsonès, Alt Urgell, Bages and Berguedà regions, fig. 2) proceeded mainly from adjacent Pyrenean mountain ranges (N = 238 recoveries from 2,368 birds ringed at wintering grounds and 12,648 birds ringed at alpine localities from 1977–2004). We also had some distant recoveries: three birds from the Western Pyrenees (Navarra), two from central Pyrenees (Pallars and Vall d’Aran) and two birds from the Eastern Pyrenees (Girona). We also identified three birds from trans–Pyrenean populations (from the Alps) (table 3, figs. 13, 14).

Capture/recapture efforts additionally provided information on movements of Citril finches in or away from our study area, not directly related to the wintering season (table 4). Such data interconnected our study area with far–apart populations (table 4; fig. 15). Most movements between areas referred to birds originally marked as juvenile or first–year birds (tables 3, 4)

Discussion

Citril finch winter distribution and the role of pines

The low detectability of the Citril finch in wintering areas coupled with the low familiarity of ornithologists with this elusive species has made it difficult to locate their wintering ranges (Benoit & Märki, 2004; Dejonghe, 1991). Extensive surveys of Citril finches carried out in northeast Spain show that the species typically winters in mountainous areas (300–1,200 m a.s.l.) at continental ranges in submediterranean and Mediterranean habitats, in clearly xerophilous environments (figs. 3, 11). The species favours sunny slopes, avoiding foggy plains with frequent thermal inversions (e.g.: Vic, Bages and Lleida plains at the Central Depression). This preference for thermophilous areas is also typical of the French areas, where the population north of the Pyrenees winters (Crousaz & Lebreton, 1963; Dejonghe, 1991; Märki, 1976; Praz & Oggier, 1973).

The typical habitat used by the species in Catalonia includes farmland and fragmented forests of Black pine (Pinus nigra), Scots pine (Pinus sylvestris), Pubescent oak (Quercus pubescens Willd.) and Lusitanian oak (Quercus faginea Lam.), with ruderal and arvensic (nitrophilous) communities from which they feed (Borras & Junyent, 1993). Sporadically, the species may be found during autumn migration in the mountain ranges close to the coast (Serralada Litoral and Prelitoral) (fig. 3).

Although this is the general description of the winter habitat of the species, discriminant analysis showed the high importance of the presence of the Black pine, and to a lesser extent of the Scots pine, in the winter distribution of the Citril finch. The abundance of these two mountain pines allowed to predict the wintering presence of the Citril finch with an accuracy of 93%. The marked preference for the Black pine over the Scots pine may be due to the combined ef-
Fig. 4. Distribution and relative abundance of Black pine (A) and Scots pine (B) in Catalonia. The 10 x 10 km UTM grid is displayed: black squares, occupation by pines ≥ 25%; large circles, occupation ≥ 10 and < 25%; small open circles, occupation ≥ 5 and < 10%. Squares with a pine abundance < 5% are not displayed. As a reference, we provide a map with the distribution of each pine on the Iberian peninsula.

Fig. 4. Distribución y abundancia relativa del pino negral (A) y el pino silvestre (B) en Cataluña. Se incluye la cuadrícula de 10 x 10 km UTM: cuadrados negros: ocupación de los pinos ≥ 25%; círculos grandes, ocupación ≥ 10 y < 25%; círculos pequeños abiertos, ocupación ≥ 5 y < 10%. No se han consignado los cuadrados con una ocupación de pinos < 5%. Como referencia se incluye un mapa con la distribución de cada pino en la península ibérica.
Fig. 5. Distribution of pure and mixed conifer forests of Black pine and Scots pine in Catalonia. Black–lined squares refer to UTM 10 x 10 km squares where the Citril finch was detected in winter (> 5 observational records) during the study period (1972–2009) (see fig. 3).

Fig. 5. Distribución de bosques de coníferas puros y mixtos de pino negral y pino silvestre en Cataluña. Los cuadrados con líneas negras son los de 10 x 10 km UTM en los que se detectó la presencia del verderón serrano en invierno (observaciones > 5) durante el periodo de estudio (1972–2009) (ver fig. 3).
The effect of the differences between these two pines. The Black pine, for instance, produces larger and hence more energetic seeds than the Scots pine (Ceballos & Ruiz de la Torre, 1971). Competition with other pine–seed eaters can also have a role; red squirrels (*Sciurus vulgaris*), for instance, appear to be more abundant among Scots pine than in Black pine forests, presumably because of the higher interannual stability in crop production of the former (Ceballos & Ruiz de la Torre, 1971) (J. Pique, pers. comm.). This association of the Citril finch with the Black pine is remarkable not only in NE Spain but in the whole range of the species in Iberia, with several records in Spain of wintering birds being linked to the distributional area of this pine (e.g. Cuenca [García–Rúa, 1974], Cazorla [Muñoz–Cobo, 1976], Gúdar, Javalambre and Albarracín [T. Polo, pers. comm.] [García–Páez, 1999]). The main wintering area for birds north of the Pyrenees, Cevennes and the region from the south of Vercors to the plains of Vaucluse (Crousaz & Lebretón, 1963; Märki, 1976), is interestingly also linked to the main French distribution area of the Black pine (Isajev et al., 2003). This could perhaps be related to the fact that this tree species was very abundant and widely spread in the Mediterranean after the last glaciation (Carrión, 2003; Carrión & Van Geel, 1999; Regato–Pájares & Elena–Rosselló, 1995; Soto et al., 2010), so that in addition to ecological factors, there may be some kind of atavistic preference for this coniferous species.

However, although the Citril finch showed a preference for the Black pine, MaxEnt analysis stressed the importance of the presence of both species of pines in mixed–conifer forests (fig. 5). This is probably due to the fact that although the seeds of the Black pine may befavoured as a food source, this tree only produces a high crop every 3–5 years (Borras et al., 1996; Kerr et al., 2008). The additional presence of Scots pine, with a more regular yearly fructification (Kantorowicz, 2000), could therefore act as a buffer, ensuring food availability in other years. We should point out here that in the years in which the Black pine produces very small crops and the Scots pine has high cone availability (Borras et al., 1996), the Citril finch can be found to exploit Scots pine in more hygrophilous areas. This would explain the observation by Benoit & Märki (2004) of birds wintering in Scots pine in the south–east of Spain during late January 2001, interestingly, a year when the Black pine had a low fructification. It is of interest to stress that in other areas of Spain (e.g. Alto Tajo and Central Range), the Citril finch may winter in forests of Scots pine (L. M. Carrascal, pers. comm.), indicating that the presence of the Black pine is not indispensable.

MaxEnt analysis also stressed the need for open forests and the presence of grasses. This can be linked to the fact that the Citril finch needs both seed plants and conifer seeds to survive the winter. Ruderal and arvensic plants are heavily used during autumn (Borras & Senar, 1991). However, at the start of the wintering period (January), ruderal and arvensic plants reduce their seed offer just when pines start opening their cones. It is by then when

Fig. 6. Graphical plot of the sensitivity for a binary classifier system as its discrimination threshold for Model 1. The figure displays the Receiver Operating Characteristic (ROC) curve for both the training and the test presence records of the Citril finch.

Fig. 6. Registro gráfico de la sensibilidad para un sistema de clasificación binario como su umbral de discriminación para el Modelo 1. Esta figura muestra la curva ROC (Receiver Operating Characteristic) para los registros tanto de entrenamiento como de frecuencia para el verderón serrano.
the species shifts its diet to pine seeds (Borras et al., 2003b; Borras & Senar, 1991).

The presence of pines seems to be necessary for the presence of wintering Citril finches. Discriminant analysis showed that the probability for Citril finch wintering appearance is very low when Black and Scots pines are not present. However, it is not sufficient; the inclusion of topo-climatic variables in MaxEnt approach stressed that in addition to these pines, a warm general temperature and some summer rain is basic to model the presence of wintering Citril finches. This is partly because these climatic variables are largely responsible for submediterranean climate and hence for the occurrence of these two species of pines in these areas (García López & Allué Camacho, 2008; Grau et al., 1999; Regato et al., 1995; Rouget et al., 2001; Thuiller et al., 2003). The warm temperature, specially at the end of win-

Table 2. Heuristic estimates of relative contributions of the environmental variables to the MaxEnt models 1 and 2. Variables used in the models include presence/absence of pure forests (when a given species makes > 70% of the total number of trees) of: (i) Pinus nigra; (ii) P. sylvestris; (iii) P. uncinata; and (iv) presence / absence of mixed conifer forest (including these three pines and deciduous trees). Land–cover percentages by: (v) woody cover and (vi) herbaceous cover. Topo–climatic predictive variables including: (vii) annual precipitation, Pann; (viii) precipitation of the driest month, Pmin; (ix) precipitation of the wettest month, Pmax; (x) maximum annual solar radiation, Rmax; (xi) minimum annual solar radiation, Rmin; (xii) maximum temperature of the hottest month, Tmax; (xiii) minimum temperature of the coldest month, Tmin; (xiv) annual temperature, Tann; (xv) topographic exposure; and (xvi) topographic wetness index, TWI.

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<tr>
<td>Puncinata</td>
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</table>
Fig. 7. Response curves displaying the probability of Citril finch occurrence (under Model 1) in relation to the main variables explaining its current distribution (table 2). The variables included presence/absence of pure forests (when a given species makes > 70% of the total number of trees) of: (i) *Pinus nigra*; (ii) *Pinus sylvestris*; and (iii) *Pinus uncinata*; (iv) presence / absence of mixed conifer forest (including these three pines and deciduous trees). Land–cover percentages by (v) woody cover and by (vi) herbaceous cover.

*Fig. 7. Curvas de respuesta que muestran la probabilidad de presencia del verderón serrano (con el Modelo 1) en relación con las variables principales que explican su distribución actual (tabla 2). Las variables incluyen presencia / ausencia de bosques puros (cuando una especie dada constituye > 70% del número total de árboles) de (i) *Pinus nigra*; (ii) *Pinus sylvestris* y (iii) *Pinus uncinata*; (iv) presencia / ausencia de bosque mixto de coníferas (incluyendo estos tres pinos y árboles caducifolios). Porcentajes de cubierta vegetal (v) cubierta leñosa y (vi) cubierta herbácea.*
Fig. 8. Habitat suitability map for the Citril finch according to Model 1 (see table 2 and figs. 6 and 7). The scale on the right shows values that vary from 0 (minimum habitat quality) to 100 (maximum habitat quality). The scores were reclassified into four classes of suitability, so the map shows areas that are of: very low habitat suitability (0–25); low habitat suitability (26–50); high habitat suitability (51–75); very high habitat suitability (76–100).

Fig. 8. Mapa de idoneidad del hábitat para el verderón serrano según el Modelo 1 (ver tabla 2 y figs. 6 y 7). La escala de la derecha muestra valores que varían de 0 (calidad mínima del hábitat) a 100 (calidad máxima del hábitat). Los registros se reclasificaron en cuatro clases de idoneidad, de manera que el mapa muestra áreas que son de: idoneidad del hábitat muy baja (0–25); idoneidad del hábitat baja (26–50); idoneidad del hábitat alta (51–75); idoneidad del hábitat muy alta (76–100).
Fig. 9. Graphical plot of the sensitivity for a binary classifier system as its discrimination threshold for Model 2. The figure displays the Receiver Operating Characteristic (ROC) curve for both the training and the test presence records of the Citril finch.

Fig. 9. Registro gráfico de la sensibilidad para un sistema de clasificación binario como su umbral de discriminación para el Modelo 2. Esta figura muestra la curva ROC (Receiver Operating Characteristic) para los registros tanto de entrenamiento como de frecuencia para el verderón serrano.

ter, is basic for the Citril finch, because the typical anticyclonic stability (in positive NAO years) in this period reduces precipitation and increases insolation and hence spontaneous opening of cones and making pine seeds easily available to the species (Kerr et al., 2008).

Summarising, the presence of mixed open forests of Black and Scots pines in typical submediterranean areas, where the warm temperatures at the end of the winter open the cones, are the key ecological and bioclimatic variables responsible for the distribution of the Citril finch in winter.

What is the origin of central Catalonia wintering birds?

Birds wintering in our area mainly came from the nearby Pyrenean Mountains, located just a few kilometers away. This seems to suggest that the species carries out simple altitudinal or transhumance movements. This is in accordance with the view of the species in some earlier publications (Bernis, 1972; Tellería et al., 1999). However, reports on recoveries of ringed birds and on visible directional movements in the north of the Pyrenees led several authors to suggest that the species could also entail a true (short) migration from breeding to wintering areas (Baccetti & Märki, 1997; Bourrillon, 1961; Crousaz & Lebreton, 1963; Fornasari et al., 1998; Praz & Oggeri, 1973; Schifferli, 1961; Spina & Volponi, 2008). This "migration hypothesis" (Fornasari et al., 1998) would explain the recovery in our area of ringed birds from many different locations across the distributional range of the species (table 3, figs. 13, 14), including even birds coming from the Alps and crossing the Pyrenees (Borràs et al., 2005a).

Citril finch movements in or away from our study area, not directly related to the wintering season, stress even more that the species may be highly mobile within Iberia (table 4, fig. 15). Our E–Pyrenees mountain ranges have exchanged birds with Central Range (Guadarrama), NW Iberian Range (Urbión) and central (Vall d’Aran) and W–Pyrenees (Navarra) (table 4, fig. 15). Additionally, there are records between SE Iberian Range (Cuenca) and W–Pyrenees (Navarra) (Alonso & Arizaga, 2004) and between the SE Iberian Range (Teruel) and E–Pyrenees (Andorra) (Toni Polo & Roger Sanmartí, pers. comm.), and an additional record of a bird ringed in coast of Liguria (Italy) and recovered during winter in Valencia (E Spain) (Spina & Volponi, 2008). All these ring–recovery data stress the apparent exchange of individuals between the different Iberian populations. This could be caused by the movement of juvenile birds in post–natal dispersal (table 4), as in other more widespread species (Newton, 2008). Indeed, analysis of movements of the Citril finch at more local scales stresses that while adult birds are very site–faithful, a high proportion (30%) of juveniles may disperse to adjacent areas (Senar et al., 2002). Future studies will test to what point this exchange of individuals can revert in gene flow.

Citril finch conservation biology and management

The presence and abundance of the Citril finch, as with other Cardueline finches (Newton, 1972), has
been historically linked to man–induced environmental changes. The species suffered a drastic bottleneck during the Middle Holocene (Förschler et al., 2010), when human–induced fires and climatic changes devastated great extensions of pine forests (mainly Black pines) (Carcaillet et al., 2002; Carrion et al., 2001a; Carrion et al., 2001b; Carrión, 2003; Carrión & Van Geel, 1999). Conversely, the desertion of large extensions of vineyards in the Mediterranean area at the end of 19th c. and early 20th c. because of the damage caused by the grape phylloxera (Dactyllosphaera vitifoliae) favoured the resurgence of many secondary woods of Black pine which then favoured the spread of the Citril finch (Borras et al., 2005b; Borras & Junyent, 1993). Economic development in Spain during the 1950s brought about changes that again favoured Citril finches; extensive pine reforestation was undertaken in the Iberian Peninsula (Tapias et al., 2001) and subalpine skiing stations were built, creating openings in available pine forests. Currently, human activities and climatic changes again seem to be acting detrimentally on the species. Since any conservation strategy concerning wildlife should be based on a dynamic view of the biological cycle of the species, both from a spatial and a temporal perspective, we should look into the current conservation needs of Citril finch on the basis of its biological cycle.

According to previously published information on the species (Borras et al., 2003a, 2003b, 2005b; Borras & Junyent, 1993; Borras & Senar, 1991, 2003; Förschler et al., 2005) the annual biological cycle of the Citril finch in Iberia comprises four phases (or quadrants) (fig. 16):
Fig. 11. Model 2. Habitat suitability map for the Citril finch according to Model 2 (see table 2 and figs. 9, 10). The scale on the right shows values that vary from 0 (minimum habitat quality) to 100 (maximum habitat quality). The scores were reclassified into four classes of suitability, so the map shows areas that are of: very low habitat suitability (0–25); low habitat suitability (26–50); high habitat suitability (51–75); very high habitat suitability (76–100).

Fig. 11. Modelo 2. Mapa de idoneidad del hábitat para el verderón serrano según el Modelo 2 (ver tabla 2 y figs. 9, 10). La escala de la derecha muestra valores que varían de 0 (calidad mínima del hábitat) a 100 (calidad máxima del hábitat). Los registros se reclasificaron en cuatro clases de idoneidad, de manera que el mapa muestra áreas que son de: idoneidad del hábitat muy baja (0–25); idoneidad del hábitat baja (26–50); idoneidad del hábitat alta (51–75); idoneidad del hábitat muy alta (76–100).
Fig. 12. Frequency distribution of Citril finch captures in different months in typical wintering areas (< 1,500 m a.s.l.). Data based on 2,368 captures from 1977 to 2004: O. October; N. November; D. December; J. January; F. February; M. March; A. April; M. May.

Table 3. Movements of Citril finches between wintering and breeding areas. We provide the ring number of the bird, the date and locality where the bird was captured during winter, and the date, locality and location where the bird was captured away from the wintering study area. The distance and direction of the movement are also given: Rf. Labels in figures 7 and 8 mapping the location of each ringing and recovery. Localities: B. Barcelona; Gi. Girona; F. France; N. Navarra; S. Switzerland; Ll. Lleida.

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<tr>
<td>Z24710</td>
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Fig. 13. Citril finch movements in winter, showing the original location (marked as a number) of the different birds either captured or recaptured at our wintering study area (marked as a rectangle). Numbers correspond to that in table 3 and in fig. 14. The contour lines refer to 1,500 m a.s.l.

Fig. 13. Desplazamientos del verderón serrano en invierno, mostrando la localización original (indicada con un número) de las distintas aves capturadas o recapturadas en nuestra área de estudio de invernada (marcada como un rectángulo). Los números corresponden a los de la tabla 3 y la fig. 14. Las líneas de contorno indican la altitud de 1,500 m s.n.m.

Fig. 14. Map of the wintering study area (as in fig. 2), showing the exact location of capture (marked as numbers) of birds originally captured or later recaptured during the breeding season away from our study area. Numbers correspond to those in table 3 and fig. 13. The contour lines refer to 1,500 m a.s.l.

Fig. 14. Mapa del área de estudio de invernada (como en la fig. 2), mostrando las localizaciones exactas de captura (marcadas en forma de números) de las aves originalmente capturadas o recapturadas más tarde durante la estación de cría lejos de nuestra área de estudio. Los números corresponden a los de la tabla 3 y la fig. 13. Las líneas de contorno indican la altitud de 1,500 m s.n.m.
Table 4. Movements of Citril finches between our study area and distant localities, exemplifying the potential for dispersal of the species. We provide the ring number of the bird, the date and locality where the bird was captured within our study area, and the date, locality and location where the bird was captured away from our study area. We additionally provide the distance and direction of the movement: Ar. Age at ringing; Rf. Labels in figures 8 and 9 mapping the location of each ringing and recovery. Localities: S. Soria; N. Navarra; M. Madrid; Gi. Girona; Ll. Lleida.

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<th>Ar</th>
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Quadrant 1
In spring (vernal period), the species breeds in subalpine open coniferous forests with abundant meadows. The species relies then on Pinus uncinata seeds complemented by herbaceous seeds from meadow grasses (e.g. Taraxacum officinale Weber ex F. H. Wigg.) (Borras et al., 2003b).

Quadrant 2
In late summer (serotinal period), Citril finches disperse over the tree line, on alpine meadows and heaths, feeding on a great variety of grassland plants, including nitrophilous plants linked to cattle (e.g. Chenopodium bonus-henricus L.; some individuals, mainly juvenile birds, may move to feed on ruderal communities of Compositae plants (e.g. Cirsium sp., Carduus sp.). During this period the birds moult.

Quadrant 3
By autumn, the birds move to lower altitudes (300–1.200 m a.s.l.) to winter. In this period they feed on ruderal and arvensic communities on fallow fields (e.g. Inula viscosa L., Chenopodium sp. and Amaranthus sp.) (Borras et al., 2003b).

Quadrant 4
Well into the winter, when herbaceous resources become exhausted, Citril finches shift diet to pine seeds (Pinus nigra and Pinus sylvestris) as cones start to open during this period (Borras et al., 2003b). Then, in the prevernal period, provided that pine fructification is abundant and meteorological conditions are adequate, the species may undergo opportunistic breeding in those montaneous areas (Borras & Senar, 1991). In Central Europe, the fourth quadrant in figure 10 has not been described. At the end of the winter, Citril finches move again to subalpine areas (Quadrant 1).

This cycle has two main components: an altitudinal component, with birds moving from subalpine/alpine areas (highland) to mountainous areas (lowland), and a trophic component, with birds shifting from pine to herbaceous resources (fig. 16).

We stressed earlier (see introduction) that most discussion on the conservation of the species has focused on the highland component. However, as in many other species, a good knowledge of the habitat requirements during the winter period may be equally important (Dolman & Sutherland, 1995), especially so in species like the Citril finch, which like other
Cardueline finches, mate during the winter (Senar & Borras, 2004).

The present study has shown that the distributional range of the Citril finch in winter is closely related to montane pines, mainly *Pinus nigra*. This link is largely trophic, occurring mainly during the second half of winter (Borras et al., 2003b). These forests are therefore critical to conservation of the species, and any threat to them, specially forest fires, will have acute detrimental effects on Citril finch populations. The devastating forest fires in Catalonia in the 1980s and 1990s, within our study area, greatly reduced availability of Black pine forest (Borras et al., 2005b). The non-serotinous cones of this pine, which open in absence of fire, increases the effect of forest fires in these trees even more (Tapias et al., 2001). Traditional Spanish forest management practices increase canopy density, thereby also favouring the frequency and intensity of these fires (Tapias et al., 2001, 2004). The slow growth of this pine and its difficulties for reforestation (Ceballos & Ruiz de la Torre, 1971) lead us to predict a marked decline in the availability of suitable habitat for the Citril finch in coming years. This will affect not only Citril finch survival over winter, but also opportunistic breeding activities (Quadrant 4).

During autumn, the main threats to the species come from the recently introduced agricultural practices of plowing fields and using herbicides, which reduce the availability of arvensic grassland communities on fallow fields. Given the importance of these dietary resources for the species at this time of year (Quadrant 3) (Borras et al., 2003b), we should advise a return to traditional agricultural practices (Borras et al., 2003b, 2005b).

During the vernal and estival seasons (Quadrant 1), the threats to the species are mainly related to a loss of pastures due to extensive reforestations and a reduction in cattle and sheep transhumance (Förschler, 2007), and to the destruction of the typical flower–rich meadows brought about by changes in ski–station management aiming to improve the retention of snow (Bezzel & Brandl, 1988; Rolando et al., 2007).

The framework we have presented for the conservation of the Citril finch stresses the need to match conservation activities with the dynamic nature of the annual cycle of the species. A conservation policy can only succeed, therefore, if actions are integrated within the different seasonal, habitat and trophic levels.
Fig. 16. Schematic diagram of the annual biological cycle of the Citril finch. The diagram shows the different periods of the year, along with the trophic sources and habitats used within each period, and the biological events that characterize that period. The diagram is divided in four quadrants which represent four main periods within the biological cycle of the species. The cycle is based on previously published information on the species (Borras et al., 2003a, 2003b, 2005b; Borras & Junyent, 1993; Borras & Senar, 1991, 2003; Förschler et al., 2005).

Fig. 16. Diagrama del ciclo biológico anual del verderón serrano. El diagrama muestra los distintos períodos a lo largo del año, junto con los recursos tróficos y los habitats utilizados en cada período, y los sucesos biológicos que caracterizan el período. El diagrama está dividido en cuatro cuadrantes, que representan los cuatro periodos principales del ciclo biológico de esta especie. El ciclo se ha basado en información sobre la especie previamente publicada (Borras et al., 2003a, 2003b, 2005b; Borras & Junyent, 1993; Borras & Senar, 1991, 2003; Förschler et al., 2005).
Acknowledgements

We wish to thank Jose Molina, Jordi Calaf, Miquel Cabrera, Carles Serrasolsas, Dolors Camps, Montse Mateu, Alex Borras and Eduard Borrás for assistance ringing the birds and Anna Moreso, Albert Solé, Alex Mazzuchan, Toni Beltran, Mar Masanés, Jordi Garcia, Iolanda Garcia, Albert Garcia, Jordi Cereira, Mariona Monròs and Olga Nicolas for field assistance; Hans Märki, Luis María Carrascal and Lluís Brotons for comments on the paper; Ramón Monell, Josep Codina, Florenci Codina, Schmith de Solanes, Isidre de Serinyana and Joan Perramón for allowing us to work in their properties; Toni Polo, Roger Sanmartí, Lluís Gustamante, Ponç Felu, Victor Sanz, Jaume Soler, Josep Bosch and Joan Perramón for providing data on the observations of wintering birds and Raúl Aymi (ICO) and Xavier Ferror (Vertebrcat, UB) for providing information from their data--bases; Toni Polo (Grupo de Anillamiento Liebeig), Roger Sanmartí, Juanjo Calleja (Grupo Ornitológico Monticola), Juli Merino (Societat "El Passerell" de Solsona), Daniel Alonso and Juan Arizaga (Sociedad de Ciencias Aranzadi) for providing data on Citril finch ring recovery; Oscar Gordo and Jordi Calaf for providing UTM databases on the distribution of land use, meteorological data and abundance of pines; the Cos d'Agents Forestals, Generalitat de Catalunya, especially Daniel Mañas, Josep Gilibets and Lluís Novellas, for facilities during field work. Birds were handled with the permission of the Catalan Ringing Office (ICO) and the Departament de Medi Ambient, Generalitat de Catalunya. This work was supported by grants from the Ministerio de Ciencia e Innovación (CGL 2009–10652).

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Appendix. References used to map the distribution of the Citril finch in Catalonia during the winter (see fig. 3).

Apéndice. Referencias utilizadas para maapear la distribución del verderón serrano en Cataluña durante el invierno (ver fig. 3).
Appendix. (Cont.)