

Improving management plans by downscaling hunting yield models: a case study with the red-legged partridge *Alectoris rufa* in southern Spain

Miguel Á. Farfán, Juan M. Vargas, Jesús Duarte & Raimundo Real

The aim of our work is to predict potentially optimal areas for red-legged partridge *Alectoris rufa* hunting success in Andalusia (southern Spain) according to topographic, climatic and vegetation factors and their interaction. We analysed 32,134 annual hunting reports from the period 1993-2001 reported by 6,049 game estates to estimate the average hunting yields of red-legged partridge in each Andalusian municipality (N = 771). We modelled the favourability for obtaining good hunting yields using generalised linear models (GLM) on a set of climatic, topographic, land use and vegetation variables. The variables that affected hunting yields of red-legged partridge were dry herbaceous and wood crops, annual number of frost days, altitude and mean annual temperature. Vegetation was the most important factor of those considered in our study explaining the distribution of good hunting yields of the red-legged partridge in Andalusia. The favourability equation was used to create a downscaled image representing the favourability of obtaining good hunting yields for the red-legged partridge in 1 × 1-km squares in Andalusia, using the Idrisi Image Calculator. Downscaling the model from municipalities to 1 × 1-km squares provided a much higher spatial resolution when predicting the optimal areas for good hunting yields for the red-legged partridge.

Key words: *Alectoris rufa*, Andalusia, downscaling, favourability, GLM models, hunting yields, optimal area, red-legged partridge

Miguel Á. Farfán & Jesús Duarte, Biogea Consultores, S.C., Calle Navarro Ledesma, 243, P4, 3° C, 29010 Málaga, Spain - e-mail addresses: biogea@biogea-consultores.com (Miguel Angel Farfán); jddbigea@gmail.com (Jesús Duarte)

Juan M. Vargas & Raimundo Real, Departamento de Biología Animal, Facultad de Ciencias, Universidad de Málaga, E-29071 Málaga, Spain - e-mail addresses: jmvvy@uma.es (Juan Mario Vargas); rrgimenez@uma.es (Raimundo Real)

Corresponding author: Juan Mario Vargas

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The red-legged partridge *Alectoris rufa* occurs throughout the Iberian Peninsula, where the species probably originated from and where it reaches its highest natural densities (Aebischer & Lucio 1997, Vargas et al. 2006). It is reported as a breeding species in Spain in 86% of the UTM 10 × 10-km squares, but rarely above 1,500 m a.s.l. (Blanco-Aguilar et al. 2003). This species is associated with cultivated

areas and mainly selects open regions where agriculture is moderately intensive and the landscape is heterogeneous (Lucio & Purroy 1992b, Lucio 1998, Borralho et al. 1999, Fortuna 2002).

In the Iberian Peninsula, the red-legged partridge has a large number of predator species typical of the Mediterranean ecosystem (Calderón 1977). It also generates economically important hunting activity,

mainly in those rural areas where other agrarian uses are only marginally important (Delibes 1992, Lucio & Purroy 1992a, Fungesma 2001, Vargas 2002).

Red-legged partridge populations have declined substantially since the early 1970s (Aebischer & Potts 1994, Tucker & Heath 1995). The Spanish population suffered about a 25% reduction during 1990-2000 (BirdLife International 2004). The main factors causing this reduction were habitat change due to human activity and excessive hunting pressure (Tucker & Heath 1995, Lucio & Purroy 1992a, Lucio et al. 1996, Borralho et al. 1997). However, the key demographic factors regulating population levels varied at different sites within its range (Putala & Hissa 1998).

Red-legged partridge is experiencing high hunting pressure in Spain (Peiró 1997), where >30,000 private game estates cover >70% of the territory (Villafuerte et al. 1998). Hunting regulations are based on local quotas fixed by individual hunting associations during the hunting season, which are established by each Regional Government. Quotas are included in a technical hunting plan, which is mandatory and must take into account management guidelines based on a 3-5-year forecast of game harvests and must be presented in annual hunting reports (AHR). However, regulations governing quotas and length of the hunting season are not supported by specific scientific studies about their effects on wild populations of red-legged partridge and other small-game species, but are rather based on local traditions and on hunters' intuition (Angulo & Villafuerte 2003).

In Andalusia (southern Spain), which is an autonomous community with a great hunting tradition (Metra Seis 1985), the red-legged partridge is the most popular small-game species (Vargas & Muñoz 1996). Between 1998-2005, an average of 976,610 individuals were harvested annually in Andalusia (Junta de Andalucía 2005).

Currently, management based on predator control and restocking has failed to recover the red-legged partridge. This management model is also problematic because it only takes into account factors operating on a very local scale (game estates have an average area of 722.1 ha in Andalusia). However, other factors operating at a regional scale have not been considered. Ricklefs (1987) and Levin (1992) pointed out that local populations are likely to be affected by historical and environmental processes that act on a regional scale. Thus, the study of regional-scale processes is important to comple-

ment local studies and to envision a broader management approach (Vaughn & Taylor 2000).

The game potential of the territory within a regional context has barely been investigated up to now (López-Ontiveros & García-Verdugo 1991). Recently, this new perspective in the management of game species was considered by Vargas et al. (2006). They identified areas in Andalusia where game yields for the red-legged partridge are high, and established environmental and land-use factors that determine these yields using municipalities as the operational work units. However, this scale of work is too coarse for real conservation and management planning applications. An alternative to this approach is to downscale the hunting yield model to another spatial resolution (e.g. Pearson et al. 2002, Barbosa et al. 2003, Araújo et al. 2005, Oja et al. 2005).

Our aim was to predict optimal areas for the red-legged partridge in Andalusia according to topography, climate, actual vegetation and land use, as well as their interactions using empirical modelling techniques. We downscaled the final model to 1 × 1-km squares to provide a much higher spatial resolution with the above aim, to be used in the regional and local management plans for this species for both hunting and conservation purposes.

Material and methods

Study area

Our work was carried out in Andalusia (Fig. 1), which covers 87,268 km² and is divided into 771 municipalities grouped into eight provinces. It has a Mediterranean climate, with mild winters and severe summer droughts. There is a decreasing west-to-east precipitation gradient. Medium-size mountain ranges predominate in the Andalusian landscape, covering 42% of its total surface area. The Sierra Morena range is situated along the northern fringe of Andalusia (range 400-1,300 m a.s.l) and has poor and moderately acid soils. The dominant vegetation includes evergreen oak forests *Quercus spp.* and scrubland, and the area is currently used for extensive livestock grazing and hunting. The Betic System range presents greater lithological heterogeneity and is sub-divided into two ranges, sub-Betic and Penibetic, separated by the intra-Betic ridge, which is a set of discontinuous depressions with most of the area used for agriculture (Ortega 1991). The dominant vegetation is comprised of pine forests

Pinus sp., evergreen oak forests and scrubland, and the hilly areas are dedicated to dry farming woody crops (mainly olive groves, almond groves, and vineyards). The maximum elevation (3,479 m a.s.l.) occurs in the Penibetic range. The Sierra Morena and the Betic System are NE-SW-oriented and mainly occupy the eastern part of Andalusia. The Guadalquivir Valley is oriented longitudinally between the Sierra Morena and Betic System. The valley bottom is covered by herbaceous crops and river terraces, and the hill slopes by woody crops. The Andalusian surface area is comprised of 47% agricultural land (Instituto de Estadística de Andalucía 2002). Olive groves and cereals are the main crops, which are fundamentally dry farming. The agricultural land is covered with 38% mountains with the crops generally restricted to the inner valleys or to hillsides with shallow slopes.

Hunting yields

We analysed 32,134 AHR from 1993-2001 reported by 6,049 game estates distributed throughout Andalusian municipalities. This information covers 4-9 hunting seasons for each municipality. Hunting season lengths were the same for every estate. Because digital maps of game estates were not available, we assigned each game estate to its corresponding municipality and estimated the average hunting

yields (HY) of red-legged partridge in each Andalusian municipality (N = 771), according to the following equation:

$$HY = \frac{\sum \text{mean annual number of partridges shot per game estate}}{\sum \text{areas of the game estates}} \times 100$$

where HY is the hunting yield per municipality expressed in numbers of red-legged partridges actually reported harvested per 100 ha of game estate. As our aim was to detect areas favourable to good hunting yields, which differs from predicting expected hunting yield values, we established six classes of hunting yields using a logarithmic scale between the extreme values obtained in the Andalusian municipalities (Farfán et al. 2004, Vargas et al. 2006). We considered the three highest classes, i.e. those with $HY > 12$, as representative of municipalities with good yields and the three lowest as representative of municipalities with poor yields. Then we produced a new binomial variable, good hunting yield (GHY), with a value of 1 in the municipalities with $HY > 12$ and 0 in those with $HY \leq 12$, to be used as the target variable in the modelling procedure. We preferred using a binary variable instead of modelling the continuous response of HY because the values of game harvest



Figure 1. Study area, showing the main mountain ranges (Sierra Morena and the Betic System, sub-divided into two ranges, Sub-betic and Penibetic) and the Guadalquivir valley.

reported in the AHR did not always correspond to true values, as some estates inflate the values to a certain extent while others tend to underestimate yields, so that actual reported values were not fully reliable. However, it is less likely that an estate with actual poor harvest reported good hunting yields and vice versa.

Predictive models

We characterised municipalities with good yields with respect to those with poor yields using stepwise logistic regression (Hosmer & Lemeshow 1989) on a set of climatic, topographic, land use and vegetation variables that were available as digital coverages (Table 1). Logistic regression is a widely used tool for modelling species distribution (e.g. Franco et al. 2000, Teixeira et al. 2001, Barbosa et al. 2003, Farfán et al. 2004, Monzón et al. 2004, Vargas et al. 2006, Vargas et al. 2007), including binary data that may be different from presence/absence of the species (Romero & Real 1996, Real et al. 2005). Altitude is released as a digital coverage by the Land Processes Distributed Active Archive Center, located at the US Geological Survey's EROS Data Center, <http://LPDAAC.usgs.gov>. Slope was calculated from altitude through the Idrisi SLOPE command (Eastman 2004). Climatic data variables result from records of 30 years and are generally representative of present climatic conditions (Font 2000) and were digitised using CartaLinx 1.2 software and processed using the Idrisi32 GIS software (Barbosa et al. 2003). Variables related to land use and vegetation cover expressed as the percentage of surface occupied were obtained by transforming the corresponding digital vector polygons into raster images. All variables were rasterised with a spatial resolution of 1 pixel = 1 km² and we averaged quantitative variable values for each municipality and extracted the proportion of each type of land use and vegetation cover in each municipality.

We used these variables to assess the variation in hunting yields due to overall influences of environment and human activity. Models constructed with these types of spatially-structured variables may have the same validity as those where the spatial autocorrelation is explicitly considered (Diniz-Filho et al. 2003). We did not include spatial variables, because they can reveal a geographical trend in distribution that does not reflect the spatial structure of the environmental predictor variables (Borcard et al. 1992, Diniz-Filho et al. 2003, Kühn 2007), but instead are related to historical events or migrations

Table 1. Variables available to model the potential distribution of red-legged partridge hunting yields on 1 × 1-km squares in Andalusia. Sources: 1) U.S. Geological Survey (1996), 2) Font (1983), 3) Montero de Burgos y González-Rebollar (1974), 4) Junta de Andalucía (1999).

Code	Variable
ALTI	Altitude (m) ⁽¹⁾
BL	Built land (% area) ⁽⁴⁾
CW	Conifer wood (% area) ⁽⁴⁾
DFRO	Mean annual number of frost days (minimum temperature < 0°C) ⁽²⁾
DDHER	Dry herbaceous crops (% area) ⁽⁴⁾
DHET	Dry heterogeneous crops (% area) ⁽⁴⁾
DS	Dense scrub (% area) ⁽⁴⁾
DSWC	Dense scrub with conifers (% area) ⁽⁴⁾
DSWD	Dense scrub with diverse trees (% area) ⁽⁴⁾
DSWO	Dense scrub with oaks (% area) ⁽⁴⁾
DWC	Dry wood crops (% area) ⁽⁴⁾
HCWO	Herbaceous crops with oaks (% area) ⁽⁴⁾
HJAN	Mean relative air humidity in January at 07:00 hours (%) ⁽²⁾
HJUL	Mean relative air humidity in July at 07:00 hours (%) ⁽²⁾
HRAN	Annual relative air humidity range (%) (= HJAN-HJUL) ⁽²⁾
IHER	Irrigated herbaceous crops (% area) ⁽⁴⁾
IHET	Irrigated heterogeneous crops (% area) ⁽⁴⁾
INSO	Mean annual insolation (hours/year) ⁽²⁾
IWC	Irrigated woody crops (% area) ⁽⁴⁾
MCNV	Mosaic of crops and natural vegetation (% area) ⁽⁴⁾
OAKW	Oak wood (% area) ⁽⁴⁾
PAST	Pasture (% area) ⁽⁴⁾
PET	Mean annual potential evapotranspiration (mm) ⁽²⁾
PIRR	Pluviometric irregularity ⁽³⁾
PREC	Mean annual precipitation (mm) ⁽²⁾
PWC	Pasture with conifers (% area) ⁽⁴⁾
PWO	Pasture with oaks (% area) ⁽⁴⁾
ROFF	Mean annual run-off (mm) ⁽²⁾
SLOP	Slope (%)
SRAD	Mean annual solar radiation (kwh/m ² /day) ⁽²⁾
SS	Sparse scrub (% area) ⁽⁴⁾
SSWC	Sparse scrub with conifers (% area) ⁽⁴⁾
SSWD	Sparse scrub with diverse trees (% area) ⁽⁴⁾
SSWO	Sparse scrub with oaks (% area) ⁽⁴⁾
TEMP	Mean annual temperature (°C) ⁽²⁾
TJAN	Mean temperature in January (°C) ⁽²⁾
TJUL	Mean temperature in July (°C) ⁽²⁾
TRAN	Annual temperature range (°C) (= TJUL-TJAN) ⁽²⁾
WETL	Wetlands (% area) ⁽⁴⁾

(Legendre 1993, Barbosa et al. 2001, Real et al. 2003), which are outside management scope.

We dealt with the familywise error rate (i.e. the increase in type I errors under repeated testing) by controlling the false discovery rate (FDR; Benjamini & Hochberg 1995, García 2003) using the procedure for all forms of dependency among test statistics proposed by Benjamini & Yekutieli (2001). We used the significant variables under an FDR of $q < 0.05$ to build a stepwise multiple logistic model of the species distribution, and selected the model corresponding

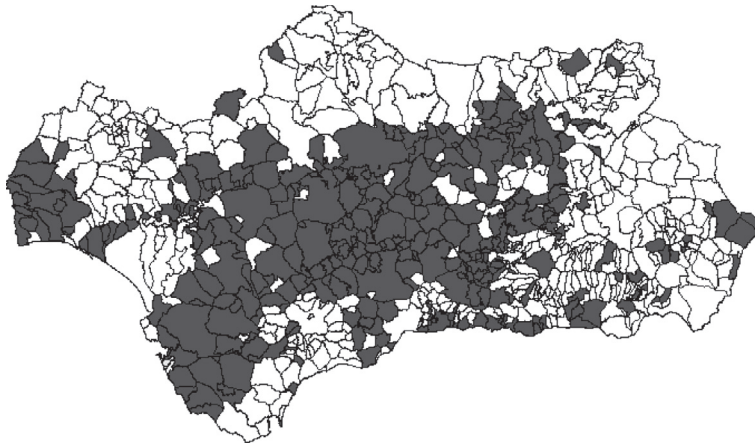


Figure 2. Municipalities with good hunting yields (GHY) for red-legged partridge in Andalusia (in dark).

to the step with the best Akaike information criterion (AIC) score (Akaike 1973, Burnham & Anderson 1998). The estimation of the parameters in the equation y was by maximum likelihood and was assessed using the test of Wald (1943).

We modelled the favourability for obtaining good hunting yields of red-legged partridge using the environmental favourability function described by Real et al. (2006), which may be obtained by performing logistic regression on good and poor hunting yields (ones and zeros, respectively) on a series of predictor variables, and then eliminating the effect of the uneven proportion of ones and zeros in the dataset from the model. The favourability for a good hunting yield in each municipality is obtained from the formula:

$$F = (P/(1-P))/((N_1/N_0) + (P/(1-P)))$$

where P is the probability value given by logistic regression, and N_1 and N_0 are the number of municipalities with good and poor hunting yields, respectively (Real et al. 2006).

Variables introduced into the final predictive model were grouped into topographic, climatic and

vegetation factors. We produced partial models based on variables related to these factors, and these partial models were evaluated using the Akaike information criterion (Akaike 1973). To account for interactions (Borcard et al. 1992, Legendre 1993), we performed a variation partitioning procedure to specify how much of the variation of the final model was explained by the pure effect of each explanatory variable, which proportion was attributable to their interaction, and how these factors interact affecting distribution of good hunting yields of red-legged partridge (Legendre 1993, Legendre & Legendre 1998; see an application in Muñoz et al. 2005).

The favourability equation obtained in the regression performed on municipalities was then introduced into the Idrisi Image Calculator and used to downscale the final model and create an image representing the expected favourability of obtaining good hunting yields of the red-legged partridge in 1×1 -km squares in Andalusia. This was a deductive application of the model based on the municipalities, applying the inferences obtained inductively at the municipality level to a finer scale level (Barbosa et al. 2003, Araújo et al. 2005).

Table 2. Variables and their coefficients (β) selected by stepwise logistic regression to predict the distribution of red-legged partridge hunting yields in 1×1 -km squares of Andalusia. The variables are ranked according to their order of entrance in the model and is coded as in Table 1. Wald shows the Wald test values. R^2 indicates the squared Pearson's correlation coefficients between the favourability predicted by a model including the variable and those that entered before it and the favourabilities predicted by the final model.

Variable	Coefficient (β)	SE	Wald	P	R^2
DHER	3.460	0.439	62.185	$3.127e^{-15}$	0.331
DWC	3.234	0.356	82.309	$1.164e^{-19}$	0.713
DFRO	-0.043	0.011	14.543	0.000137	0.947
ALTI	-0.002	0.0005	12.306	0.000452	0.969
TEMP	-0.308	0.111	7.748	0.00538	1.000

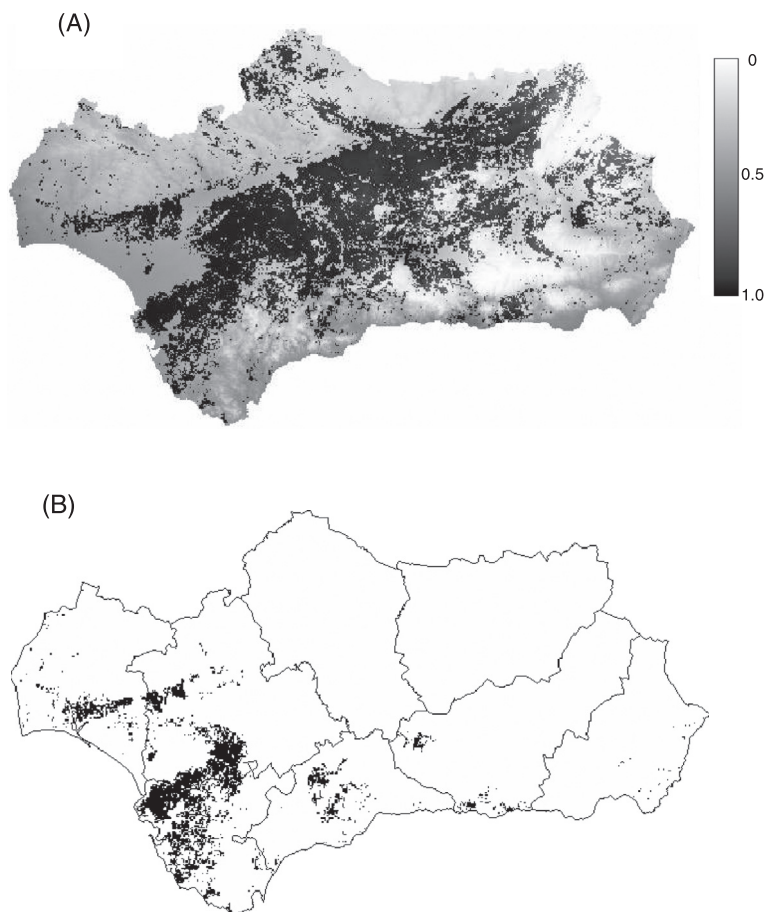


Figure 3. A) Favourability values for red-legged partridge good hunting yields in each 1×1 -km square of Andalusia, shown on a scale ranging from 0 (white) to 1 (black). B) Only the 1×1 -km squares where the favourability to obtain good hunting yields is ≥ 0.95 are shown (in black). Black lines correspond to province limits.

Results

Good hunting yields (GHY) for the red-legged partridge was found in 43% of Andalusian municipalities (Fig. 2). The step with the lowest AIC value ($AIC=917.15$) produced by the stepwise procedure included five variables (Table 2). The most favourable areas for obtaining good hunting yields are, according to this function, cultivated zones composed of dry herbaceous and wood crops (DHER, DWC), located at low altitudes (ALTI) with warm winters (DFRO) and mild summers (TEMP). Favourable areas are mainly located along the Guadalquivir valley and in the plains between the sub-Betic and Penibetic ranges (Fig. 3A). However, the 1×1 -km squares with favourability values >0.95 (Fig. 3B) are basically situated in the western-most regions in these areas.

Figure 4 shows the favourability models obtained for the topographic, climatic and vegetation factors. The similarity of Figures 3A and 4C suggests that the

grouped distribution of good hunting yields seems to be caused mainly by the vegetation effect. In fact, the model based on the vegetation had the lowest AIC value ($AIC=978.60$), followed by the model based on topography ($AIC=1060.79$), and that based on climate ($AIC=1082.97$).

Variation partitioning of the final model (Fig. 5) indicates that climate and topography have a positive interaction, as well as topography and vegetation, and climate, vegetation and topography together. However, pure climate has a negative interaction with pure vegetation.

Discussion

The large-scale modelling of species' hunting yields may be a fundamental tool for game management and conservation as it provides a broader geographic perspective that works as a context for local studies. Spatial modelling has undergone a great advance in recent years with the progresses in spatial

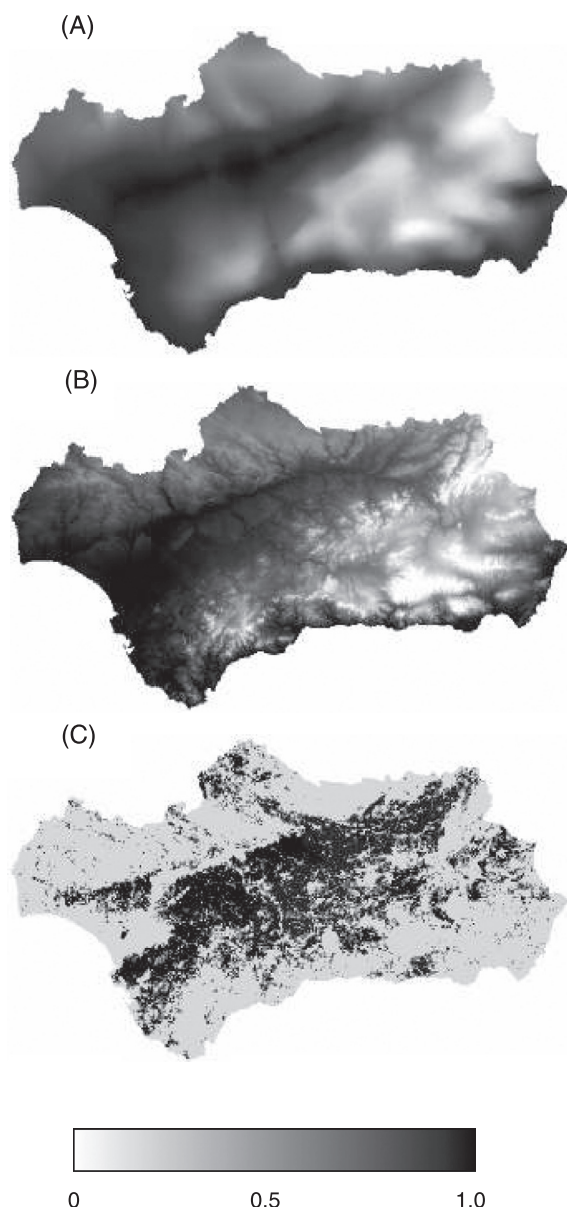


Figure 4. Favourability maps predicted by the climatic (A), topographical (B) and vegetation (C) factors in each 1 × 1 km-square of Andalusia.

statistics and the generalisation of the use of Geographic Information Systems (GIS). These systems are designed to store, transform, analyse and represent geographically referenced data, and allow for a greater scope and precision in forecasting hunting yields in several kinds of geographical units. With the help of GIS and large-scale models, game management may obtain more satisfactory results as the factors that affect game populations on a larger scale are taken into account.

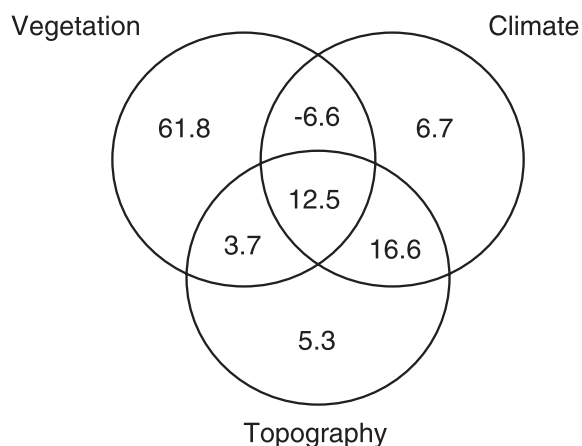


Figure 5. Results of the variation partitioning of the final model. Values shown in the diagrams are the percentages of variation explained by the indicated factors and by their interactions.

The distribution of good hunting yields (GHY) in the municipalities of Andalusia provides an acceptable representation of the current good and poor hunting areas for red-legged partridge in this region (Vargas et al. 2006). Density and hunting yield are not always equivalent parameters (Lucio 1991), but at a macrospatial scale, when relative abundance values per unit area are lacking, hunting yields obtained from AHR provide a realistic image of both potential and current good and poor areas (Farfán et al. 2004, Vargas et al. 2006). Therefore, this is an easy and inexpensive method for assessing relative abundance of partridge at a regional scale (Gortázar et al. 2002). However, hunting yields are affected by human-induced land use and environmental conditions. This is why we included land-use variables in our models.

Red-legged partridge restocking may also mask the actual scarcity of native individuals in some localities, which might hinder the use of hunting yield models to infer partridge abundance. However, if restocking effort were homogeneously distributed, then the model would not be affected by it, and geographical variation in restocking effort not related to the variables used in this study would cause variation in hunting yields regardless of the modelled environmental conditions, thus forming part of the residuals not explained by the environmental model, but not affecting the model itself. In contrast, if restocking effort were higher in municipalities with certain environmental conditions measured in this study, then the areas modelled as favourable for the partridge would include areas where partridge release is more likely. However,

releases are performed basically to maintain traditional hunting yield levels (Nadal 1998), so that the releases are more or less proportional to the hunters' expectancy of hunting success, which, in turn, are related to favourable conditions for the partridge. Nevertheless, most game estates are hunting above their current carrying capacity, since the decline in hunting yield over the last 20 years (Blanco-Aguilar et al. 2003), close to 42% in Andalusia (Vargas et al. 2006), has not resulted in a diminished hunting pressure. This is why the threshold we used to consider a hunting yield as good was obtained in relation to all reported hunting yields, and should be understood as a relative rather than an absolute threshold.

We used the AHR as information source, because it is an indirect sampling method that provides homogenous data in a large temporal series, with evident savings in material and human resources. Indirect sampling methods have been successfully used in game research (Tellería & Sáez-Royuela 1985, Vargas & Muñoz 1996, Oleson & He 2004). Nevertheless, Landry (1983) and Bravo & Peris (1998b) question the accuracy of these data and, therefore, their validity in this kind of study. The AHR contain omissions and errors, although many of these can be corrected by filtering the data. This allows us to discard from the analysis the game estates whose AHR have questionable data on hunting yields. Thus, the AHR provide a valid database for conducting some statistical analyses, particularly when the study area, sample size and temporal series are large (Bravo & Peris 1998a,b) as in our study.

Using the information included in the AHR, Vargas et al. (2006) showed that good hunting yields of red-legged partridge in Andalusia are obtained in municipalities located along the lower and middle basin of the Guadalquivir valley and in the plains situated between the sub-Betic and Penibetic ranges. According to their model, good hunting yields were obtained mainly in highly mechanised and intensively farmed dry cropland in low-elevation areas. These results are concordant with the habitat requirements of the species at a smaller scale in other areas of their current range (Rands 1987, Ricci et al. 1990, Meriggi et al. 1991, Lucio & Purroy 1992b) and should be considered in the development of future regional management plans for this species.

Considering the current status of this species, Vargas et al. (2006) suggested that there is a need to create protected areas to ensure maintenance of high

density groups and the genetic characteristics of wild populations of red-legged partridge in Andalusia. Management measures in these areas would involve maintenance of habitat heterogeneity, controlling hunting pressure and thorough quality control regarding restocking practices (Pépin & Blayac 1990, Borralho et al. 1997, Lucio 2002). An effort should also be made to encourage agricultural practices that benefit partridge. Partridges thrive in areas with small fields and maximised woody/shrubby edge. Nevertheless, if agricultural practices drift toward larger fields or convert to row-crops (i.e. soybeans), partridge populations may decline (Gortázar et al. 2002, Ricci & Garrigues 1986). However, the scale of the distribution map and favourability model (Vargas et al. 2006) are too coarse to determine the exact location and size of proposed protected areas. A predictive model with more precise spatial resolution for management and conservation planning applications would be useful. Downscaling the model to 1×1 -km squares provided a much higher spatial resolution in predicting good hunting yields for this species, although the variables related to human activities used by Vargas et al. (2006), which were not available at this resolution scale, could not be used. Previous studies have used environmental variables to construct predictive models (Laurance 1991, Purvis et al. 2000, Pearson et al. 2002, Norris & Harper 2004). However, this approach only considers one aspect of a complex problem, since predictive models constructed with both environmental and human variables better reflect the complexity of factors involved, thereby increasing the predictive power of such models (Barbosa et al. 2003, Cardillo et al. 2004, Keane et al. 2005, Muñoz et al. 2005, Vargas et al. 2006). As Araújo et al. (2005) pointed out, losses and gains of information arise from downscaling procedures and, consequently, the usefulness of the process depends on the goals and the ability to test results.

Traditional land use has changed during the second half of the 20th century in agricultural and forest areas in Andalusia (Fernández-Ales et al. 1992). Such changes have mainly consisted of intensified activity in the most productive agricultural areas, in the Guadalquivir valley and the plains of the Betic range, abandoning traditional uses in mountain areas, plus the natural regeneration of scrubland (Fernández-Ales et al. 1992, BCH 2000). Abandonment of traditional agrarian activities in medium-sized mountains resulted in habitat homogenisation and patchiness reduction, negatively

affecting red-legged partridge (Lucio et al. 1996, Duarte & Vargas 2002).

Positive interactions between factors (see Fig. 5) mean that characteristics of these factors that favour good hunting yields of red-legged partridge tend to be present simultaneously. Our results suggest vegetation is the most important factor of those considered explaining the distribution of good hunting yields of red-legged partridge in Andalusia. From a mathematical point of view, negative interactions measure the amount in which the effect of a factor is obscured by another factor through interrelationships among variables (Cartron et al. 2000, Bárcena et al. 2004). The negative interaction between pure vegetation and climate suggests that, given similar topographic conditions, the effects of vegetation and climate on good hunting yields conflict with one another. In other words, favourable climatic conditions tend to not coincide with the favourable vegetation conditions given constant topography.

Our results could be used to improve current management of red-legged partridge in Andalusia in three ways. First, habitat management is the fundamental element necessary for maintaining and increasing wild populations of this species (Lucio 1992, Vargas 2002). This study shows that most of the variation observed in the distribution of good hunting yields is exclusively explained by vegetation, indicating that habitat should play an important role in future regional management plans. Up to the present, local initiatives individually undertaken in game estates to recover red-legged partridge have mainly included predator control and restocking with partridge reared on farms to maintain harvest rates.

Second, favourable areas should be used as recovery areas for wild populations of red-legged partridge. Although restocking may be justified and beneficial in some cases (Carvalho et al. 1998), this practice is rarely carried out with scientific rigour following good conservation practices. Consequently, restocking is counterproductive for wild populations of red-legged partridge (Gortázar 1998, Blanco-Aguilar et al. 2003, Alonso et al. 2005). Thus, restocking should follow a sound protocol (Gortázar et al. 2000) and individuals should be released in the most favourable areas for the species, since outside these, the probability of obtaining good results is lower, especially if the factors which caused the decline are still present (Goñi et al. 1997, Duarte & Vargas 2001).

Third, hunting pressure should be regulated in relation to the potential of the territory, especially in those areas less favourable for the species where maintaining the presence of wild populations is difficult. Thus, knowing the potential of the territory for this species at a fine-resolution scale may be useful to adopt different game management strategies according to the local characteristics of the territory. This research approach provides regional governments with a new tool for devising more suitable local game management policies for this species.

References

- Aebischer, N. & Lucio, A. 1997: Red-legged partridge (*Alectoris rufa*). - In: Hagemeyer, E.J.M. & Blair, M.J. (Eds.); The EBBC Atlas of European Breeding Birds: Their Distribution and Abundance. - T & AD Poyser, London, pp. 208-209.
- Aebischer, N.J. & Potts, G.R. 1994: Red-legged Partridge *Alectoris rufa*. - In: Tucker, G.M. & Heath, M.F. (Eds.); Birds in Europe: their conservation status. - BirdLife International, Cambridge, pp. 214-215.
- Akaike, H. 1973: Information theory and an extension of the maximum likelihood principle. - In: Petrov, B.N. & Csaki, F. (Eds.); Proceedings of the Second International Symposium on Information Theory. - Akademiai Kiado, Budapest, Hungary, pp. 267-281.
- Alonso, M.E., Pérez, J.A., Gaudioso, V.R., Diéz, C. & Prieto, R. 2005: Study of survival, dispersal and home range of autumn-released red-legged partridges (*Alectoris rufa*). - British Poultry Science 46: 401-406.
- Angulo, E. & Villafuerte, R. 2003: Modelling hunting strategies for the conservation of wild rabbit populations. - Biological Conservation 115: 291-301.
- Araújo, M.B., Thuiller, W. & Williams, P.H. 2005: Downscaling European species atlas distributions to a finer resolution: implications for conservation planning. - Global Ecology and Biogeography 14: 17-30.
- Barbosa, A.M., Real, R., Márquez, A.L. & Rendón, M.A. 2001: Spatial, environmental and human influences on the distribution of otter (*Lutra lutra*) in the Spanish provinces. - Diversity and Distributions 7: 137-144.
- Barbosa, A.M., Real, R., Olivero, J. & Vargas, J.M. 2003: Otter (*Lutra lutra*) distribution modeling at two resolution scales suited to conservation planning in the Iberian Peninsula. - Biological Conservation 114: 377-387.
- Bárcena, S., Real, R., Olivero, J. & Vargas, J.M. 2004: Latitudinal trends in breeding waterbird species richness in Europe and their environmental correlates. - Biodiversity and Conservation 13: 1997-2014.

- BCH (Banco Central Hispano) 2000: Los árboles en el espacio agrario. Importancia hidrológica y ecológica. - Servicio Agrario y Medioambiental-BCH, Madrid, 96 pp. (In Spanish).
- Benjamini, Y. & Hochberg, Y. 1995: Controlling the false discovery rate: a practical and powerful approach to multiple testing. - Journal of the Royal Statistical Society 57: 289-300.
- Benjamini, Y. & Yekutieli, D. 2001: The control of the false discovery rate in multiple testing under dependency. - The Annals of Statistics 29: 1165-1188.
- BirdLife International 2004: Birds in Europe: population estimates, trends and conservation status. - Cambridge, U.K., BirdLife International, BirdLife Conservation Series No. 12, 374 pp.
- Blanco-Aguilar, J.C., Virgós, E. & Villafuerte, R. 2003: Perdiz roja, *Alectoris rufa*. - In: Martí, R. & del Moral, J.C. (Eds.); Atlas de las aves reproductoras de España. - Dirección General de Conservación de la Naturaleza-Sociedad Española de Ornitología, Madrid, pp. 212-213. (In Spanish).
- Borcard, D., Legendre, P. & Drapeau, P. 1992: Partialling out the spatial component of ecological variation. - Ecology 73: 1045-1055.
- Borrallho, R., Carvalho, S., Rego, F. & Vaz-Pinto, P. 1999: Habitat correlates of red-legged partridge (*Alectoris rufa*) breeding density on Mediterranean farmland. - Revue de Ecologie (Terre Vie) 54: 59-69.
- Borrallho, R., Rego, F. & Vaz-Pinto, P. 1997: Demographic trends of Red-legged partridge (*Alectoris rufa*) in Southern Portugal after implementation of management actions. - Gibier Faune Sauvage 14: 585-600.
- Bravo, F. & Peris, S.J. 1998a: El valor de los planes cinegéticos. - Trofeo 120: 25-28. (In Spanish).
- Bravo, F. & Peris, S.J. 1998b: Los planes cinegéticos: su interés en la evaluación demográfica de la perdiz roja (*Alectoris rufa*). (In Spanish with an English summary: Game planning: their importance about demographic evaluation of the red-legged partridge (*Alectoris rufa*). - Ecología 12: 413-421.
- Burnham, K.P. & Anderson, D.R. 1998: Model selection and inference. A practical information theoretic approach. - Springer Verlag, New York, USA, 353 pp.
- Calderón, J. 1977: El papel de la perdiz roja (*Alectoris rufa*) en la dieta de los predadores Ibéricos. - Doñana, Acta Vertebrata 4: 61-126. (In Spanish).
- Cardillo, M., Purvis, A., Sechrest, W., Gittleman, J.L., Bielby, J. & Mace, G.M. 2004: Human population density and extinction risk in the world's carnivores. - Public Library of Science, Biology 2: 909-914.
- Cartron, J.-L.E., Kelly, J.F. & Brown, J.H. 2000: Constraints on patterns of covariation: a case study in strigid owls. - Oikos 90: 381-389.
- Carvalho, J., Castro-Pereira, D. & Borrallho, R. 1998: Red-legged partridge *Alectoris rufa* restocking programs: their success and implications on the breeding population. - Gibier Faune Sauvage 15: 465-474.
- Delibes, J. 1992: Gestión de los cotos de perdiz roja. - In: Fundación 'La Caixa' (Ed.); La perdiz roja. Gestión del hábitat. Fundación 'La Caixa', Barcelona, pp. 141-146. (In Spanish).
- Diniz-Filho, J.A., Bini, L.M. & Hawkins, B.A. 2003: Spatial autocorrelation and red herrings in geographical ecology. - Global Ecology and Biogeography 12: 53-64.
- Duarte, J. & Vargas, J.M. 2001: Estudio de poblaciones, gestión del hábitat y depredación en explotaciones extensivas de caza. Las repoblaciones como herramienta de gestión cinegética. - In: Linares, D., Zurita, F. & Ramón, J. (Eds.); Actividades cinegéticas. - Grupo Editorial Universitario, Universidad de Granada, Granada, pp. 133-145. (In Spanish).
- Duarte, J. & Vargas, J.M. 2002: Los sumideros de perdiz roja a lo largo del ciclo anual. - In: Lucio, A. & Sáenz de Buruaga, M. (Eds.); Aportaciones a la gestión sostenible de la caza en España. FEDENCA-EEC, Madrid, pp. 55-71. (In Spanish).
- Eastman, J.R. 2004: Idrisi Kilimanjaro GIS, User Guide and Software. - Clark Labs, Clark University, USA, 328 pp.
- Farfán, M.A., Guerrero, J.C., Real, R., Barbosa, A.M. & Vargas, J.M. 2004: Caracterización del aprovechamiento cinegético de los mamíferos en Andalucía. (In Spanish with an English summary: Game harvest characterisation of the mammals in Andalusia). - Galemys 16: 41-59.
- Fernández-Ales, R., Martín, A., Ortega, F. & Ales, E.E. 1992: Recent changes in landscape structure and function in a mediterranean region of SW Spain (1950-1984). - Landscape Ecology 7: 3-18.
- Font, I. 1983: Atlas climático de España. - Instituto Nacional de Meteorología, Madrid, 47 pp. (In Spanish).
- Font, I. 2000: Climatología de España y Portugal. - Ediciones Universidad de Salamanca, Salamanca, 422 pp. (In Spanish).
- Fortuna, M.A. 2002: Selección de hábitat de la perdiz roja *Alectoris rufa* en periodo reproductor en relación con las características del paisaje de un agrosistema de la Mancha (España). (In Spanish with an English summary: Red Partridge *Alectoris rufa* habitat selection during the breeding season in relation with the landscape traits of an agricultural area in La Mancha (Spain). - Ardeola 49: 59-66.
- Franco, A.M.A., Brito, J.C. & Almeida, J. 2000: Modeling habitat selection of common cranes *Grus grus* wintering in Portugal using multiple logistic regression. - Ibis 142: 351-358.
- Fungesma (Fundación para la Gestión y Protección del Medio Ambiente) 2001: Buenas Prácticas Cinegéticas. - Mundiprensa, Madrid, 236 pp. (In Spanish).

- García, L.V. 2003: Controlling the false discovery rate in ecological research. - *Trends in Ecology and Evolution* 18: 553-554.
- Goñi, M., Gortázar, C., Marco, J. & Fernández de Luco, D. 1997: Su efectividad en la práctica: repoblaciones con perdiz roja. - *Trofeo* 326: 24-31. (In Spanish).
- Gortázar, C. 1998: Las repoblaciones con perdiz roja. - In: FEDENCA/Grupo Editorial V (Eds.); *La perdiz roja*. I Curso, Madrid, pp. 119-131. (In Spanish).
- Gortázar, C., Villafuerte, R. & Martín, M. 2000: Success of traditional restocking of Red-legged partridge for hunting purposes in areas of low density of Northeast Spain Aragón. - *Zeitschrift für Jagdwissenschaft* 46: 23-30.
- Gortázar, C., Villafuerte, R., Escudero, M.A. & Marco, J. 2002: Post-breeding densities of the Red-Legged Partridge (*Alectoris rufa*) in agrosystems: A large-scale study in Aragón, Northeastern Spain. - *Zeitschrift für Jagdwissenschaft* 48: 94-101.
- Hosmer, D.W. & Lemeshow, S. 1989: Applied logistic regression. - John Wiley and Sons, Inc., New York, 307 pp.
- Instituto de Estadística de Andalucía 2002: Anuario Estadística de Andalucía, 2002. - Junta de Andalucía, Sevilla, 735 pp. (In Spanish).
- Junta de Andalucía 2005: Estadísticas de caza en Andalucía. - Número de piezas cazadas en actividades cinegéticas. Available at: <http://www.juntadeandalucia.es/medioambiente/site/web/>. (In Spanish).
- Junta de Andalucía 1999: Mapa de usos y coberturas vegetales del suelo de Andalucía 1999. - Consejería de Medio Ambiente, Sevilla, 18 pp. (In Spanish).
- Keane, A., Brooke, M. de L. & McGowan, P.J.K. 2005: Correlates of extinction risk and hunting pressure in gamebirds (Galliformes). - *Biological Conservation* 126: 216-233.
- Kühn, I. 2007: Incorporating spatial autocorrelation may invert observed patterns. - *Diversity and Distributions* 13: 66-69.
- Landry, P. 1983: Les méthodes et les données disponibles sur les statistiques relatives aux tableaux de chasse dans les pays européens. - *Bulletin de la Office National de la Chasse* 70: 33-42. (In French).
- Laurance, W.F. 1991: Ecological correlates of extinction proneness in Australian tropical rain-forest mammals. - *Conservation Biology* 5: 79-89.
- Legendre, P. 1993: Spatial autocorrelation: trouble or new paradigm? - *Ecology* 74: 1659-1673.
- Legendre, P. & Legendre, L. 1998: Numerical ecology. 2nd English Edition. - Elsevier Science, Amsterdam, 853 pp.
- Levin, S.A. 1992: The problem of pattern and scale in ecology. - *Ecology* 73: 1943-1967.
- López-Ontiveros, A. & García-Verdugo, F.J. 1991: Geografía de la caza en España. - *Agricultura y Sociedad* 58: 81-112. (In Spanish).
- Lucio, A. 2002: Caza y conservación de la naturaleza. Nuevas tendencias en ordenación cinegética. - In: Lucio, A. & Sáenz de Buruaga, M. (Eds.); *Aportaciones a la gestión sostenible de la caza en España*. - FEDENCA-EEC, Madrid, pp. 295-312. (In Spanish).
- Lucio, A. 1992: Gestión de las poblaciones de perdiz roja. - In: Fundación 'La Caixa' (Ed.); *La perdiz roja. Gestión del hábitat*. Fundación 'La Caixa', Barcelona, pp. 109-115. (In Spanish).
- Lucio, A. 1991: Ordenación y gestión en caza menor. - In: Fuentes, A., Sánchez, I. & Pajuelo, L. (Eds.); *Manual de ordenación y gestión cinegética*. IFEBA, Badajoz, pp. 219-255. (In Spanish).
- Lucio, A. 1998: Recuperación y gestión de la perdiz roja en España. - In: FEDENCA/Grupo Editorial V (Eds); *La perdiz roja*. I Curso, Madrid, pp. 63-90. (In Spanish).
- Lucio, A. & Purroy, F.J. 1992a: Caza y conservación de aves en España. (In Spanish with an English summary: *Hunting and bird conservation in Spain*). - *Ardeola* 39: 85-98.
- Lucio, A. & Purroy, F.J. 1992b: Red legged partridge (*Alectoris rufa*) habitat selection in northwest Spain. - *Gibier Faune Sauvage* 9: 417-429.
- Lucio, A., Purroy, F., Sáenz de Buruaga, M. & Llamas, O. 1996: Consecuencias del abandono agroganadero en áreas de montaña para la conservación y aprovechamiento cinegético de las perdices roja y pardilla en España. - *Revista Florestal* 9: 305-318. (In Spanish).
- Meriggi, A., Montagna, D. & Zacchetti, D. 1991: Habitat use by partridges (*Perdix perdix* and *Alectoris rufa*) in an area of northern Apennines, Italy. - *Bollettino di Zoologia* 58: 85-90.
- Metra Seis 1985: Turismo cinegético en España. - Secretaría General de Turismo. Ministerio de Transportes, Turismo y Comunicaciones, Madrid, 276 pp. (In Spanish).
- Montero de Burgos, J.L. & González-Rebollar, J.L. 1974: Diagramas bioclimáticos. - ICONA, Madrid, 379 pp. (In Spanish).
- Monzón, A., Fernández, P. & Rodríguez, N. 2004: Vegetation structure descriptors regulating the presence of wild rabbit in the National Park of Peneda-Gerês, Portugal. - *European Journal of Wildlife Research* 50: 1-6.
- Muñoz, A.R., Real, R., Barbosa, A.M. & Vargas, J.M. 2005: Modelling the distribution of Bonelli's eagle in Spain: implications for conservation planning. - *Diversity and Distributions* 11: 477-486.
- Nadal, J. 1998: La bioecología de la perdiz roja. - In: Federación Española de Caza. (Ed.); *La perdiz roja*. Madrid: Federación Española de Caza, pp. 33-45. (In Spanish).
- Norris, K. & Harper, N. 2004: Extinction processes in hot spots of avian biodiversity and the targeting of pre-emptive conservation action. - *Proceedings of the Royal Society of London, Series B* 271: 123-130.

- Oja, T., Alamets, K. & Pärnamets, H. 2005: Modelling bird habitat suitability based on landscape parameters at different scales. - *Ecological Indicators* 5: 314-321.
- Oleson, J.J. & He, C.Z. 2004: Space-time modeling for the Missouri Turkey Hunting Survey. - *Environmental and Ecological Statistics* 11: 85-101.
- Ortega, F. 1991: El medio físico. - *Geografía de España: Andalucía. Canarias*, Editorial Planeta, Barcelona, Volume 8: 83-109. (In Spanish).
- Pearson, R.G., Dawson, T.E., Berry, P.M. & Harrison, P.A. 2002: SPECIES: a Spatial Evaluation of Climate Impact on the Envelope of Species. - *Ecological Modelling* 154: 289-300.
- Peiró, V. 1997: Gestión ecológica de los recursos cinegéticos. - Universidad de Alicante, Alicante, 138 pp. (In Spanish).
- Pépin, D. & Blayac, J. 1990: Impacts d'un aménagement de la garrigue et de l'instauration d'un plan de chasse sur la démographie de la perdrix rouge (*Alectoris rufa*) en milieu méditerranéen. (In French with an English summary: Impacts on habitat improvement and game management on the demography of a red-legged partridge (*Alectoris rufa*) mediterranean population). - *Gibier Faune Sauvage* 7: 145-158.
- Purvis, A., Gittleman, J.L., Cowlshaw, G. & Mace, G.M. 2000: Predicting extinction risk in declining species. - *Proceedings of the Royal Society of London, Series B* 267: 1947-1952.
- Putala, A. & Hissa, R. 1998: Breeding dispersal and demography of wild and hand-reared grey partridges *Perdix perdix* in Finland. - *Wildlife Biology* 4: 137-145.
- Rands, M. 1987: Hedgerow management for the conservation of Partridges. - *Biological Conservation* 4: 127-139.
- Real, R., Barbosa, A.M., Martínez-Solano, I. & García-París, M. 2005: Distinguishing the distributions of two cryptic frogs (Anura: Discoglossidae) using molecular data and environmental modeling. - *Canadian Journal of Zoology* 83(4): 536-545.
- Real, R., Barbosa, A.M., Porras, D., Kin, M.S., Márquez, A.L., Guerrero, J.C., Palomo, L.J., Justo, E.R. & Vargas, J.M. 2003: Relative importance of environment, human activity and spatial situation in determining the distribution of terrestrial mammal diversity in Argentina. - *Journal of Biogeography* 30: 939-947.
- Real, R., Barbosa, A.M. & Vargas, J.M. 2006: Obtaining environmental favourability functions from logistic regression. - *Environmental and Ecological Statistics* 13: 237-245.
- Ricci, J.C. & Garrigues, R. 1986: Influence de certaines caractéristiques des agrosystèmes sur les populations des perdrix grises (*Perdix perdix* L.) dans la région nord-bassin parisien. - *Gibier Faune Sauvage* 3: 369-392. (In French).
- Ricci, J.C., Mathon, J., García, A., Berger, F. & Esteve, J. 1990: Effect of habitat structure and nest site selection on nest predation in red-legged partridges in french mediterranean farmlands. - *Gibier Faune Sauvage* 7: 231-253.
- Ricklefs, R.E. 1987: Community diversity: relative roles of local and regional processes. - *Science* 235: 167-171.
- Romero, J. & Real, R. 1996: Macroenvironmental factors as ultimate determinants of distribution of common toad and natterjack toad in the south of Spain. - *Ecography* 19: 305-312.
- Teixeira, J., Ferrand, N. & Arntzen, J.W. 2001: Biogeography of the golden-striped salamander, *Chioglossa lusitana*: a field survey and spatial modelling approach. - *Ecography* 24: 618-623.
- Tellería, J.L. & Sáez-Royuela, C. 1985: L'évolution démographique du sanglier (*Sus scrofa*) en Espagne. (In French with an English summary: The demographic evolution of the wild boar (*Sus scrofa*) in Spain). - *Mammalia* 49: 195-202.
- Tucker, G.M. & Heath, M.F. 1995: Birds in Europe: their conservation status. - Cambridge, U.K., Birdlife International Birdlife Conservation Series no 3, 600 pp.
- U.S. Geological Survey 1996: GTOPO30. - Land Processes Distributed Archive Center. Available at: <http://edcdaac.usgs.gov/gtopo30/gtopo30.asp>
- Vargas, J.M. 2002: Alerta cinegética. Reflexiones sobre el futuro de la caza en España. - Otero, Madrid, 398 pp. (In Spanish).
- Vargas, J.M., Farfán, M.A., Guerrero, J.C., Barbosa, A.M. & Real, R. 2007: Geographical and environmental correlates of big and small game in Andalusia (southern Spain). - *Wildlife Research* 34: 498-506.
- Vargas, J.M., Guerrero, J.C., Farfán, M.A., Barbosa, A.M. & Real, R. 2006: Land use and environmental factors affecting red-legged partridge (*Alectoris rufa*) hunting yields in Southern Spain. - *European Journal of Wildlife Research* 52: 188-195.
- Vargas, J.M. & Muñoz, A.R. 1996: Panorámica de la caza menor en Andalucía. - In: Federación Andaluza de Caza (Eds.); La caza en Andalucía y su problemática. Federación Andaluza de Caza, Archidona, pp. 1-19. (In Spanish).
- Vaughn, C.C. & Taylor, C.M. 2000: Macroecology of a host-parasite relationship. - *Ecography* 23: 11-20.
- Villafuerte, R., Viñuela, J. & Blanco, J.C. 1998: Extensive predator persecution caused by population crash in a game species: the case of Red kites and Rabbits in Spain. - *Biological Conservation* 84: 181-188.
- Wald, A. 1943: Tests of statistical hypotheses concerning several parameters with applications to problems of estimation. - *Transactions of the American Mathematical Society* 54: 426-482.