

Long-Term Changes in Game Species Over a Long Period of Transformation in the Iberian Mediterranean Landscape

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Received: 23 June 2008 / Accepted: 27 March 2009
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Abstract Agricultural change has transformed large areas of traditional farming landscapes, leading to important changes in the species community assemblages in most European countries. We suspect that the drastic changes in land-use that have occurred in Andalusia (southern Spain) over recent decades, may have affected the distribution and abundance of game species in this region. This article compares the distribution of the main game species in Andalusia during the 1960s and 1990s, using data from maps available from the Mainland Spanish Fish, Game and National Parks Service and from recent datasets on hunting yield distributions, respectively. Big-game and small-game species were significantly segregated in southern Spain during the 1990s, as two clearly independent chorotypes (groups of species whose abundances are similarly distributed) were obtained from the classification analysis. In contrast, big-game and small-game species were not significantly segregated several decades ago, when there was only one chorotype consisting of small-game species and wild boar. The other three ungulates did not constitute a significant chorotype, as they showed positive correlations with some species in the group mentioned above. These changes seem to be a consequence of the transformations

that have occurred in the Iberian Mediterranean landscape over the last few decades. The abandoning of traditional activities, and the consequent formation of dense scrubland and woodland, has led to an expansion of big-game species, and a decrease of small-game species in mountain areas. Moreover, agricultural intensification has apparently depleted small-game species populations in some agricultural areas. On the other hand, the increasingly intensive hunting management could be artificially boosting this segregation between small-game and big-game species. Our results suggest that the conservation and regeneration of traditional agricultural landscapes (like those predominating in the 1960s) should be a priority for the conservation of small-game species.

Keywords Agricultural intensification · Chorotypes · Hunting yield distributions · Land abandonment · Spain · Traditional farming landscapes

Introduction

In most European countries, the intensification of agriculture has transformed large areas of traditional farming landscapes (Fernández-Alés and others 1992). The habitats maintained by traditional agricultural activities were species-rich areas which harbored species associations with different biogeographical and ecological origins (Schmitt and Rákosy 2007). However, agriculture intensification has caused important changes in species communities (Matson and others 1997), decreasing α -diversity and favoring the dominance of generalist species (Schmitt and Rákosy 2007). As a result of this process, traditional agricultural habitats are now considered one of the most important natural heritages of Europe and hence represent a major

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conservation priority (WallisDeVries and others 2002; Cremene and others 2005). Traditional landscapes in the Mediterranean region are of particular relevance as they maintain high biological diversity (Pineda and others 1981) in one of the global biodiversity hotspots (Myers and others 2000).

At the opposite extreme, many of the places which were used for crops or pastures have now become scrubland and forest as a consequence of traditional practices being abandoned (Romero-Calcerrada and Perry 2004). This has been especially evident in Mediterranean countries (Sirami and others 2007), where large areas of land were dedicated to marginal agriculture with poor competitive value (Vargas 2002). The disappearance of traditional activities in the mountain areas has led to changes in habitat heterogeneity, and species assemblage. The α -diversity has either increased or decreased depending on the magnitude of habitat change and the animal group studied, as some species were favored by the increase in scrubland and forest, whilst others were displaced (Laiolo and others 2004; Sirami and others 2007, 2008).

Groups of species which are sensitive to habitat change can make reliable bioindicators, highlighting environmental change (Cremene and others 2005; Schmitt and Rákosi 2007). The impact of land-use change on game species in the Iberian Peninsula and elsewhere in Europe has been the subject of increasing concern, and, consequently, research (e.g., Edwards and Berny 2000). This suggests that game species can be considered as a reliable indicator system of environmental change due to their sensitivity to such changes. Agricultural intensification, for example, is thought to be the main cause of the decline in the numbers of European hare (*Lepus lepus*) throughout Europe (Smith and others 2004). Moreover, some ungulates, such as wild boar (*Sus scrofa*), have become widespread following land abandonment in some European regions (Sáez-Royuela and Tellería 1986). Therefore, we suspect that the drastic changes in land use that have occurred over recent decades in Andalusia (southern Spain; Fernández-Alés and others 1992), may have affected the distribution and abundance of game species in this region.

Studying the changes in the distribution and abundance of game species is important not only because these changes affect the composition and function of the associated ecosystem (e.g. Delibes-Mateos and others 2008a), but also because hunting in Spain is a traditional activity of cultural, social and economic importance (Vargas 2002), with more than 30,000 private game estates covering >70% of the country (Villafuerte and others 1998). Currently, hunting is practiced by as much as 2.3% of the total Spanish population (around a million hunters), with more than 25,000 foreign hunters visiting each year (Vargas and others 2007), especially in the southern regions. One of

these regions, with a great game tradition in Spain, is Andalusia. Nearly 9000 game estates cover >90% of Andalusia (Guirado and Ortega 2002), where approximately 250,000 hunting licenses have been issued annually for the last 15 years (Junta de Andalucía 2003). The intensity of hunting management has increased in Andalusia over recent decades (Angulo 2003), with different strategies, such as translocations, becoming very frequent (Delibes-Mateos and others 2008b). We suspect that these changes in management practices could be also affecting the distribution and abundance of game species in this region.

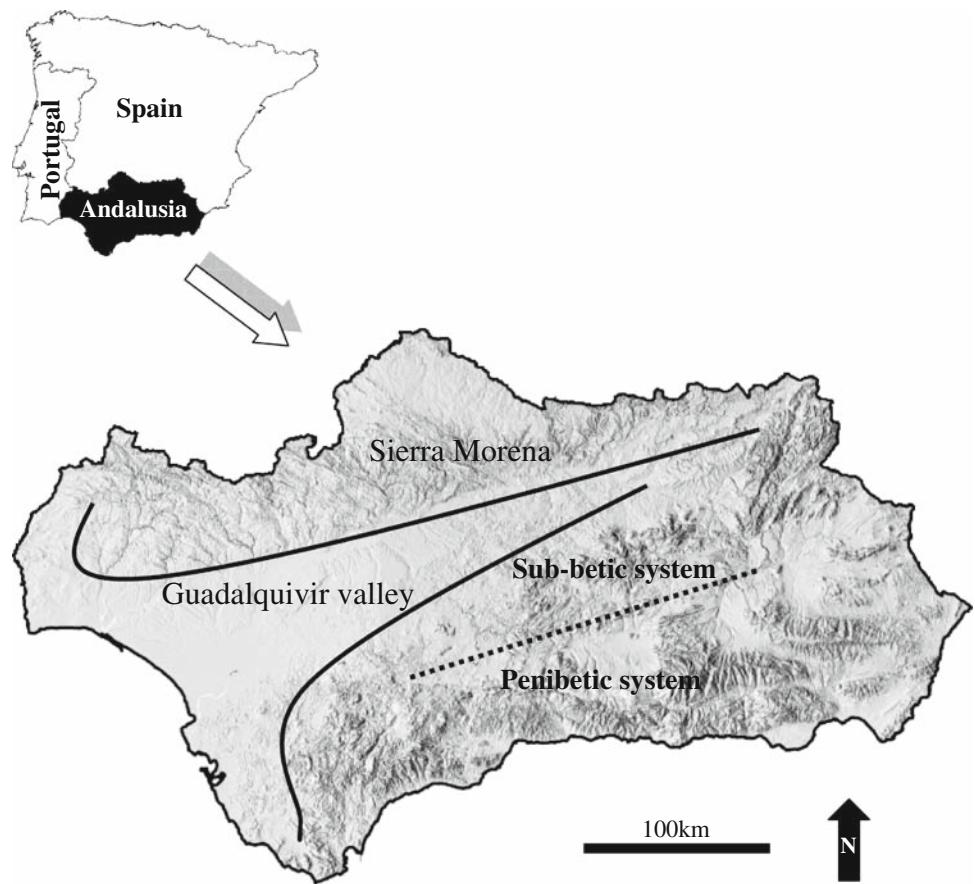
This article analyzes how the associations between the main game species have changed over recent decades in Andalusia. Using data taken from maps available from the Mainland Spanish Fish, Game and National Parks Service (Ministerio de Agricultura 1968; see also Gortázar and others 2000) and recent datasets on hunting yield distributions (Vargas and others 2006, 2007), we compare the distributions of the main game species in Andalusia during the 1960s and 1990s, respectively. In Andalusia, which is the main agricultural region in Spain (www.mapa.es), there has been a large reduction in landscape diversity over recent decades, as agricultural intensification and land abandonment have occurred in different areas (Fernández-Alés and others 1992). We hypothesize that this homogenization of the landscape has led to a segregation between big-game and small-game species, with big-game species mainly located in mountain areas, and small-game species associated with agricultural areas, as suggested by Vargas and others (2007). In contrast, we suggest that both groups would have been less spatially segregated during the 1960s than during the 1990s, as the landscape was more heterogeneous and diverse (Fernández-Alés and others 1992). Finally, we also discuss how the recent intensification in hunting practices could have contributed to the changes in the distribution of game species in Andalusia.

Materials and Methods

Study Area

This study was conducted in Andalusia (southern Spain; Fig. 1) which covers 87,268 km². Physiographically, medium-sized mountains predominate in the Andalusian landscape. The main mountain ranges are the Sierra Morena and the Baetic System (Fig. 1). Natural vegetation, mainly formed by evergreen oak and pine forest and scrubland, is typically restricted to mountain ranges. The most important plain is the Guadalquivir Valley, which is mainly oriented longitudinally between the Sierra Morena and the Baetic System (Fig. 1). The valley bottom is

Fig. 1 Study area. Schematic representation of the main mountain ranges (the Sierra Morena and the Baetic System, sub-divided into two ranges, Sub-betic and Penibetic) and the largest plain (the Guadalquivir valley)



covered by herbaceous crops and river terraces, and the hill slopes by woody crops. This region has a Mediterranean climate, with mild winters and severe summer droughts (for more details on the study area see Vargas and others 2006, 2007).

Differences Between Hunting Yields in the 1990s and the Abundance of Game During the 1960s

In order to evaluate how the associations between the main game species have changed over recent decades in Andalusia, we analyzed hunting yields from the 1990s and the abundance of the ten most representative game species during the 1960s. These were the Iberian wild goat (*Capra pyrenaica*), red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*) within the big-game group; and the European wild rabbit (*Oryctolagus cuniculus*), Iberian hare (*Lepus granatensis*), red-legged partridge (*Alectoris rufa*), woodpigeon (*Columba palumbus*), turtle dove (*Streptopelia turtur*) and quail (*Coturnix coturnix*) within the small-game group.

Density and hunting yield are not always equivalent parameters (Lucio 1991), as abundances and hunting yields are not the same quantitative variable. However, good hunting yields may be linked to high abundances. A serious

objection to this could come from the influence of restocking on hunting yields, but this does not seem the case of our study area, where restocking apparently provides a small percentage of hunted animals (see Farfán and others 2008). On the other hand, hunting yields are recorded equally for all species, which means that the relationship between the bag data and abundance estimate is the same for each species. Therefore, hunting yields in Andalusia provide a realistic picture of good and poor areas, especially at the macrospatial scale, when relative abundance values are usually lacking (Farfán and others 2004; Vargas and others 2006). We analyzed 32,134 annual hunting reports (AHRs) for the period 1993/2001 from 6049 game estates to estimate the average hunting yields of the above-mentioned species in each Andalusian municipality ($n = 771$), according to the following equation:

$$HY = \frac{\sum \text{mean annual number of individuals hunted per game estate}}{\sum \text{areas of the game estates}} * 100$$

where HY is the hunting yield per municipality expressed as the number of individuals captured per 100 ha of game estate where the species is hunted (Vargas and others 2007).

The abundance of game species during the 1960s was obtained from maps available from the Mainland Spanish Fish, Game and National Parks Service (Ministerio de Agricultura 1968; see also Gortázar and others 2000). These maps show the abundance of the main game species during the 1960s in Spain on a 1-6 scale (1: absent, 2: rare, 3: scarce, 4: common, 5: abundant, and 6: very abundant). The maps were scanned and the abundance of each game species was digitally converted onscreen into ArcGis 9.0 shapefiles (ESRI, Redlands, CA, USA). We transformed the corresponding digital polygons into raster images using Idrisi software (Clark Labs, Worcester, MA, USA). Finally, for each species we extracted the mean value of abundance in each municipality through the Idrisi EXTRACT command (Eastman 2004).

The correlations between the geographical distributions of the recent hunting yields (*HY*) of the game species included in the present study and the geographical distributions of the abundance of the same species during the 1960s were checked using Spearman's correlation coefficient. The correlation values were then transformed into a statistical significance matrix in which we replaced the actual correlation values by “+”, “-” and “0” signs, according to whether the correlation was significant and positive, significant and negative, or nonsignificant, respectively.

Classification Analysis of Species

Following Márquez and others (1997), we used UPGMA (unweighted pair-group method using arithmetic averages) as the classification method to determine similarities between the distribution patterns of the game species included in the study, using the distribution of the recent hunting yields and the abundance of game species during the 1960s (see above). We searched for “chorotypes,” which are groups of species whose distributions overlap more than expected at random in space (Vargas and others 1997). For our purposes, the interpretation of “chorotypes” is quantitative, and refers to groups of species whose abundances (or hunting yields) are similarly distributed.

The UPGMA results were displayed as dendograms: one for the recent situation and another for the situation during the 1960s. To detect quantitative chorotypes, we explored all clusters of distributions in the dendograms and selected those that combined the following characteristics: a high proportion of positive significant correlations (+) within the cluster, a low proportion of negative significant correlations (-) within the cluster, and a low proportion of positive significant correlations (+) between the distributions of the cluster and the distributions of the most similar cluster. The degree to which a cluster combines these conditions is provided by the internal homogeneity parameter IH. For the mathematical expansion of this

parameter, see “DW(AxA)” in Olivero and others (1998). We re-scaled the IH values to range between -1 and +1. In this way, we computed the IH values for every branch of the dendrogram. A cluster was considered a quantitative chorotype if: (a) IH = 1; or else (b) IH was positive, had higher values than those of the other clusters including the distributions involved, and the proportion of “+” signs between the cluster and the most similar cluster was significantly lower than the proportion of “+” signs within the cluster (evaluated using a G-test of independence). The distributions that did not fulfill these conditions did not constitute any chorotype, and therefore were considered as following a more gradual pattern rather than a discrete spatial one.

In addition, we used a consensus dendrogram to determine if the relationships between the abundance of the main game species during the 1960s and their recent hunting yields have remained stable over time. In particular, we used the so-called “agreement subtree” (Kubicka and others 1995) method, which provides the largest sub-dendrogram common to both dendograms.

Predictive Models

Following the same criterion as Farfán and others (2004) and Vargas and others (2006), we characterized municipalities with good recent hunting yields and those with poor yields for the species groups detected in the consensus dendrogram. This way, for each species, the range of hunting yield values, using a logarithmic scale, was split into six equal intervals. Then, values within the three higher intervals were considered good, whereas values within the three lower intervals were considered poor.

For the group of species in a same consensus cluster (either of big game or of small game), we quantified as 1 to every municipality where all these species showed good hunting yields, and 0 where at least one of them showed poor hunting yields. The environmental implications of this binomial variable were analyzed using logistic regression (Lawless and Singhal 1978, 1987; Hosmer and Lemeshow 1989). Recent land use and vegetation variables were used for this (Consejería de Medio Ambiente 1999; see Table 1). These variables, expressed as the percentage of surface area occupied, were obtained by transforming the corresponding digital vector polygons into 1 × 1 km resolution raster images. We averaged the quantitative variable values for each municipality and extracted the proportion of each type of land use and vegetation cover in each one (see Vargas and others 2006). Logistic regression generates a probabilistic model predicting a dichotomous dependent variable from a set of independent variables. Thus, we modeled the probability of obtaining good hunting yields for the species groups detected in the consensus dendrogram. To avoid problems derived from the

Table 1 Variables available to characterize vegetation and land use in municipalities with good hunting yields for the three small-game species and two big-game species resulting from the consensus dendrogram (see the Results section and Fig. 6)

Code	Variable
BL	Built land
CW	Conifer wood
DHER	Dry herbaceous crops
DHET	Dry heterogeneous crops
DS	Dense scrub
DSWC	Dense scrub with conifers
DSWD	Dense scrub with diverse trees
DSWO	Dense scrub with oaks
DWC	Dry wood crops
HCWO	Herbaceous crops with oaks
IHER	Irrigated herbaceous crops
IHET	Irrigated heterogeneous crops
IWC	Irrigated woody crops
MCNV	Mosaic of crops and natural vegetation
OAKW	Oak wood
PAST	Pasture
PWC	Pasture with conifers
PWO	Pasture with oaks
SS	Sparse scrub
SSWC	Sparse scrub with conifers
SSWD	Sparse scrub with diverse trees
SSWO	Sparse scrub with oaks
WETL	Wetlands

The variables are expressed as the percentage of surface area occupied

Source: Consejería de Medio Ambiente (1999)

multicollinearity of the predictor variables included in the logistic regression equations, we tested for Spearman rank correlations between them.

Results

Differences Between Hunting Yields in the 1990s and the Abundance of Game During the 1960s

In the 1960s, the abundances of big-game species were mainly positively and significantly correlated (Table 2; Fig. 2). The abundances of small-game species were also positively and significantly correlated in most cases (Table 2; Figs. 3, 4). The correlations of the abundance of the wild boar with those of the small-game species were all positive and significant (Table 2; Figs. 2, 3, 4). The red deer abundance was positively and significantly correlated with the abundance of the small-game species, except for quails (Table 2; Figs. 2, 3, 4). Negatively and significantly

correlated abundances only occurred between the Iberian wild goat and the European rabbit, and the Iberian hare and the turtle dove (Table 2).

As regards recent hunting yields, the correlations among the four big-game species were mainly positive and significant (Table 2; Fig. 2). Similarly, the hunting yields of all small-game species were positively and significantly correlated (Table 2; Figs. 3, 4). There were important differences in correlations between big-game and small-game species compared to those observed in the 1960s. In general, the correlations between the more representative big-game and small-game species were negative or non-significant during the 1990s, whereas they were positive in the 1960s (see above and Table 2). The hunting yields of the red deer correlated positively and significantly with those of the turtle dove and the woodpigeon, but negatively and significantly with the hunting yields of the red-legged partridge, and nonsignificantly with other small-game species. The hunting yields of the wild boar only correlated positively and significantly with those of the woodpigeon. In contrast, the correlations of the hunting yields of this ungulate and those of the red-legged partridge and the Iberian hare were negative and significant.

Classification of Species

We found only one significant quantitative chorotype in the classification analysis obtained from the abundances of game species in the 1960s (see Table 3; Fig. 5a). This group was constituted by small game species, but also included the wild boar (Fig. 5). The other three big-game species remained ungrouped (Fig. 5). On the other hand, we obtained two significant chorotypes using the recent hunting yields. In this case, all the small-game species were placed in one chorotype, whereas the big-game species formed a different one (see Table 3; Fig. 5b). We obtained two species groups in the consensus dendrogram formed from the 1990s and 1960s dendograms. One was made up of three small-game species (quail, European rabbit and red-legged partridge) and the other by two big-game species (red and roe deer; Fig. 6). Thus, only the associations between these two groups have remained unaltered over time.

Predictive Models

The logit function of the logistic regression model for the three small-game species obtained in the consensus dendrogram is as follows:

$$y = -3.74 + DHER \times 2.89 + IHER \times 3.63 + DWC \\ \times 2.17 + SSWO \times 5.26$$

where the variables are ranked according to their order of entrance in the model (the variables are abbreviated as in

Table 2 Matrix of statistical significance with correlation values replaced by “+”, “—” and “0” signs, according to whether the correlation is positive and significant, negative and significant, or nonsignificant, respectively

Species	<i>Coturnix coturnix</i>	<i>Oryctolagus cuniculus</i>	<i>Lepus granatensis</i>	<i>Streptopelia turtur</i>	<i>Columba palumbus</i>	<i>Sus scrofa</i>	<i>Alectoris rufa</i>	<i>Capra pyrenaica</i>	<i>Cervus elaphus</i>	<i>Capreolus capreolus</i>
1960	<i>Coturnix coturnix</i>	1	0	+	+	+	0	0	0	0
	<i>Oryctolagus cuniculus</i>		1	+	+	+	+	—	+	0
	<i>Lepus granatensis</i>			1	+	+	+	—	+	0
	<i>Streptopelia turtur</i>				1	+	+	—	+	0
	<i>Columba palumbus</i>					1	+	0	+	0
	<i>Sus scrofa</i>						1	0	+	+
	<i>Alectoris rufa</i>							1	0	0
	<i>Capra pyrenaica</i>								1	+
	<i>Cervus elaphus</i>									1
	<i>Capreolus capreolus</i>									1
Actual	<i>Oryctolagus cuniculus</i>	1	+	+	+	+	0	+	0	0
	<i>Alectoris rufa</i>		1	+	+	+	0	0	—	—
	<i>Streptopelia turtur</i>			1	+	+	0	0	+	0
	<i>Lepus granatensis</i>				1	+	—	0	0	—
	<i>Coturnix coturnix</i>					1	+	+	0	0
	<i>Columba palumbus</i>						1	0	+	+
	<i>Capra pyrenaica</i>							1	0	+
	<i>Capreolus capreolus</i>								1	+
	<i>Cervus elaphus</i>									1
	<i>Sus scrofa</i>									1

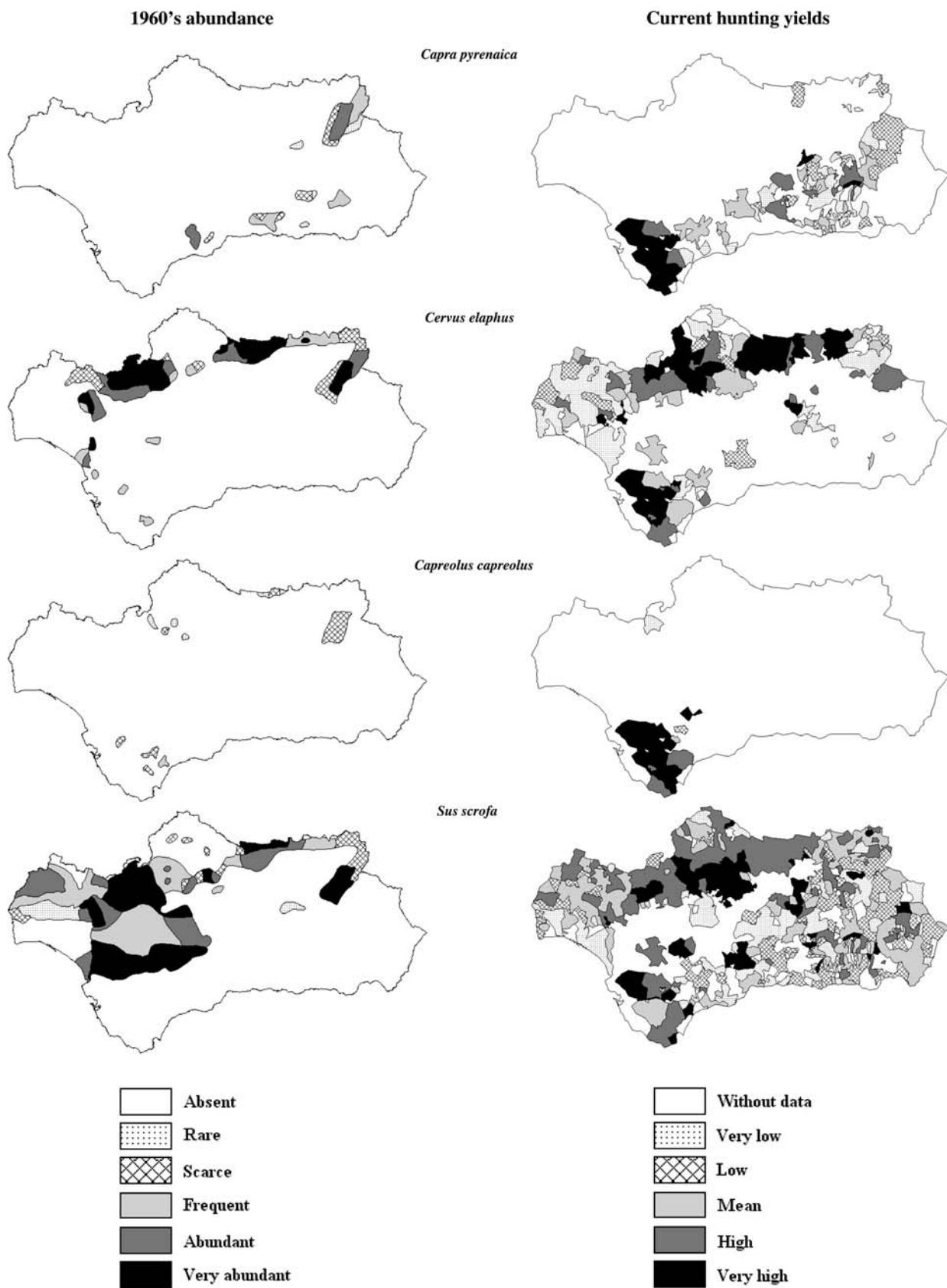


Fig. 2 Abundances during the 1960s and current hunting yields of the main big-game species in Andalusia. Hunting yield values have been transformed using a logarithmic scale, which has been split into six equal intervals for representation purposes

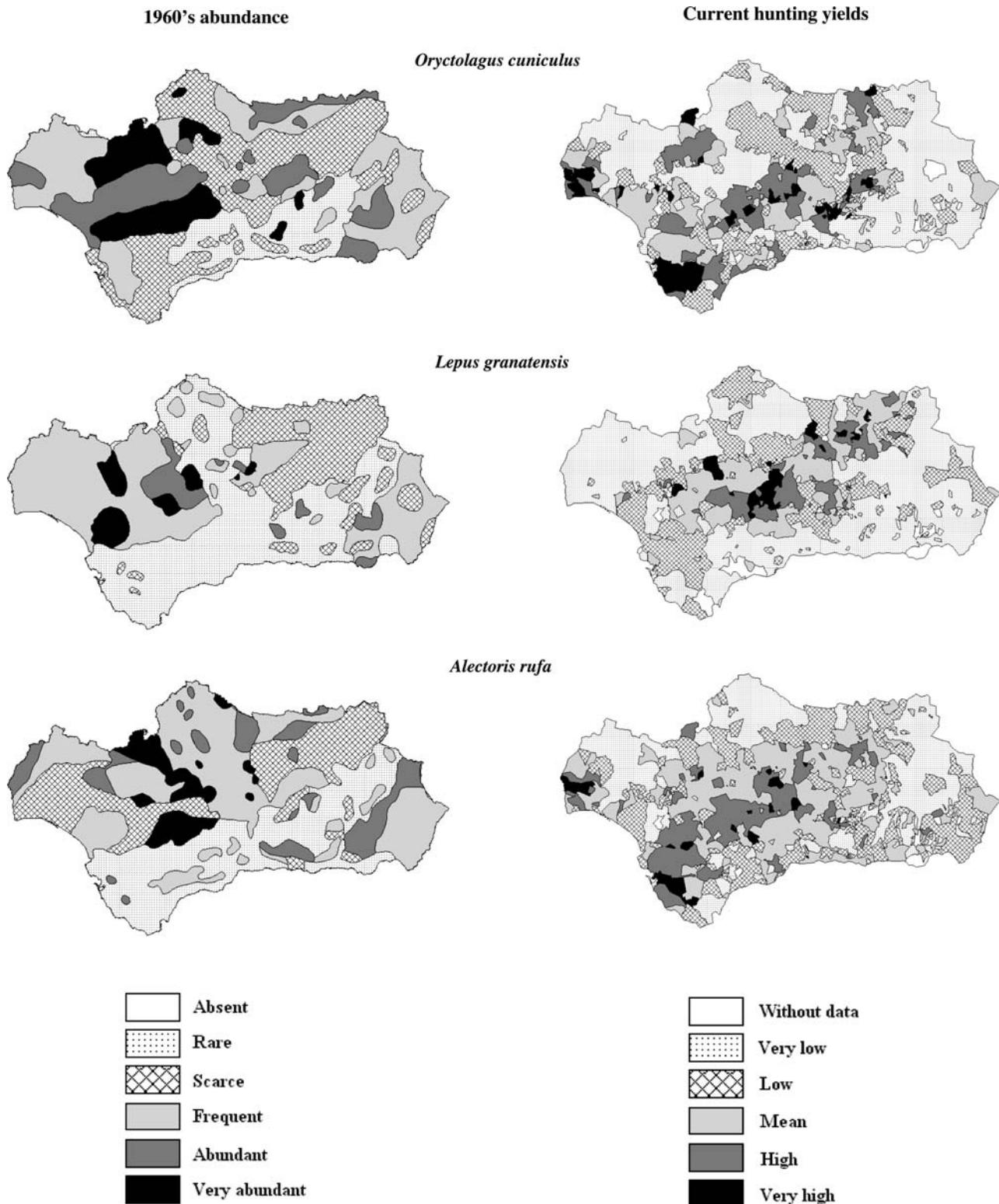


Fig. 3 Abundances during the 1960s and current hunting yields of the main resident small-game species in Andalusia. Hunting yield values have been transformed using a logarithmic scale, which has been split into six equal intervals for representation purposes

Table 1). According to this function, municipalities with good hunting yields for these three species were characterized by the presence of herbaceous and woody

crops and sparse scrub with oaks. For the consensus group constituted by the two big-game species (see above; Fig. 6), the municipalities with good hunting yields were

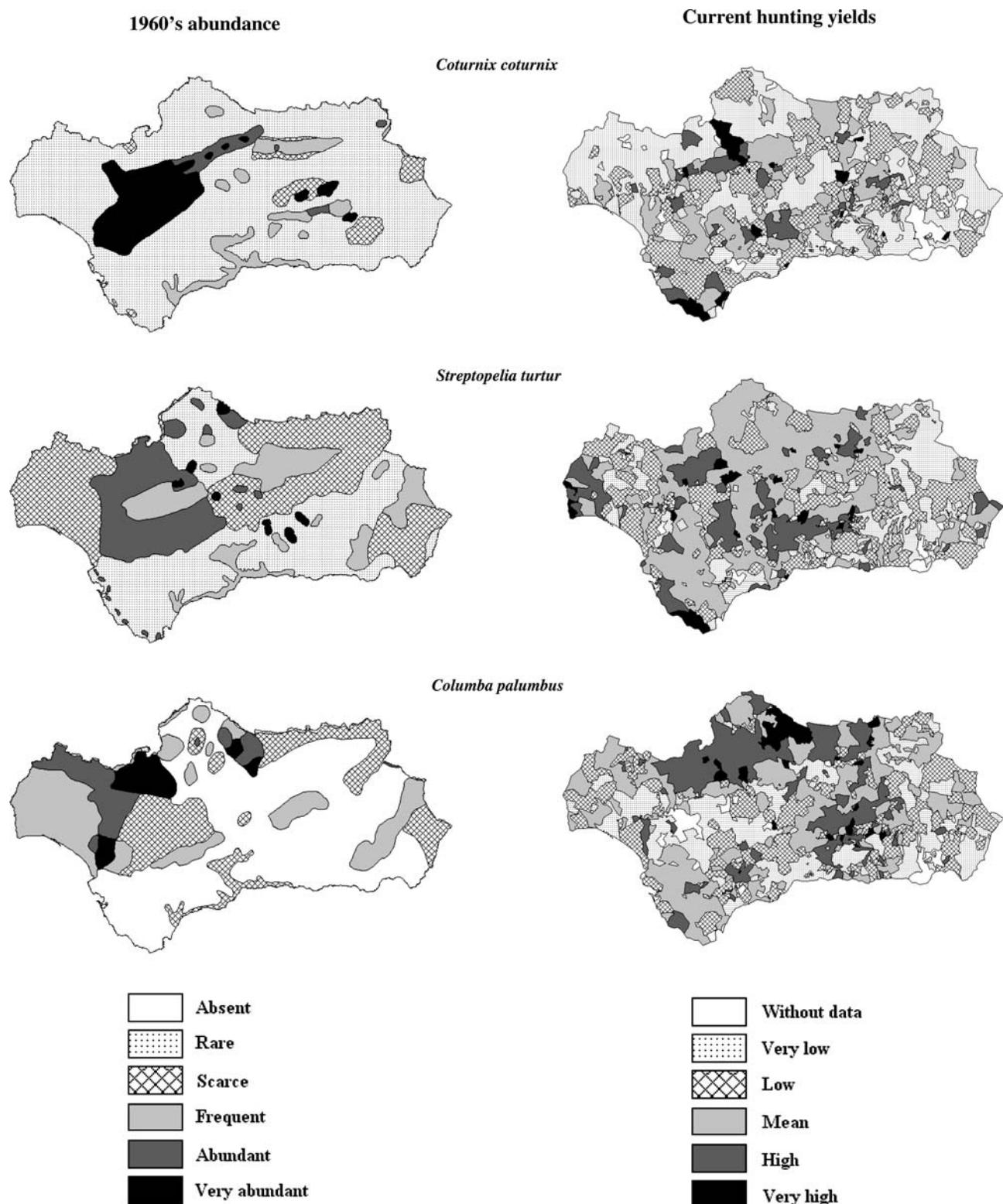


Fig. 4 Abundances during the 1960s and current hunting yields of the main migrant small-game species in Andalusia. Hunting yield values have been transformed using a logarithmic scale, which has been split into six equal intervals for representation purposes

Table 3 Internal homogeneity (IH) parameter values for the chorotypes and for the cluster of ungrouped species in the dendograms (Fig. 5)

Cluster	IH
1960s chorotype I	0.496*
1960s <i>C.pyrenaica</i> , <i>C. elaphus</i> , <i>C. Capreolus</i>	0.496 (n.s.)
Current chorotype I	0.613**
Current chorotype II	0.518***

Significant G-tests of independence are indicated as * ($P < 0.001$), ** ($P < 0.01$) and *** ($P < 0.05$); n.s.: nonsignificant G-test

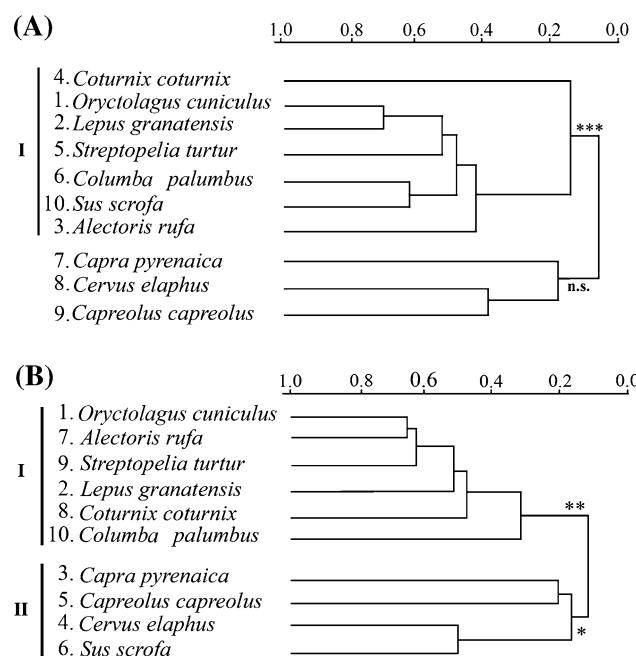


Fig. 5 (a) Dendrogram of the distributional similarities of the abundances of game species in the 1960s; (b) Dendrogram of the distributional similarities of current hunting yields of game species. Significant G-tests of independence are indicated as * ($P < 0.05$), ** ($P < 0.01$) and *** ($P < 0.001$); n.s.: nonsignificant G-test

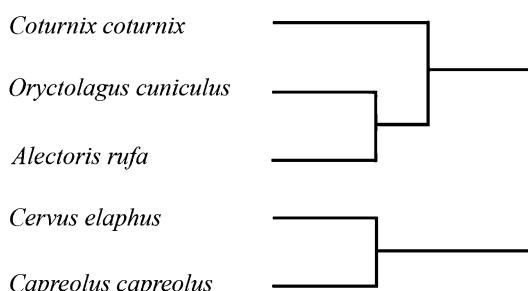


Fig. 6 Consensus dendrogram of the abundance of game species in the 1960s and current hunting yields of the same game species

Table 4 Spearman correlations (r) between the predictor variables included in the logistic regression equations

	OAKW	PAST	DSWO	DHER
<i>Big-game</i>				
OAKW	1	0.386	0.651	-0.026
PAST		1	0.499	0.093
DSWO			1	0.044
DHER				1
<i>Small-game</i>				
DHER	1	0.325	0.260	0.082
IHER		1	0.071	-0.119
DWC			1	-0.018
SSWO				1

Names of variables are abbreviated following Table 1

characterized by oak woods, pasture, dense scrub with oaks and dry herbaceous crops:

$$y = -8.38 + \text{OAKW} \times 14.22 + \text{PAST} \times 18.50 + \text{DSWO} \times 17.86 + \text{DHER} \times 6.19$$

Spearman correlation matrices for the predictor variables included in the two equations are shown in Table 4. The highest correlations between variables are 0.26 for small-game species, and 0.65 for big-game species. Even the later is not an excessively high correlation, and moreover both variables (oak wood and dense scrub with oaks) describe different habitats that are used differentially by big-game species.

Discussion

According to the distribution of the hunting yields, during the 1990s there was a significant segregation between big-game and small-game species in southern Spain, with two clearly independent chorotypes: one consisting of the four species of ungulates and the other of the small-game species (Fig. 5b; see also Vargas and others 2007). In contrast, our findings show that big-game and small-game species were not significantly segregated previously (Fig. 5a). Only one chorotype was identified in the 1960s, and this consisted of the small-game species and the wild boar (Fig. 5a), which was included in the big-game species group during the 1990s (Fig. 5b). The other 3 ungulates were closely associated with each other, but did not constitute a significant chorotype, probably because some of them showed positive correlations with species in the group mentioned above (Table 2). This was corroborated by the results of the consensus dendrogram; only the

associations between red and roe deer, and between rabbit, red-legged partridge and quail remained stable during the study period (Fig. 6). Thus, the relationship between the abundances of the species within the same consensus groups have remained stable (Kubicka and others 1995), independently of whether or not they may have increased or decreased. The contrary has happened to the species formerly in the chorotypes but later excluded from the consensus tree. A paradigmatic example of conflictive species is the wild boar, which has been excluded from its 1960s chorotype (where it coincided with small-game species) because the distribution of its recent hunting yields coincided more with those of big-game species (Fig. 5b).

So the highest hunting yields of both small-game and big-game species occurred in different areas in southern Spain, whereas in the 1960s their areas of greatest abundance were more evenly distributed. It is noteworthy that no municipality in the study area obtained good hunting yields for small-game and big-game during the 1990s (Vargas and others 2007), whereas previously both were successfully hunted in the same zones. For instance, the Sierra Morena was not only an important area for big-game species during the 1960s, but also for small-game species such as rabbit, hare or partridge (Figs. 2, 3, 4).

Species abundance and distribution depend to a great extent on environmental factors (e.g., climatic factors, landscape characteristics, etc.), and relevant factors may differ from one species to another such as for small-game and big-game species (e.g., Acevedo and others 2006; Vargas and others 2006). The recent segregation of the highest hunting yield areas of both big-game and small-game species in southern Spain has been attributed to their different habitat requirements. Big-game species are basically distributed in mountainous regions covered by Mediterranean woodlands, whereas the most characteristic small-game species are restricted to agricultural plains and some agro-forestry areas (Vargas and others 2007). Similar patterns have been reported in other Spanish regions (see Acevedo and others 2006; Gortázar and others 2007), and have been also shown by the results of the logistic models for the consensus groups obtained in this study. Nevertheless, when traditional agriculture was common, both kinds of environments existed in the same places significantly more often than recently, since crop production has been either intensified or abandoned (e.g., Fernández-Alés and others 1992). This made that, several decades ago, both small-game and big-game species inhabited the same landscapes; e.g., mosaics of pastures or agricultural lands with a high proportion of natural vegetation (Delibes-Mateos and others, unpublished work; see also Fernández-Alés and others 1992). Therefore, the segregation of the highest hunting yield areas of both big-game and small-game species observed in this study seems to have been the

result of the spatial segregation of their preferred habitats over recent decades.

In this study, we have found that big-game species have greatly expanded across Andalusia in recent decades, both in density and geographical range (Fig. 2). The wild boar, for example, has colonized all the mountain systems in the region (Fig. 2). The formation of dense Mediterranean scrubland and woodland as a consequence of land abandonment seems to be one of the main factors explaining the current trend of increasing populations of these ungulates in Andalusia, as has occurred in other areas of Spain (Gortázar and others 2000; Acevedo and others 2005). The increase of scrubland and woodland areas has also benefited some small-game species, such as the woodpigeon (Fig. 4), which is highly dependent on this habitat. However, the loss of traditional management of scrubland seems to be one of the main factors explaining the decline in the most characteristic small-game species across the mountain areas of southern Spain (Fig. 3; Moreno and Villafuerte 1995). The current scarcity of rabbits, hares and partridges is a major conservation concern in the Sierra Morena, where they reached high densities several decades ago (Fig. 3), and where several endangered predators such as the Iberian lynx (*Lynx pardinus*) and the Spanish Imperial Eagle (*Aquila adalberti*) still coexist (e.g., Fernández and others 2006).

Agricultural intensification has also been reported as a critical constraint for small-game populations (e.g. Smith and others 2004). Agricultural intensification has resulted in an increase in average crop area, and a decrease in edge and marginal area, per property in Spain (Andrés and others 2002). In Andalusia, total crop area and the average patch size has increased in the most fertile areas (Fernández-Alés and others 1992). This may explain the declines of small-game species in some regions (Buenestado and others 2008). This situation could be currently becoming stabilized, as most important changes in the Spanish agriculture (e.g., smallholding merging, crop irrigation, mechanization, and the use of chemical fertilizers) were mainly concentrated from the 1960s to the 1980s, and started to stabilize after the 1980s, when Spain joined the European Union (Junta de Andalucía 1995, 1996; Vargas 2002; Zambrana and others 2002).

Until a few decades ago, local non-profit hunting societies were predominant in most areas of southern Spain. However, hunting management has become a new agrarian land use of great economic importance in these areas (López-Ontiveros 1991), and consequently the number of private hunting estates has greatly increased in recent years. Private hunting areas devoted to big-game species are particularly common in mountain areas. Here, the owners aim to increase ungulate densities through management practices, such as translocations or food supplementation within

fenced areas (Carranza 1999). Intensive management of small-game species is currently associated with areas where some of these species remain at high densities (Delibes-Mateos and others 2008c). Here, management is mainly based on supplementary feeding, restocking and predator control. Translocations of small-game species have increased in southern Spain during recent decades (Delibes-Mateos and others 2008b), and this could explain the high hunting yields observed in some lowland areas, where abundances were low in the 1960s (Figs. 3 and 4; see also Buenestado and others 2008). Therefore, hunting management could be indirectly contributing to the recent segregation between big-game and small-game species, promoting the expansion of some big-game species into mountain areas, and boosting small-game species in farming zones.

In summary, the recent segregation between the highest hunting yield areas of both big-game and small-game species seems to be a consequence of the land use changes that have occurred in Spain in recent decades. Furthermore, hunting management could be artificially boosting such segregation. This situation appears to be detrimental to the conservation of the most characteristic small-game species. Species such as rabbit, partridge and hare require urgent measures to conserve or improve their populations, and this is especially important in some mountain systems, where endangered predators are reliant upon them as preys. According to our results, changes in habitat management provide a strong explanation for the game species segregation. For this reason, we suggest that the conservation of open Mediterranean scrubland and habitat heterogeneity in the agroecosystems should be a priority to preserve the populations of small-game species. On the other hand, and although the role of traditional forms of game management is not addressed in this article, the only employment of management strategies such as supplementary feeding, restocking and predator control does not seem enough to recover small-game species, especially in areas where their preferred habitats have been lost. In such situations, vegetation should be managed to increase habitat heterogeneity, with pasture encouraged in areas dominated by dense scrubland. This would recreate the landscape predominant during the 1960s (Fernández-Alés and others 1992) and would facilitate the recovery of small-game populations. Additionally, current models of hunting management should be revised to make them compatible with biodiversity conservation. We recommend that the management of game species should be mainly based on the creation and maintenance of wildlife habitats, which is in the common interest of hunters, governments and environmental associations aimed at biodiversity conservation (Martínez and others 2002). National and regional regulations already include the potential application of strategies for the

conservation of habitat as a tool for hunting management. Most game estates in southern Iberian Peninsula are in lands with other uses than hunting, hence belonging to owners other than the hunting managers. Because of this, the management of habitats is strongly conditioned by interests around agriculture, cattle-raising or forestry. Specific actions to promote hunting might have negative effects on these land uses, and in such cases this should be economically compensated, either with investments made by game estates, or with a regional policy of economical incentives to landlords.

Acknowledgments M. Delibes-Mateos was supported by a post-doctoral grant funded by the regional government of Castilla la Mancha (JCCM) and the European Social Fund. Special thanks go to E. Martínez for providing us the maps of the abundance of game species during the 1960s, and to the Consejería de Medio Ambiente de la Junta de Andalucía for supplying the Annual Hunting Reports. We also thank Virginia H. Dale, Dave Parish, and two anonymous reviewers for helpful comments on previous drafts of the Manuscript.

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