



## Modelling seasonal changes in the distribution of Common Quail *Coturnix coturnix* in farmland landscapes using remote sensing

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Species' distribution models are widely used in landscape ecology but usually lack explicit information about species' responses to ecosystem dynamics, leading to uncertainty when applied to the prediction of seasonal change in distributions. In this study, we aimed to build a species' distribution model for the Common Quail *Coturnix coturnix*, a farmland species that shows changes in its distribution in response to seasonal changes in habitat suitability. During the course of three breeding seasons we collected temporal replicates of presence–absence data in 13 sampling locations in four countries (Morocco, Portugal, Spain and France). We used generalized linear mixed models to relate the species' presence or absence to environmental variables and to the normalized difference vegetation index at each sampling location through the seasons, the latter variable being an indicator of within- and between-season habitat changes. The preferred model showed that occurrence was highly dependent on habitat changes associated with crop seasonality, as measured by the normalized difference vegetation index. Common Quail selected areas with dense vegetation and warm climate and tracked spatial changes in these two parameters. The model allows accurate mapping of within- and between-season distribution changes. Such changes are related to habitat variations caused mainly by drought and agricultural practices. Our results demonstrate that seasonal changes in farmland ecosystems can be incorporated into a simple distribution model, and our approach could be applied to other species to predict the effects of agricultural changes on the distribution of birds inhabiting farmland landscapes.

**Keywords:** agriculture, cereal, crop seasonality, generalized linear mixed model, normalized difference vegetation index, species' distribution models.

Attempts to gain insight into the processes that determine the distribution of organisms in dynamic ecosystems and to map responses to habitat and climate change have focused on the development of species distribution modelling (SDM) techniques (Guisan & Zimmermann 2000, Pearce & Ferrier 2000, Segurado & Araújo 2004, Elith *et al.*

2006, Araújo & New 2007). These methods are commonly used in a temporally static way and often lack explicit information on causes of change in distribution. For example, farmland landscapes are habitat mosaics in which various habitat components change throughout the course of the year as a consequence of agricultural operations and crop growth (Benton *et al.* 2003, Flade *et al.* 2006). In this context, the species inhabiting these landscapes face rapid changes in the distribution of

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resources, including food and vegetation cover (Wilson *et al.* 1996, 2007, Benton *et al.* 2003, Green *et al.* 2005). These changes in resources then determine the temporal and spatial distribution of farmland species.

Agricultural landscapes dominated by cereals or forage crops and grass show strong seasonal changes throughout the year. These agricultural habitats are usually ephemeral, due to harvesting, showing changes from one year to another or even within the same season. Thus, species that breed in these crops must respond to a rapidly changing habitat. Several studies of farmland and steppe birds have explicitly taken into account seasonal agricultural changes through SDMs (Tella & Forero 2000, Osborne *et al.* 2001, Suárez-Seoane *et al.* 2002, Brotons *et al.* 2004, Bota *et al.* 2005). However, SDMs based on static variables may provide an overly simplistic view of species responses to rapid habitat changes, as they only capture species requirements at a given time. Thus, often they do not incorporate information about system dynamics and relevant biotic processes (Zurell *et al.* 2009).

One means of measuring phenological change in these dynamic landscapes is through the use of the normalized difference vegetation index (NDVI) as a proxy for seasonal vegetation change on farmland. NDVI is a simple numerical index of photosynthetic activity (Rouse *et al.* 1974), and thus primary production, detected via satellite by multiple sensors such as the advanced very high resolution radiometer (AVHRR). This index is suitable for obtaining information about changes in vegetation structure (Pettorelli *et al.* 2005) and for detecting patterns in vegetation development on farmland, and thus for overcoming the problem of using static variables in dynamic agricultural landscapes. For example, as cereal crops ripen and dry at the end of the growing season they lose chlorophyll and become yellow. However, while NDVI changes, the biomass in the crop field remains more or less constant until harvest occurs. Consequently, NDVI can be used as an indicator of cereal crop maturation and to predict when harvesting will occur.

In this study, we aim to build a simple model of Common Quail *Coturnix coturnix* distribution that incorporates temporal variability in environmental variables and illustrates how a farmland species tracks changes in its environment over the course of the year.

The Common Quail is widely distributed in the Palearctic. It winters in the Sahel and, after migration, it reaches its breeding grounds in northern Africa and Eurasia (Guyomarc'h *et al.* 1998). Arrival dates are later at higher latitudes. Once in the breeding areas, Quails mainly inhabit cereal crops (usually wheat and barley) and behave secretively within the dense vegetation. During the breeding season, which continues until the end of August, males sing to announce their presence to females and other males (Guyomarc'h *et al.* 1998). Moreover, there is a marked and constant inflow and outflow of individuals, especially males, in breeding locations throughout the breeding season (Rodríguez-Teijeiro *et al.* 1992). The estimated length of stay is 7–10 days among males, as males move on if they do not succeed to mate or as soon as the female begins incubation, and 2.5 months among females. Thus, male calls indicate their attempts to breed, and the absence of male calls at the beginning and end of the breeding season indicates an absence of males. Moreover, the mean date on which cereal crops approach their asymptotic height matches the modal date for male calling activity, expressed as the day of the breeding season when the highest density of calling males is reported (Puigcerver *et al.* 1989). When habitat suitability is reduced, for example due to harvesting, most Quails move and search for a more suitable habitat in a different location; only females with broods will remain in their breeding areas to raise their chicks (Rodríguez-Teijeiro *et al.* 2009). In accordance with these nomadic habits (Dean 2004), the species reaches sexual maturity in the natal year and can even reproduce in the first year of life (Guyomarc'h & Saint-Jalme 1990).

In areas with continental and Atlantic climates, crops are less dependent on water supply due to the high precipitation regime and therefore crop seasonality and productivity are dictated mainly by crop type and/or farming practices (Chamberlain *et al.* 2000). However, Mediterranean areas have lower annual precipitation rates and thus crop seasonality and productivity are mainly dictated by climate and weather (De Juana & García 2005), and maturation occurs each season from south to north and from lower to higher altitudes (Rodríguez-Teijeiro *et al.* 2009).

In this study, we predicted that changes in NDVI will reflect changes in the temporal development of crop vegetation (Pettorelli *et al.* 2005).

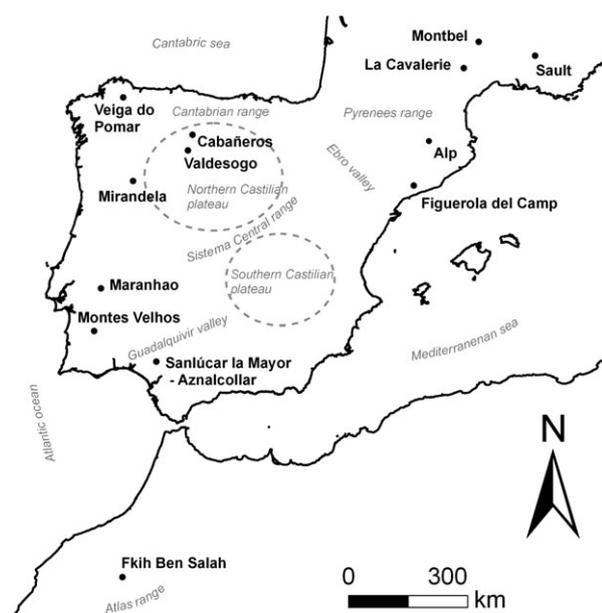
We also predicted that the Quail, which is generally limited by the presence of suitable habitat (Sardà-Palomera & Vieites 2011), would track recorded changes in vegetation cover as the major determinant of the species' seasonal distribution changes. We also predicted that seasonal changes in vegetation cover would interact with abiotic factors (e.g. climate) to determine the species' distribution. Thus, using continuous occurrence data through the course of the seasons should make it possible to relate occurrence to a broad range of environmental data within and between seasons to develop an SDM that predicts distribution changes.

To test this prediction, we built a generalized linear mixed model (GLMM) for this nomadic species of dynamic and ephemeral habitats to estimate environment–species relationships across space and time. The data were collected over 3 years in 13 sampling locations in four countries on two continents (Morocco, Portugal, Spain and France).

## METHODS

### Study area

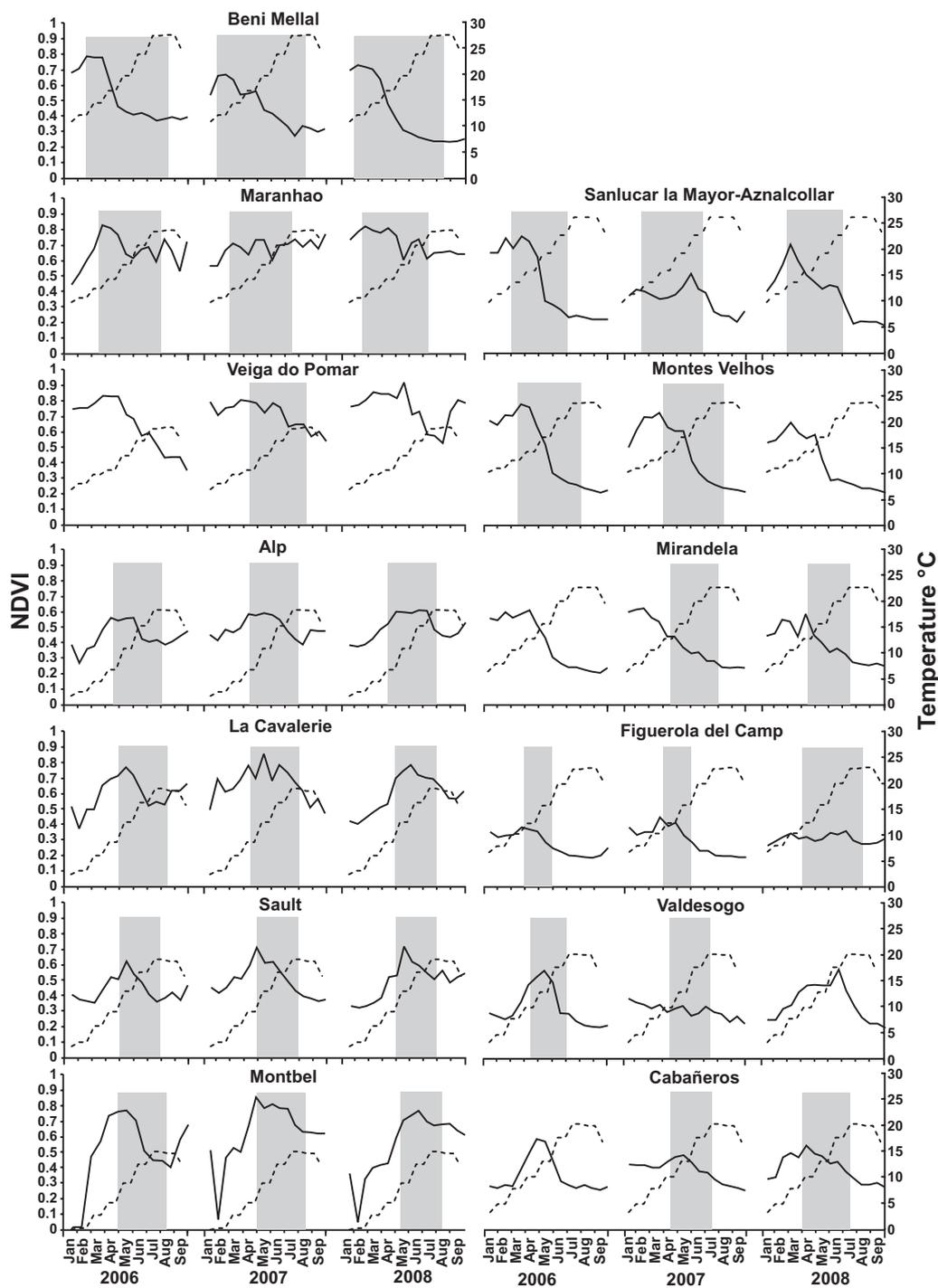
The study area covered Morocco, Portugal, Spain and southern France (Fig. 1). These countries



**Figure 1.** Map of the study area showing the sampling locations (black) and the main geographical features (grey).

comprise the most important areas in terms of the density of the western population of the Common Quail (Guyomarc'h *et al.* 1998, Guyomarc'h 2003). Morocco, most of the Iberian Peninsula (Spain and southern Portugal) and the Mediterranean coast of France have a Mediterranean climate characterized by dry winters and summers, and intermediate annual precipitation (400–800 mm), which falls mainly in spring and autumn. The north and northwestern part of the Iberian Peninsula and the rest of France have a temperate climate with higher precipitation (500–1000 mm). Relief in the study area varies from sea level to 4165 m above sea level (a.s.l.) in the Atlas range in Morocco. The Iberian Peninsula contains a large area (the Castilian plateau), which has a mean altitude of 700 m a.s.l. and is divided into two parts (northern and southern) by the Sistema Central range. The Peninsula is delimited to the north by the Pyrenees (3300 m) and the Cantabrian Range (2600 m). The dominant agricultural systems in the area are cereal crops, especially in the Mediterranean area and the northern Castilian plateau. However, in the temperate area the dominance of cereal crops decreases and cereals are grown alongside other field types such as grassland, meadows and pastures.

Fieldwork was carried out during the 2006–08 breeding seasons (which encompasses the months February to August, depending on location) in 13 different sampling locations in these four countries (Fig. 1). The sampling locations were chosen because they were known to be breeding areas from sampling carried out in previous years. These areas show different levels of habitat suitability for the species, ranging from areas with low Quail densities that vary greatly between years (e.g. Figuerola del Camp) to areas with high and constant densities between years (e.g. Fkih Ben Salah). Eight locations were sampled for all three study years; four locations were sampled for 2 years and one location for 1 year only (Fig. 2). The locations can be classified into two groups according to water supply (Table 1): dry areas (< 700 mm), in which only wheat and barley crops can be grown (Montes Velhos, Sanlúcar la Mayor – Aznalcollar, Valdesogo, Cabañeros and Figuerola del Camp), and areas in which cereal crops can be mixed with other herbaceous crops (alfalfa, vetch, meadow, etc.), due to a higher mean precipitation (> 700 mm; Veiga do Pumar, Mirandela, Alp, La Cavalerie, Montbel and Sault) or irrigation (Fkih Ben Salah and Maranhao).



**Figure 2.** Common Quail presence (grey shaded area), NDVI pattern (solid line) and the monthly mean temperature (1950–2000) from WORLDCLIM (dotted line) for each sampling location. Periods with no data are non-sampled periods.

**Field methods**

Ten point counts (Bibby *et al.* 2000) were established at each sampling location, and were visited

every sampling day. Within the sampling location, point counts were located in places surrounded by crop fields potentially suitable for Common Quail breeding. At each point count, a digital female

**Table 1.** Mean annual accumulated precipitation (Accumulated prec.), mean temperatures (Mean temp.) obtained from WORLDCLIM Version 1.4 (1950–2000) and habitat description of the sampled breeding sites in Morocco (Mo), Portugal (Po), Spain (Sp) and southern France (Fr). Crop species mentioned are wheat (*Triticum* spp.), barley (*Hordeum* spp.), rye (*Secale cereale*), triticale (hybrid *Triticum* spp. × *Secale* spp.), millet (*Panicum* spp.), alfalfa (*Medicago sativa*), vetch (*Vicia* spp.) and lavender (*Lavandula* spp.).

Location	Accumulated prec. (mm)	Mean temp. (°C)	Habitat description
Cabañeros (Sp)	474	11	Wheat and barley crops and set-aside
Fkih Ben Salah (Mo)	478	19	Irrigated wheat and alfalfa crops
Valdesogo (Sp)	545	11	Wheat and barley crops and set-aside
Montes Velhos (Po)	548	17	Wheat and barley crops
Sanlúcar la Mayor – Aznalcóllar (Sp)	558	18	Wheat and barley crops
Figuerola del Camp (Sp)	596	14	Barley crops
Maranhao (Po)	645	17	Irrigated wheat, alfalfa, millet and vetch crops
La Cavalerie (Fr)	784	10	Triticale, barley crops and alfalfa
Sault (Fr)	831	10	Lavender crops, wheat crops and meadow
Montbel (Fr)	858	7	Wheat and barley crops, alfalfa and meadow
Mirandela (Po)	868	14	Wheat, rye and barley crops
Alp (Sp)	916	9	Wheat, rye, barley, maize crops and meadow
Veiga do Pumar (Sp)	1022	12	Meadow and forage crops

decoy (PQ-10 with E-36X chip, Mundi Sound Ca. Pa.Di., S.L. Spain) was played to elicit song from any males that did not call spontaneously. These digital decoys have an approximate range of 350 m radius, and point counts were separated from each other to avoid overlap problems ( $\geq 700$  m). The presence or absence of calling male Quails was recorded. Quails are only detectable by male calls and they only call during the breeding season. Sampling locations were visited

once every 10 days (except Fkih Ben Salah, which was visited once a month), from before the arrival of Quails from their winter quarters until the end of the breeding season, when harvesting occurred or Quails left the area to return to winter quarters (except Fkih Ben Salah, where the species could also winter, see Guyomarc'h 1992). When no advertising call was heard and thus no male Quails were detected in any of the point counts in a certain sampling location, we considered that they were absent from this location and their breeding attempts were over. When a minimum of one male Quail was detected in a count point, this was considered evidence of the presence of the species in the sampling location. We included all absences (zero values) detected in the field prior to arrivals of Quails and after they left, with the aim to encompass the maximum range of environmental variables across the study area to estimate environment–species relationships. Thus, we obtained a temporal series of Quail presence and absence data for each sampling location and sampling day throughout the entire season for each study year. These presence/absence data were used as the dependent variable.

### Predictor variables

NDVI was used to quantify vegetation cover suitability. NDVI data were obtained from the Moderate Resolution Imaging Spectroradiometer (MODIS, <http://modis.gsfc.nasa.gov/>). We used Version-5 MODIS/Terra Vegetation Indices at 1-km spatial resolution for the study area for 2006, 2007 and 2008. These data are provided in a grid format for each 16-day period. This grid is created from a maximum value accumulation process so that each pixel has the highest NDVI value recorded over the 16-day accumulation period. This helps to reduce error from clouds, mist and other atmospheric effects, as well as view angle differences. Therefore, we could relate each sampling day at the different sampling locations to its respective NDVI value, with a maximum difference of 8 days. NDVI values range from zero to one, where zero indicates the absence of photosynthetic activity, and therefore the absence of living vegetation, and high values equate to high photosynthetic activity.

Monthly mean temperature and monthly mean accumulated precipitation for each location were taken as climatic variables. These values, with a

spatial resolution of 1 km<sup>2</sup>, were obtained from WORLDCLIM Version 1.4 (<http://www.worldclim.org/>) (Hijmans *et al.* 2005). This is an interpolated climate dataset with high spatial resolution, which is widely used in species distribution modelling, especially from a climatic perspective (Daly 2006, Elith *et al.* 2006, Broennimann *et al.* 2007, Pearson *et al.* 2007). Altitude, at a resolution of 1 km<sup>2</sup> (also provided by WORLDCLIM), was included in the dataset as a geographical variable, and latitude was also included in the model to control for possible spatial effects related to migration timing.

As sampling locations were homogeneous farmland areas ranging from approximately 15 to 50 km<sup>2</sup>, we selected the central point of each sampling location to relate species presence/absence data with the predictor variables. The mean value of the centre cell and all the adjacent cells was used to obtain a mean value for a 9-km<sup>2</sup> area for each variable. This mean value provided average information of the environmental conditions in the sampling locations that was suited to the ecology of this mobile species.

## Data analysis

Correlates of distribution presence/absence were modelled using GLMMs with the GLIMMIX (SAS Institute, Cary, NC, USA) macro. A model with a binomial error distribution and a logit link function was specified with presence–absence at each location for each sampling day as the dependent variable. Sampling locations were included as a random effect to control for variation between locations and to account for non-independence in the data collected at given locations. Year (2006, 2007 and 2008) and season (winter, spring and summer) were included as categorical fixed effects to control for possible interactions. Because breeding individuals were detected in winter in the sampled locations at lower latitudes (Fkih Ben Salah and Sanlúcar la Mayor – Aznalcóllar), and in spring and summer in locations at higher latitudes, seasons were considered to be winter (from January to March), spring (from April to June) and summer (from July to September). Autumn was excluded because the species was not detected in any locations in the study area. The remaining variables (NDVI, mean temperature, precipitation and altitude) were included as covariates. To control for possible curvilinear relationships we also calculated the quadratic and cubic terms for

the NDVI variable and ran the model again for each case. We finally selected the model that better explained the deviance.

Full models that included all the variables and possible interactions were reduced by sequentially removing non-significant terms ( $P$ -values < 0.01) (Sol *et al.* 2005, Pons *et al.* 2008). Although model selection approaches have been widely discussed (see Whittingham *et al.* 2006, Murtaugh 2009 among others), we considered that a backward stepwise procedure would be appropriate in our case.

We additionally performed a temporal cross-validation to test how well occupancy in each year was estimated from the other 2 years in turn. The dataset was divided into 3 years, one of which we used as independent data to test the model run using training data from the remaining 2 years, and repeating the process for all three combinations. This made it possible to assess how well the model predictions used to generate maps fit the observed data. Using the predictions and test data obtained, we performed the area under the receiver operating characteristic curve (AUC) test using the R package ‘presence–absence’ version 1.1.3 in R version 2.14.0 (R Development Core Team 2011).

Occurrence probability maps were created by projecting the minimum adequate model over the corresponding raster variables using ESRI ARCGIS 9.2. (ESRI, Redlands, CA, USA). These probabilities of occurrence were interpreted as a habitat suitability index. The model was only projected onto areas that contained potential habitats for the species (Guyomarc’h *et al.* 1998), which were selected from CORINE Land Cover 2000 (from the European Environment Agency, <http://www.eea.europa.eu/>) for Europe, and from the US Geological Survey (<http://www.usgs.gov/>) for Africa.

## RESULTS

### Relationships between land use and NDVI

Drier areas (mean annual accumulated precipitation below 700 mm and without supplementary water support), where only cereal crops were cultivated, showed lower NDVI values than areas with more water availability, where cereal crops were mixed with other herbaceous crops (Mann–Whitney  $U$ -test:  $z = 3.0$ ,  $P < 0.01$ ,  $n_1 = 6$ ,

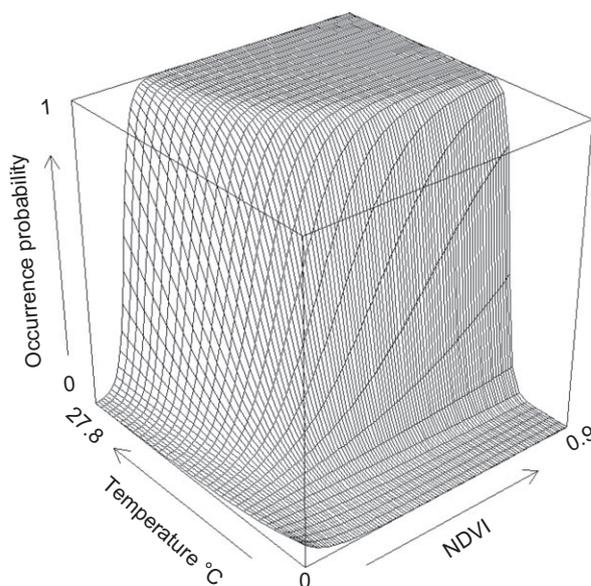
$n_2 = 7$ ). In drier areas, the median NDVI was 0.41 and ranged from 0.18 to 0.77. However, in wetter areas (with accumulated precipitation over 700 mm or with supplementary water support) the median NDVI value was 0.59 and ranged from 0 to 0.90. Quails were recorded at locations with NDVI values between 0.24 (minimum in Mirandela in July 2007) and 0.83 (maximum in La Cavalerie in May 2007).

The ratio of presence/absence data was 1.81 : 1, with 245 presences and 135 absences. The minimum adequate model for the presence-absence response variable (Table 2) explained 73.5% of the deviance, and the AUC values obtained from the temporal cross-validation analyses were 0.89, 0.83 and 0.91. This model indicates that the interaction between NDVI and temperature is strongly related to Common Quail occurrence, having accounted for seasonal variation (Fig. 3), with the highest occurrence probability when NDVI is high and conditions are warm (Figs 2 and 3). These results also suggest that there are some thresholds in both NDVI and temperature below which Quail will not occur. Quails seem not to be present when NDVI falls below 0.24 and/or mean temperature falls below 7 °C. In the case of NDVI, the lowest value during spring and summer coincides with harvesting.

The variable 'season' also entered into the model, with occurrence higher in spring (in fact the species was present in all the sampling

**Table 2.** Results for the minimum adequate model for the Common Quail obtained from a GLMM with a binomial (presence or absence) error distribution and a logit link function, and applying a backward stepwise procedure.

Effect	Estimate	se	Type III, F	P
<b>Fixed</b>				
Intercept	-6.704	2.693		0.0824
NDVI	-12.667	4.385	8.34	0.0041
Temperature	-0.013	0.013	0.92	0.3375
NDVI × Temperature	0.198	0.037	28.53	<0.0001
Season			20.23	<0.0001
Winter	2.988	1.395		0.0329
Spring	6.092	1.082		<0.0001
Summer	0			
<b>Random</b>				
Location	2.721	1.883		



**Figure 3.** Response of Common Quail occurrence probability to the predictor variables (NDVI and temperature), taking into account the interaction between both variables.

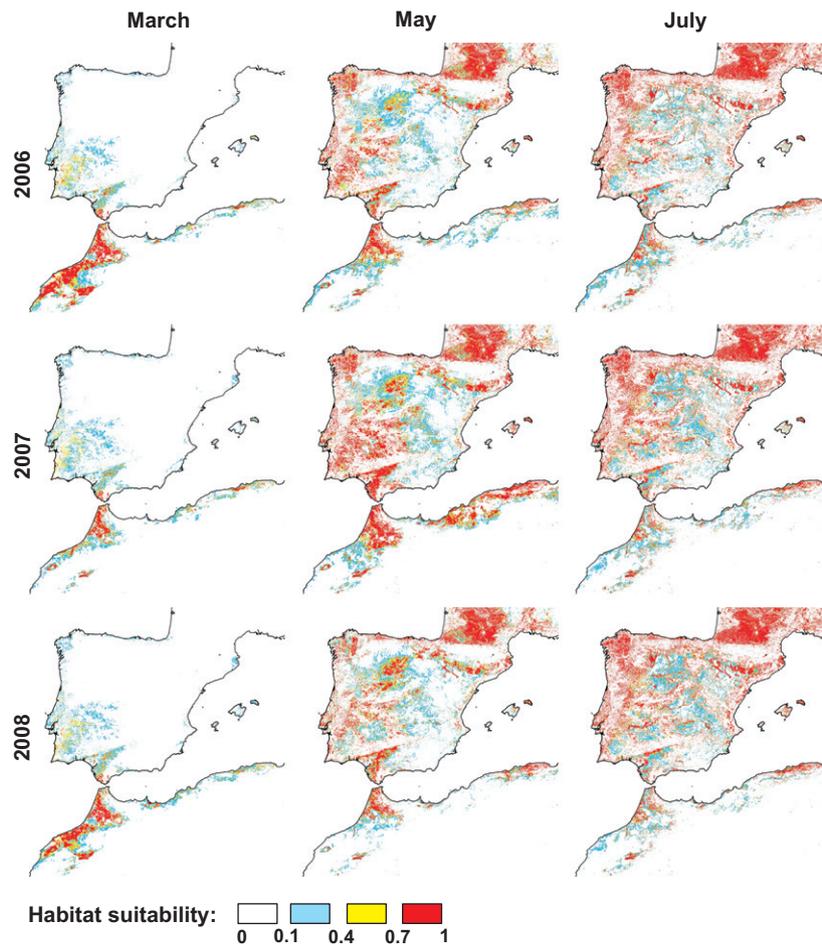
locations throughout this season) than at other seasons.

We obtained habitat suitability maps for every 16-day period during the length of the species' stay in the study area. The resultant habitat suitability maps showed spatial and temporal variations in Quail population distribution during the breeding season in farmland areas (Fig. 4).

## DISCUSSION

### Responses to seasonal habitat changes

The results show that NDVI is the main factor of those considered in the model that determines the occurrence of male Common Quails during the breeding season, the onset of which is determined by temperature. Thus, Quails prefer agricultural areas with high NDVI values but within a range of high temperatures, which determine the beginning of the breeding season but not the end. In this context, NDVI reflects the life cycle of the cereal crops, decreasing when crops begin to ripen and dry. Crop maturation reduces habitat suitability for Quails and their ability to reproduce (Puigcerver *et al.* 1989). NDVI reaches its lowest values at the time of harvesting, the ultimate event that causes breeding attempts to end due to habitat



**Figure 4.** Habitat suitability maps for the Common Quail obtained from the GLMM and projected onto different months (March, May and July) and years (2006, 2007 and 2008) during the study period for herbage areas. Habitat suitability ranges from 0 (no suitability) to 1 (maximum suitability).

destruction, and compels remaining individuals to move (Rodríguez-Teijeiro *et al.* 2009), other than females with dependent chicks.

Our results strongly suggest that, in the study area, each agricultural system is associated with a particular temporal NDVI pattern. Temperature also varies throughout the year and at different locations, depending on altitude and latitude, which may explain why the arrival of Quails is delayed in some areas where they would be under climatic stress, even though vegetation cover might be suitable for the species. Like many other migrating species, Quails begin to breed earlier in southern latitudes due to climatic conditions. Habitat changes and cereal drying also begin earlier in southern breeding areas, and from lower to higher altitudes (Rodríguez-Teijeiro *et al.* 2009).

Thus, optimal breeding conditions change in a wave-like manner throughout the species' range during a single breeding season. However, wide variations can appear between years, depending on rainfall. Quails rapidly adapt to this regime through their continuous nomadic movements, which allow them to exploit emerging habitats (Puigcerver *et al.* 1989, Rodríguez-Teijeiro *et al.* 2009). The case of Figuerola del Camp is a clear example of this. In this sampling location, Quails tripled the length of the stay due to an abnormal weather that affected vegetation. They took advantage and their breeding success also showed an enormous increase as compared with other years (Rodríguez-Teijeiro *et al.* 2010).

Some sampling locations have a higher water supply, and cereals are mixed with other crops

with different cultivation patterns (lucerne, vetch, meadow, etc.). This is the case in some areas that are influenced by the Atlantic climate and in higher altitude areas, which show higher precipitation rates. It also occurs close to rivers or in artificially irrigated areas. In general, these areas show higher and more constant NDVI values throughout the seasons and thus a higher probability of the species' presence during the breeding season. Moreover, when cereal harvesting occurs in these areas, other suitable crops remain for the species.

Although we could not validate map projection beyond the sampling locations, the projection of the model across the whole study area allows us to understand how variation in vegetation cover (NDVI) can affect habitat suitability and the distribution of Quails. Apart from identifying temporal and spatial variation in the species' distribution during the breeding season, the projection of the model in sequential maps showed that some areas that were not suitable or had lost habitat suitability during the spring became more suitable in the summer. This may be due to increasing temperatures and weeds growing after harvesting in the open cereal fields, or the fact that other crops, such as maize, are frequently sown in some areas after cereal harvesting. The model identified areas within the species' range that presented suitable conditions for the species after harvesting and that could contain high numbers of Quail before post-breeding migration occurred (Rodríguez-Teijeiro *et al.* 2009).

### Contribution to species distribution models

As previous studies have demonstrated, NDVI is a very useful index for modelling habitat suitability for farmland and pseudo-steppe land-birds (Osborne *et al.* 2001, Suárez-Seoane *et al.* 2002, Osborne & Suárez-Seoane 2007). In Mediterranean agricultural landscapes it is also an indicator of water input (Smith *et al.* 1995, Palumbo *et al.* 2008), often representing a more effective measure than precipitation, as it enables areas under irrigation to be identified. However, in this study we incorporate gradual NDVI changes into the model and relate these changes to a temporal series of presence-absence data.

Recently, concerted efforts have been made to test and develop the best models for predicting species distributions, especially under climate

change scenarios and from a conservation perspective (Fielding & Bell 1997, Pearson & Dawson 2003, Araújo *et al.* 2005). However, these models have been based on presence-absence occurrence in a single time period, which, to obtain a broad range of environmental information, has to be related to interpolated climate data taken from the means of long series (New *et al.* 1999, Hijmans *et al.* 2005). Interpolated global data can be very useful, and in fact were used in this study to obtain the climate data. However, they can also give too general a view of the species' requirements, and when such data are used indiscriminately, the models may give uncertain results (Daly 2006).

Although the model used in this study is not strictly dynamic, incorporating temporal replicates in SDM and relating them to seasonal environmental changes allows us to include a larger range of conditions to estimate environment-species relationships, and in consequence to reproduce species distribution dynamics. Using a single time period in the middle of the breeding season would restrict environmental data variability. Using data from throughout several breeding seasons makes it possible to relate a broad range of environmental data to presences and absences. If the whole potential range of conditions in the model is not included, we would lose most of the absence cases, which could lead to misleading conclusions (Barbet-Massin *et al.* 2010).

Our results show that it is possible to build a species distribution model of the reproductive presence of a species with a high movement capacity that depends on a dynamic ecological niche. In this case, a predictive model based on specific data over time and static variables would miss important information. The model that we have developed provides valuable information about the ecological requirements of Common Quail and its temporal habitat dynamics. Moreover, it is a useful tool for optimal conservation management of the species (e.g. in relation to the timing of the hunting season and of agricultural operations such as mowing) because it allows us to detect important breeding and pre-migration concentration areas.

This study was funded by the Spanish Hunting Federation (2006), the Euskadi Hunting Federation (2007 and 2008), the Dirección General de Investigación Científica y Técnica (projects CGL2004-05308/BOS, CGL2007-

63199 and CGL 2008-05506-02), the EU FP7 project SCALES, the FGCSIC, Banco Santander and CSIC (Steppe-ahead project), the Direcció General de Recerca (2005-SGR-00090) and the Àrea d'Activitats Cinegètiques of the Generalitat de Catalunya. We thank two anonymous reviewers who read the first draft and provided useful comments and suggestions. We also thank Mohammed Maghnouj (Centre National de la Recherche Forestière, Haut Commissariat aux Eaux et Forêts et à la Lutte Contre le Désertification, Morocco), Inácio Alves and Agostinho Beça (Federação de Caçadores da Primeira Região Cinegética, Portugal), Pedro Colaço and Antonio Guerreiro (Confederação Nacional dos Caçadores Portugueses, Portugal), Yannick Bay, Bernard Borgogne, Jacky Gleize and Christophe Rieutort (Fédération Départementale des Chasseurs de La Lozère, France), Bernard Blanchy and Bernard Bourgeon (Fédération Départementale des Chasseurs de L'Aveyron, France) and Denis Roux (Office National de la Chasse et de la Faune Sauvage, France) who carried out the fieldwork in each respective sampling location. We are also grateful to Victor Sazatornil, Emilio Garcia and Oscar Rivas who selflessly carried out the fieldwork in Veiga do Pumar, Spain, in 2007. The English version of this manuscript has been revised by the University of Barcelona Language Service.

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Received 21 September 2010;  
 revision accepted 12 June 2012.  
 Associate Editor: Simon Butler.