

Natural, human and spatial constraints to expanding populations of otters in the Iberian Peninsula

Miguel Clavero^{1,2,3*}, Virgilio Hermoso⁴, Lluís Brotons¹ and Miguel Delibes^{3,5}

¹Grup d'Ecologia del Paisatge, Àrea de Biodiversitat, Centre Tecnològic Forestal de Catalunya, Carretera vella de Sant Llorenç de Morunys km 2, 25280 Solsona, Catalonia, Spain, ²Departament de Ciències Ambientals, Universitat de Girona, Campus de Montilivi, 17071 Girona, Catalonia, Spain, ³SECEM, Sociedad Española para la Conservación y el Estudio de los Mamíferos, Apdo. de Correos 15450, 29080 Málaga, Spain, ⁴The Ecology Centre, School of Biological Sciences, The University Queensland, St Lucia, Qld 4072, Australia, ⁵Doñana Biological Station, Department of Conservation Biology, CSIC, Americo Vespucio s/n, 41092 Sevilla, Spain

ABSTRACT

Aim To determine the relationships between otter (*Lutra lutra*) distribution dynamics and environmental and spatial constraints over a 20-year period.

Location Andalusia, southern Iberian Peninsula.

Methods We synthesized otter distribution data from three otter surveys (1985, 1995 and 2005) using subcatchment areas defined by hydrological barriers. Subcatchments were characterized by two 'natural' (climatic and orographic variables) and two 'human' (land use and population density) gradients. In addition, we calculated two contagion variables (the distance to previously occupied subcatchments and the percentage of occupied subcatchments within a 50 km buffer) for consecutively surveyed subcatchments.

Results Between 1985 and 2005 the percentage of subcatchments with otters present increased from 42% to 72%. Otters tended to be rare or absent from human-dominated areas. Anthropogenic gradients were better predictors of otter distribution than natural ones. Human and natural gradients showed strong covariation, but for any value of the natural gradients otters tended to be present in subcatchments with lower human impacts. Colonization of new subcatchments was found to be strongly related to contagion variables and expansion rates were slower than those estimated in other studies. Newly colonized areas tended to be located in areas with intermediate human influence, while repeated absences occurred mainly in areas where human impact was most severe.

Main conclusions Our results suggest that recent otter expansion across Andalusia is a reflection of large-scale improvement in environmental conditions. Otter populations that survived the period of strong and generalized declines appear to be acting as sources from which neighbouring areas are colonized, probably aided by improved water quality and increases in food availability. However, the further expansion of otters into their full original range is likely to be constrained by human-impacted landscapes.

Keywords

Andalusia, freshwater environments, landscape gradients, *Lutra lutra*, mammals, Mediterranean streams, otter surveys, recolonization, recovering species.

*Correspondence: Miguel Clavero, Grup d'Ecologia del Paisatge, Àrea de Biodiversitat, Centre Tecnològic Forestal de Catalunya, Carretera vella de Sant Llorenç de Morunys km 2, 25280 Solsona, Catalonia, Spain.
E-mail: miguelito.clavero@gmail.com

INTRODUCTION

Effective conservation planning must address two main initial questions: (1) where could species find suitable habitat conditions, and (2) where they do occur (e.g. Klar *et al.*, 2008). There is a large amount of scientific literature assessing the factors causing species declines and how this knowledge could be used to improve conservation measures (e.g. Rod-

ríquez & Delibes, 2002). However, less attention has been given to factors controlling changes in the distribution of expanding populations of species, whether natural or facilitated by reintroduction programmes (Davies *et al.*, 2005; Brotons *et al.*, 2008). The majority of analyses to predict the expansion of species have been performed for invasive species (e.g. Hengeveld, 1989; Sax *et al.*, 2005; Roura-Pascual *et al.*, 2010). While range contractions result from the cumulative effects of local

extinctions, expanding ranges can be viewed as the sum of recolonization events. Recolonization relies on the dispersal potential of individuals and the availability of new habitats offering adequate conditions (Suter *et al.*, 2009). Among mammals, colonization is generally associated with the dispersal of juvenile individuals, often favoured by intra-specific competition arising in saturated populations (e.g. Ferreras *et al.*, 2004; Cote *et al.*, 2007).

Understanding the environmental and spatial factors that control range expansions can help to predict the spread of species and inform pertinent management strategies. For example, understanding the range expansion patterns of a given species can help managers to decide if species-based conservation measures are necessary or if improvement of environmental conditions alone will be sufficient to ensure natural recolonization. Because conservation funds are limited (Bottrill *et al.*, 2009), costly actions such as species reintroductions need to be justifiable and have a high likelihood of success (IUCN, 1998). In this context, the spontaneous recolonization of areas where a recovering species had previously gone extinct could possibly put into question the need for an active reintroduction project.

The Eurasian otter (*Lutra lutra* Linnaeus, 1758; henceforth otter) is a semi-aquatic mammal with a wide Palaearctic distribution range (Kruuk, 2006). In Europe, most otter populations have suffered sharp declines from the 1950s, noticed both in degraded and relatively unaltered environments. Major otter populations became restricted to peripheral areas, such as western parts of the Iberian Peninsula and the British Isles, southern Italy, eastern European countries and northern Scandinavia (Macdonald & Mason, 1990). It has been argued that the historical declines in otter populations were mainly driven by persistent bio-accumulative pollutants [dichlorodiphenyltrichloroethane (DDT) and polychlorinated biphenyls (PCBs)] strongly affecting the species due to its apex position in the freshwater trophic web (Roos *et al.*, 2001). Additional factors, such as impacts of habitat degradation on prey populations and direct persecution, might have also had a significant role in otter decline.

Due to its threatened status and favourable social perception throughout Europe, the otter has become a flagship species for nature conservation (e.g. White *et al.*, 1997). This circumstance facilitated the establishment of numerous monitoring programmes and the design of standard otter survey methods (e.g. Reuther *et al.*, 2000). Recently, these monitoring programmes have detected a change in otter population trends across most of Europe, showing a general increase in the geographic range and the proportion of river stretches occupied by the species. There are a large number of standardized datasets on otter distribution, which makes the species a valuable case study for performing large-scale analyses aimed at identifying environmental factors allowing its range expansion.

Recently, Marcelli & Fusillo (2009) assessed the influence of landscape characteristics on the expansion of otter populations in southern Italy, showing that in the last 20 years some

human-related variables have had a reduced role as main factors limiting otter distribution. However, this and other previous studies did not explicitly account for the influence of spatial variables on the expansion processes. Therefore, patterns of the dynamics of otter distribution reported to date could be influenced by: (1) the clustered distribution of otter occurrences, and (2) the species' dispersal limitations. For example, due to spatial constraints, otters might colonize suboptimal areas near saturated populations while being unable to arrive at suitable habitats located further from potential source populations.

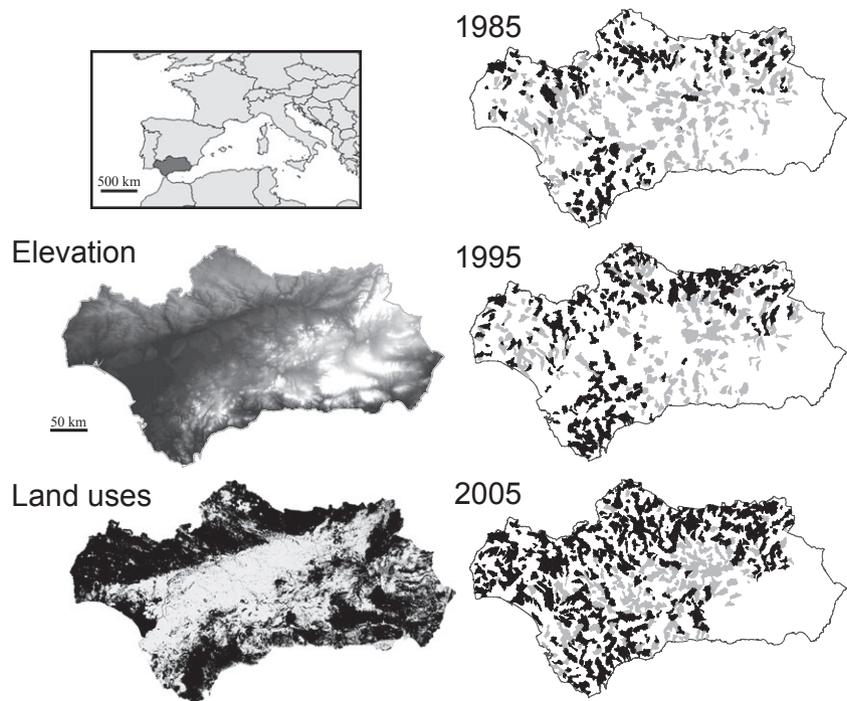
We analysed the distribution patterns of an expanding otter population in the southern Iberian Peninsula, where there have not been any direct species-based conservation measures implemented to date. We used data from three extensive otter surveys conducted in 1985, 1995 and 2005 aiming to relate the dynamics of otter distribution to different sources of landscape variation. These sources of variation were categorized as natural or human-driven, and were later used in a spatially explicit analysis of otter distribution dynamics. Our objectives were: (1) to analyse the influences of landscape gradients on otter distribution patterns and their possible changes along the three different time periods, and (2) to relate the dynamics of otter range expansion to landscape characteristics and to the spatial constraints derived from the ecology of the species.

MATERIALS AND METHODS

Study area

Andalusia, with an area of about 90,000 km², occupies the southern portion of Spain. This region has three main morpho-structural units, aligned in an east–west direction, with two main mountain ranges, the Sierra Morena to the north and the Baetic Cordillera to the south, separated by the lowlands of the Guadalquivir Depression (Rivas-Martínez *et al.*, 1997). The lowlands concentrate most agricultural areas as well as some of Andalusia's biggest urban areas. Other densely populated areas occur along both the Mediterranean and the Atlantic coasts (Fig. 1). The sparsely populated mountain areas are mainly devoted to extensive grazing, forest exploitation and game reserves. Approximately half of the region is occupied by forest and 'savanna-like' wooded grassland, called *dehesas*, mainly dominated by holm (*Quercus rotundifolia*) and cork (*Quercus suber*) oaks. The climate is typically Mediterranean, featuring a predictable seasonal variation, with mild and rainy winters and hot and dry summers. There is also a high and unpredictable inter-annual variation, which principally affects the amount of winter rain. Climatic characteristics, such as seasonal and inter-annual precipitation variability, are the main factors controlling the structure and functioning of freshwater ecosystems in Mediterranean areas (Gasith & Resh, 1999; Magalhães *et al.*, 2002), which in turn affect many aspects of otter ecology (Clavero *et al.*, 2003; Ruiz-Olmo & Jiménez, 2009).

Figure 1 Situation, environmental features and otter (*Lutra lutra*) distribution in Andalusia. In the elevation map, higher elevations are denoted by lighter areas. In the map of land uses, black areas indicate 'natural' uses (forest, *dehesas*, shrub or meadows) while white areas indicate 'human' uses (agricultural or urban) (see Table 1). Distribution maps represent the results of the three otter surveys performed in Andalusia, synthesized for subcatchments (delimited by water divides and river confluences). Black subcatchments are those with otters present, while grey subcatchments are those in which the species was not detected.



Otter surveys

Otters are largely nocturnal and difficult to observe in the field, and thus their presence is most commonly detected through the identification of their characteristic signs. Otters produce dozens of faeces (spraints) daily that are deposited in conspicuous and commonly predictable places (Kruuk, 2006). Therefore, otter records are primarily based on the detection of spraints (Lenton *et al.*, 1980; Mason & Macdonald, 1986). Survey methodologies were standardized by the IUCN/SSC Otter Specialist Group in order to achieve comparable results across Europe (Reuther *et al.*, 2000). Otter surveys performed in Andalusia followed the recommendations of the international standard method (López-Martín & Jiménez, 2008). Spraints or tracks were searched for along riverbanks (only one bank in large rivers) until found or until a maximum distance of 600 m had been covered. Surveys were performed at least 1 week after any episode of rain and, in any case, avoiding flood periods (López-Martín & Jiménez, 2008).

As the lack of otter signs is not an irrefutable proof of their absence (i.e. false negatives are possible), we used areas surveyed more than once in Andalusia to quantify the probability of recording false negatives. Applying extremely conservative assumptions (e.g. otters cannot disappear from a location where they had once been detected) we estimated a minimum detection probability of 91.6% (see Appendix S1 in the Supporting Information). We are confident that under more realistic circumstances (i.e. local extinctions are possible) false negatives constitute < 5% of absence data. Thus, due to the high detectability of the species in our data set, we used presences and absences resulting from surveys to relate otter distribution to environmental variables. In fact, presence-absence analyses are preferred to presence-only ones (e.g.

comparing presences with a set of randomly generated pseudoabsences) whenever there are data on absences available (Brotons *et al.*, 2004).

Three national otter surveys have been performed in Spain, in 1984–85, 1994–96 and 2004–06 (henceforth 1985, 1995 and 2005) (Delibes, 1990; Ruiz-Olmo & Delibes, 1998; López-Martín & Jiménez, 2008). For our purposes, we selected all river reaches surveyed across Andalusia, excluding those in Almeria, a very dry province in eastern Andalusia where the otter has not been recorded in the last few decades (Prenda & Palomo, 2008). In total, 523, 581 and 831 sites were visited in the 1985, 1995 and 2005 surveys, respectively. Although the use of Universal Transverse Mercator (UTM) 10 × 10 km cells is usual in the design of and reporting on otter surveys (Reuther *et al.*, 2000), we synthesized results using subcatchments (i.e. hydrological units delimited by water divides and river confluences) as territorial units (Linke *et al.*, 2007; Ottaviani *et al.*, 2009). Subcatchments are a more appropriate spatial unit than equal-sized cells (e.g. UTM cells) to study the distribution patterns of aquatic organisms because they are the natural areas of influence and boundaries (Linke *et al.*, 2007). We derived 2684 subcatchments in Andalusia from a 90-m digital elevation model using ARC Hydro (Maidment, 2002) in ARCGIS 9.1 (ESRI, Redlands, CA, USA). We selected subcatchments with an average elevation lower than 1500 m, because in the Iberian Peninsula otters are rarely detected above that elevation (Ruiz-Olmo, 1998). We used otter occurrence records in 424, 440 and 632 subcatchments for the 1985, 1995 and 2005 surveys, respectively. Survey intensity in an average subcatchment remained stable across the sampling periods (1.23, 1.32 and 1.31 sites/subcatchment in 1985, 1995 and 2005, respectively). Subcatchments were

considered 'positive' when otter signs were detected in at least one site within the subcatchment, even if it included other sites where the presence of otters had not been confirmed. Otherwise subcatchments were considered 'negative'. The average subcatchment area was 42.4 km² (SD 29.4 km²) and there were no statistical differences in area between positive and negative subcatchments (one-way ANOVA on square root-transformed subcatchment area; $F_{1,1036} = 0.003$; $P = 0.96$).

Environmental characterization

We estimated 23 environmental variables for all surveyed subcatchments ($n = 1038$) (Table 1). Fourteen of these variables described climate and orography, and were considered 'natural' variables (i.e. not affected by direct human impacts). The remaining nine variables, considered 'human' ones, were: (1) percentage cover of eight land-use categories (forest, *dehesas*, shrub, meadows, ligneous dry farm, herbaceous dry farm, irrigation lands and urban) in each subcatchment (Andalusian Land Cover Digital Map 1:25,000; CMA, 1999), and (2) human population density. We built environmental gradients of natural and human-related variation in landscape characteristics using two different principal components analyses (PCAs) to summarize the variation in the original variables' data sets. We transformed all non-normal variables (Table 1). In both PCAs we applied the Varimax normalized

rotation, an orthogonal rotation technique that minimizes the number of original variables used to explain each gradient, thus facilitating their interpretation (McGarigal *et al.*, 2000). The two main gradients resulting from each PCA (i.e. the first two principal components) were retained to be used as independent variables to study the patterns in otter distribution and their temporal dynamics. We used STATISTICA 6 (StatSoft Inc., Tulsa, OK, USA) to run the PCAs.

The first two components extracted by the PCA on natural variables (PC1_{nat} and PC2_{nat}) explained over 70% of the variation of the original dataset (Table 1). PC1_{nat} described a gradient going from wet areas but with high precipitation seasonality, placed towards the negative extreme, to areas with high temperature variability (both annual and diurnal) and relatively high summer precipitation. PC1_{nat} values increased both eastwards and, especially, northwards (i.e. towards more continental areas). PC2_{nat} had hotter lowland areas towards its negative extreme and cold mountain areas with relatively high summer precipitation towards its positive end. While PC2_{nat} values increased eastwards, they did not show any relationship with latitude.

The second PCA, using human-related variables, produced two gradients (henceforth PC1_{use} and PC2_{use}) that explained over 55% of the variation in the dataset (Table 1). Both gradients had more human-impacted subcatchments towards their positive extremes, and were thus interpreted as landscape indicators for human impacts. PC1_{use} had landscapes domi-

Table 1 Natural (PC1_{nat} and PC2_{nat}) and human (PC1_{use} and PC2_{use}) landscape gradients defined by means of principal components analyses (PCAs) applied to two different sets of variables describing the 1038 subcatchment units surveyed for otters (*Lutra lutra*) in Andalusia: (1) climatic and orographic variables not affected by human activity; and (2) land uses and human population density. Factor loadings of each original variable along the different resulting gradients (PCs) area are shown, and those with an absolute value larger than 0.5 are highlighted in bold. The lower cells show the correlation (Pearson's r) between factor scores of each subcatchment and its longitude and latitude.

(1) Natural gradients Climatic and orographic variables					(2) Human gradients Land uses and population density			
	Units	Transf.	PC1 _{nat}	PC2 _{nat}		Transf.	PC1 _{use}	PC2 _{use}
Mean annual temp.	°C	X^2	-0.28	-0.92	Forest	\sqrt{X}	-0.75	-0.20
Temp. seasonality	CV	X^2	0.94	0.15	<i>Dehesas</i>	\sqrt{X}	-0.32	-0.52
Annual temp. range	°C	X^2	0.93	0.17	Shrub	\sqrt{X}	-0.73	-0.49
Diurnal temp. range	°C	X^3	0.87	0.14	Meadows	\sqrt{X}	-0.68	-0.03
Temp. hottest month	°C		0.82	-0.36	Ligneous dry farm.	\sqrt{X}	0.57	0.07
Temp. coldest month	°C		-0.70	-0.68	Herbaceous dry farm.	\sqrt{X}	0.69	0.23
Mean annual precip.	mm		-0.66	0.10	Irrigation lands	\sqrt{X}	0.17	0.67
Precip. seasonality	CV		-0.80	-0.46	Urban	\sqrt{X}	-0.06	0.86
Precip. wettest month	mm		-0.79	-0.06	Population density	$\text{Log}_{10}(X)$	0.28	0.82
Precip. driest month	mm	$\text{Log}_{10}(X)$	0.64	0.72	Eigenvalue		2.58	2.47
Elevation	m	\sqrt{X}	0.46	0.86	% Variance		0.29	0.56
Slope	‰	\sqrt{X}	0.05	0.81	Correlation with X		0.21	-0.12
Drainage density	km km ⁻²	$\text{Log}_{10}(X)$	-0.06	0.32	Correlation with Y		0.08	-0.48
Drainage area	km ²	$\text{Log}_{10}(X)$	0.16	-0.44				
Eigenvalue			6.09	3.95				
% Variance			0.44	0.72				
Correlation with X			0.57	0.50				
Correlation with Y			0.86	0.001				

CV, coefficient of variation.

nated by dry agriculture towards its positive extreme, while areas with high natural vegetation cover were closer to the negative extreme. $PC2_{use}$ was positively related to irrigated and urban areas with high population density, while its negative values were related to higher cover of *dehesas* and shrub formations. $PC1_{use}$ had a slight increase moving eastwards, while $PC2_{use}$ tended to show higher values towards the southern part of Andalusia (Table 1).

To account for possible temporal changes in land use, we extracted the cover of the eight land-use categories from the 1991 Land Cover Digital Map of Andalusia and compared the PCAs from 1991 and 1999. The resulting PCAs were almost identical (see Appendix S2). Therefore, we maintained the environmental characterization based on the 1999 data for all three otter surveys.

Environmental factors and otter distribution

To ensure data independence and avoid pseudoreplication, we selected those subcatchments that had been visited in only one of the surveys, and picked up a single, randomly selected survey in those subcatchments that had been visited more than once. As a result, the number of subcatchments finally used to analyse the factors influencing otter distribution was 1038.

We tested the response of otter occurrence to environmental and temporal factors using generalized linear models (GLMs) with binomial error distribution and a logit link function, run in *SPSS 13* (SPSS Inc., Chicago, IL, USA). We followed a hierarchical procedure to fit alternative models, using different subsets of predictor variables (e.g. Naves *et al.*, 2003). Subsequent models used: (1) survey (a factor with three levels, 1985, 1995 and 2005); (2) natural gradients ($PC1_{nat}$ and $PC2_{nat}$); (3) human gradients ($PC1_{use}$ and $PC2_{use}$); (4) natural and human gradients; (5) survey and natural gradients; (6) survey and human gradients; and (7) survey and natural and human gradients (i.e. the full model). When survey and any gradient were simultaneously included in the model, we also included their interaction (i.e. factor \times covariate) to test if the influences of environmental gradients on otter distribution differed among surveys. We fitted the seven models listed above and ranked them according to Akaike's information criterion (AIC), inspecting those models having stronger support, i.e. with a difference in AIC (ΔAIC) < 2 with respect to the first-ranking model (Burnham & Anderson, 2002).

To account for the spatial component of otter distribution, we calculated the percentage of positive subcatchments within a 50-km radius in the same survey. These values were converted to a factor, 'local occupancy', with three levels: low (0–33% of positive surrounding subcatchments), medium (33–66%) and high (66–100% positive subcatchments). Local occupancy was used as a random factor to fit the final models selected through the process described above, which were thus fitted as generalized linear mixed models (GLMMs) with binomial error distribution and a logit link function using *SAS 9.1* (SAS Institute Inc., Cary, NC, USA).

We then explicitly accounted for the potential role of natural gradients ($PC1_{nat}$ and $PC2_{nat}$) as determinants of human gradients ($PC1_{use}$ and $PC2_{use}$), and analysed how these relationships may vary between positive and negative subcatchments. By doing this, we addressed the question of whether otters showed preference for any extreme of the human gradients at a given position along a natural gradient. To answer this, we ran GLMMs with normal error and identity link, using survey (three levels) as the random factor, in *SPSS 13*. We tested fixed effects as in analysis of covariance (ANCOVA), in which one of the human gradients was the dependent variable, one of the natural gradients was the covariate and the presence-absence of otters was the factor. Thus, we performed four different mixed-effects ANCOVAs. For each ANCOVA, we followed a two-step procedure (see García-Berthou & Moreno-Amich, 1993). First, we tested the homogeneity of slopes by inspecting the significance of the interaction term (factor \times covariate). Whenever this interaction term was not significant ($P > 0.1$) it was removed from the model, and standard ANCOVA designs were then applied.

Recolonization process

To evaluate the influence of environmental factors on the temporal dynamics of otter distribution we selected those subcatchments that had been visited in any two consecutive surveys [$n = 367$ subcatchments, 159 with data for 1985 and 1995 surveys (period 1) and 208 for 1995 and 2005 surveys (period 2)]. Subcatchments that were visited in the three otter surveys ($n = 103$) were used as different sampling units (one for each period). Subcatchments were then classified as: (1) 'maintenance', when otters were detected in both consecutive surveys; (2) 'colonization', when otters were detected in a survey, but not in the previous one; (3) 'extinction', when otters were not detected in a subcatchment that was positive in the previous survey; and (4) 'absence', when otters were not detected in any of two consecutive surveys. However, we excluded 'extinction' events from further analyses, due to their low numbers (12 extinction events in period 1, and 5 in period 2). We hence retained 350 subcatchment units, including 76 absences, 78 colonizations and 196 maintenances.

To account for the spatial structure of otter expansion, we used two complementary contagion variables. First, we calculated the minimum distance of every subcatchment (in metres, from the subcatchments' centroids) to any subcatchment (excluding itself) that had been positive in the previous survey. This variable, 'distance', was maintained as a continuous predictor, being \log_{10} -transformed prior to its inclusion in any analysis. The second contagion variable was calculated from the proportion of positive subcatchments in the previous survey within a 50-km radius around any given subcatchment. This variable, 'previous occupancy', was converted to a factor with three levels: low (0–33% of positive subcatchments in the previous survey), medium (33–66%) and high (66–100% positive subcatchments). Finally, an additional variable, 'anthropization', accounted for possible temporal changes in

the level of human pressure on the territory. Anthropization was the difference between the cover of human-related land uses (agricultural and urban) in 1999 and those in 1991. Positive values of this variable corresponded to subcatchments where human pressure increased between 1991 and 1999.

We treated the maintenance, colonization or absence status of subcatchments as an ordinal variable and analysed the temporal and spatial dynamics of otter distribution by means of a GLMM with an ordinal multinomial error structure and a logit link (e.g. Sol *et al.*, 2005). We used distance, natural and human gradients, and anthropization as continuous predictors, while previous occupancy was treated as a categorical predictor. Period (two levels) was included as a random factor to control for the possible variation associated with repeated surveys. We fitted a full model including all explanatory variables. The strength of the model's effect was estimated through the deviance change of a GLM (i.e. without the random factor) with the same fixed terms compared with a null model. These analyses were run using SAS 9.1.

RESULTS

Environmental factors and otter distribution

The otter has progressively expanded its distribution range across Andalusia in the last two decades (Fig. 1). In 1985, the

species was detected in 42% of the surveyed subcatchments, a percentage that increased to 58% in 1995 and again to 72% in 2005 (i.e. approximately a 70% increase in the species' range in 20 years). This trend was reflected in the strong effect of the 'survey' factor on otter occurrence (Table 2). Gradients related to human impacts were better predictors of otter distribution than natural ones and accounted for a larger proportion of the deviance than natural gradients, independently of whether survey was included as a factor in the models. However, the full model accounted for the largest amount of deviation (Table 2) and was the only one having support after inspecting the AICs of alternative models (the Δ AIC with the second ranking model was 12.6). Otter occurrence tended to be higher at the more natural end of both human gradients. Once the human gradients and survey were taken into account, otter occurrence was lower in more continental ($PC1_{nat}$ positive end) and mountain subcatchments ($PC2_{nat}$ positive end) (Table 2). There were highly significant interactions between survey and $PC2_{nat}$ and $PC1_{use}$, suggesting a temporal increase in the probability of otter occurrence at lower elevations and in dry farming areas.

The two natural gradients had strong significant effects on the two human gradients ($P < 0.001$ in all cases) and the slope of these relationships did not differ between positive and negative subcatchments in any of the four possible combinations of natural and human gradients (interaction term

Table 2 Factors affecting otter (*Lutra lutra*) distribution in Andalusia. Presence or absence of otters was modelled by means of generalized linear models (GLMs), using a binomial error structure and logit link function. Models were fitted using a combination of three groups of variables: (1) survey (categorical variable with three levels: 1985, 1995 and 2005); (2) natural gradients ($PC1_{nat}$ and $PC2_{nat}$); and (3) human gradients ($PC1_{use}$ and $PC2_{use}$). Deviance change shows the percentage deviance reduction in relation to the null model (which only included the intersection term) while the dispersion parameter shows the ratio between the residual deviance and the residual degrees of freedom. The final full model was fitted using a generalized linear mixed model (GLMM) with local occupancy (a three-level factor, based on the percentage of occupied subcatchments in a 50-km radius) as random effect. A negative direction of the relationships between predictors and the dependent variable in the full model indicates that higher predictor values are related to otter absences.

Model selection (GLMs)	d.f.	χ^2	P-value	Δ Deviance (%)	Dispersion parameter
Survey	2	81.5	< 0.001	5.7	1.29
Natural gradients	2	6.5	0.04	0.5	1.37
Human gradients	2	123.3	< 0.001	8.7	1.25
Natural + human gradients	4	185	< 0.001	13.0	1.20
Survey + natural gradients	8	109.8	< 0.001	7.7	1.27
Survey + human gradients	8	226.5	< 0.001	15.9	1.16
Full model	14	344.8	< 0.001	24.3	1.05
Fixed effects in full model (GLMM)	d.f.	F	P-value	Direction	
Survey	2	10.3	< 0.001	(85,95) < 05	
$PC1_{nat}$	1	5.2	0.022	Positive	
$PC2_{nat}$	1	20.9	< 0.001	Negative	
$PC1_{use}$	1	49	< 0.001	Negative	
$PC2_{use}$	1	52.8	< 0.001	Negative	
Survey \times $PC1_{nat}$	2	2.4	0.094	–	
Survey \times $PC2_{nat}$	2	7.5	< 0.001	05 < 95 < 85	
Survey \times $PC1_{use}$	2	4.2	0.015	05 < (95,85)	
Survey \times $PC2_{use}$	2	2.7	0.068	–	

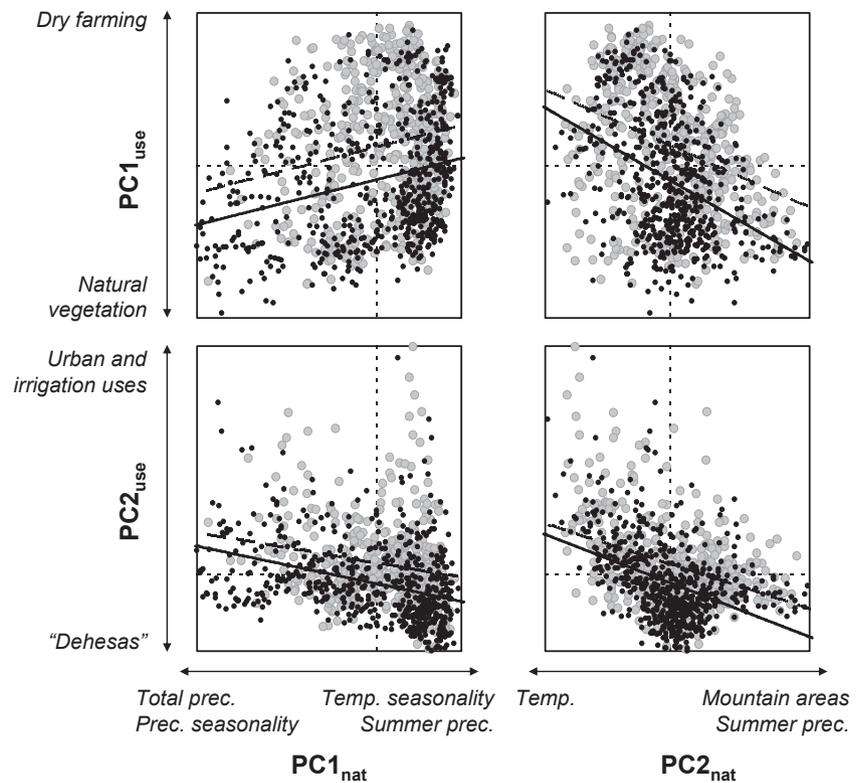


Figure 2 Relationships between natural (abscissas) and human (ordinates) gradients shown separately for positive (black circles, plain line) and negative (grey circles, dashed line) subcatchments of the otter (*Lutra lutra*) in Andalusia.

$P > 0.17$ in all cases). Interestingly, for any value of the two natural gradients, positive subcatchments always tended to be placed closer to the natural extremes of the human gradients than the negative ones ($P < 0.001$ in all four cases) (Fig. 2).

Recolonization process

Contagion variables proved to be major determinants of the temporal dynamics of otter distribution, indicating that dispersal limitation may be a critical factor in the species' expansion process (Table 3). There were no repeated otter absences recorded in areas with a high previous occupancy. At lower levels of occupation, absence subcatchments were further from previously occupied subcatchments than those that had been colonized or those in which otters maintained their presence (Fig. 3). On average, colonized subcatchments were 13.0 km away from the nearest subcatchment occupied 10 years earlier. This meant that otter expansion rate averaged 1.3 km year⁻¹, a value that remained rather constant in both periods (1.2 and 1.4 km year⁻¹ for the 1985–95 and 1995–2005 periods, respectively). The maximum distance of a colonized subcatchment from a previously occupied subcatchment was 50.9 km. However, among the 78 recorded colonization events, this distance was larger than 30 km in only five events (6.4%).

In agreement with the results depicted above, absence subcatchments usually had strong human influences, while maintenance subcatchments were mainly located towards the less impacted extreme of human gradients (Table 3). Interestingly, colonized subcatchments tended to be placed at

Table 3 Generalized linear mixed model (GLMM) analysing factors behind changes in otter (*Lutra lutra*) distribution between consecutive otter surveys in Andalusia. Period (two levels, 1985–95 and 1995–2005) was included as a random factor (covariance parameter estimate = 0.05, SE = 0.12). The model (deviance change 35.1%, dispersion parameter 0.65) was fitted using an ordinal multinomial error structure of the response variable and a logit link function, where maintenance > colonization > absence.

	d.f.	F	P-value	Direction
Previous occupancy	2	17.8	< 0.001	L < M < H
Distance	1	18.8	< 0.001	Negative
PC1 _{nat}	1	1.3	0.25	Negative
PC2 _{nat}	1	3.0	0.08	Negative
PC1 _{use}	1	4.6	0.03	Negative
PC2 _{use}	1	13.8	< 0.001	Negative
Anthropization	1	1.9	0.17	Positive

L, M and H stand for low, medium and high previous occupancy, respectively.

intermediate positions within human gradients (Fig. 3). In spite of this, the dynamic component of human impacts (i.e. anthropization) did not have any significant relationship with changes in otter distribution. The elevational gradient (PC2_{nat}) had a marginally significant negative effect on recolonization. These results imply that, once dispersal capacities have been taken into account, the colonization of new areas by otters may be limited by the intensity of human influences at the landscape scale. However, results also show that otters have colonized moderately impacted areas from where they were

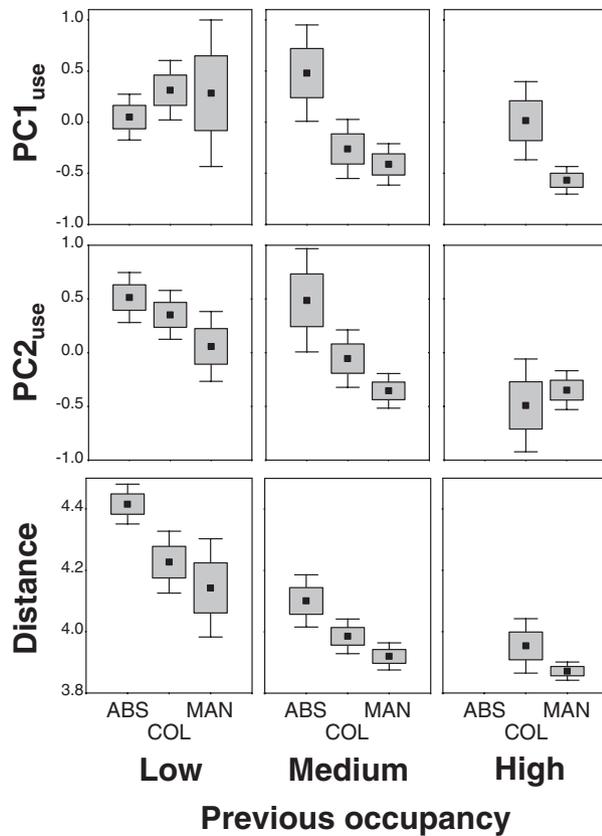


Figure 3 Mean values of human gradients and distance to nearest previously occupied subcatchment according to otter (*Lutra lutra*) distribution changes between any two consecutive surveys in Andalusia (ABS, repeated absence; COL, colonization; and MAN, maintenance) and shown separately for the different levels of previous occupancy (i.e. after the proportion of positive subcatchments in a 50-km buffer). Boxes represent standard error and whiskers represent 95% confidence intervals.

previously absent, a process that appears to be involved in the recent expansion of the distribution of the species.

DISCUSSION

Environmental factors and otter distribution

Studies analysing the relationship between environmental features and otter distribution have been performed at a range of spatial scales. Analyses have been carried out for river stretches within a particular basin (e.g. Prenda & Granado-Lorencio, 1996) at a regional scale (Barbosa *et al.*, 2001; Marcelli & Fusillo, 2009) and at a continental scale (Robitaille & Laurence, 2002). At the landscape scale, the ecological significance of many of these works has been hindered by the clustered structure of historical otter declines, which probably responded to the geographically structured impacts of factors operating at large spatial scales. For example, the amount of organochlorinated pollutants in the environment, generally accepted as the main cause of otter decline in the second half of

the 20th century, had a clear geographical component, decimating otter populations in large areas across central Europe while having less acute impacts in peripheral areas (e.g. Macdonald & Mason, 1990, 1994). As a likely consequence, pure geographical variables have often been found to be the main predictors of otter distribution patterns, while landscape features played only a secondary role (Barbosa *et al.*, 2001, 2003; Remonti *et al.*, 2008). We believe that Andalusia offers a good opportunity to explore the ecological patterns of otter distribution and its dynamics for two main reasons. First, otter populations in Andalusia were not restricted to a single geographical area within the region in any of the three surveys. Second, the expansion of otter populations has not followed a particular geographical direction (see Marcelli & Fusillo, 2009) (i.e. the size of a hypothetical polygon enclosing otter populations in Andalusia has remained relatively stable across otter surveys, see Fig. 1). In addition, the region is characterized by a wide variation of landscapes and no direct actions to reinforce the population (e.g. reintroduction programmes) have been undertaken.

Our results showed that the distribution of the expanding otter population in Andalusia could be linked to natural and, especially, human-related landscape gradients. Human gradients derived from land-use variables ($PC1_{use}$ and $PC2_{use}$) were the main factors influencing otter distribution (Table 2). Otters tended to be consistently rarer in highly cultivated and urban areas along both natural gradients (Fig. 2). Negative relationships between otter occurrence and different proxies for human landscape modification have been reported throughout the species' European range. For example, Prenda *et al.* (2001) found that otters tended to occur in unpolluted and scarcely human-disturbed streams in Córdoba, a central Andalusian province. Similarly, Barbosa *et al.* (2001) and Robitaille & Laurence (2002) described a negative relationship between road density and frequency of otter occurrences among continental Spanish and French provinces, respectively.

In our study, natural landscape gradients were poor predictors of otter occurrence when considered alone, although their effect increased notably when human gradients were also included in the models. These changes were due to the existing relationships between natural and human gradients (Fig. 2), particularly in the case of the elevational gradient defined by $PC2_{nat}$. While $PC2_{nat}$ did not have any significant influence on otter occurrences in the model that included only the effects of natural gradients or these and 'survey' ($P = 0.85$ and $P = 0.95$, respectively), it had a highly significant negative effect in the full model (Table 2). The higher probability of occurrence of otters at lower elevations reported by the full model is a predictable pattern, because higher-order river stretches offer higher prey availability, both in terms of diversity and biomass (Matthews, 1998; Ruiz-Olmo, 1998), and especially in the case of fish, the otter's staple prey (Clavero *et al.*, 2003). Similar to other carnivores, otter populations are primarily regulated by the availability of food, and thus should thrive in low-elevation areas. In fact, many local-scale studies have reported positive relationships between

different estimators of otter population density and prey availability (e.g. Prenda & Granado-Lorencio, 1996; Ruiz-Olmo *et al.*, 2001). However, our results show that the hypothetical negative relationship between elevation and otter occurrence is apparent only when human landscape gradients are also taken into account. This may result from the fact that lowland areas are also those most affected by anthropogenic land uses (Fig. 2). In fact, human-related landscape degradation is likely to affect primarily the lowland water courses favoured by otters, contributing to the apparent species' preference for middle-elevation areas, which have been repeatedly reported in the literature (e.g. Prenda *et al.*, 2001; Marcelli & Fusillo, 2009).

The positive relationship between otter occurrence and $PC1_{nat}$ denotes a higher probability of otter occurrence in areas with low precipitation seasonality and relatively high precipitation during the drier summer months. Water availability is a critical factor in otter ecology in Mediterranean habitats, especially during summer droughts (e.g. Prenda *et al.*, 2001; Ruiz-Olmo *et al.*, 2002; Ruiz-Olmo & Jiménez, 2008). As summer advances, water flow stops in most small and medium-sized Mediterranean water courses, and surface water becomes restricted to chains of isolated pools that act as refuges for aquatic organisms (Gasith & Resh, 1999; Magalhães *et al.*, 2002). Otters can initially benefit from this process due to the concentration of prey in pools. However, conditions turn progressively harsher as a combination of pool desiccation, reduction of pool water quality (i.e. frequent episodes of anoxia, high temperatures) and high predation rates lead to the collapse of prey populations (Magalhães *et al.*, 2002; Ruiz-Olmo *et al.*, 2007). These processes can cause a reduction in the biological performance of otters in most unstable freshwater environments (Clavero *et al.*, 2008; Ruiz-Olmo & Jiménez, 2008, 2009) and can explain the positive relationship between $PC1_{nat}$ and otter occurrence in Andalusia. However, it should also be noted that, as previously discussed for $PC2_{nat}$, this relationship became evident only after considering the effects of survey and human landscape gradients on otter distribution. In fact, in the model including only natural gradients $PC1_{nat}$ had a small and negative (i.e. contrary to that in the full model) effect on otter occurrence (see Table 2).

The recolonization process

Our results showed that the probability of colonization of any particular subcatchment by otters had stronger relationships with spatial contagion variables than with any other predictor. Both population maintenance and colonization of new areas were favoured by a high previous occupancy and the presence nearby of previously occupied subcatchments. Repeated absences of otters were improbable in areas with high levels of previous occupancy (Fig. 3). These patterns reflect strong spatial dynamics, based on dispersion from saturated populations and colonization of empty habitats. Low-quality habitats can be repeatedly colonized by otters whenever those areas are surrounded by high-quality habitats that act as

sources (e.g. Delibes *et al.*, 2009), resulting in a low probability of detecting otter absence.

However, the recorded expansion rate of the otter in Andalusia (1.3 km year^{-1}) seems quite slow compared with the known movement capabilities of the species. Otters are highly mobile animals that are able to travel more than 20 km in a single day and occupy linear home ranges of up to 40 km (Saavedra, 2002). High expansion rates have been reported in areas where the species had been totally depleted or where populations had been reintroduced. For example, Janssens *et al.* (2006) reported an expansion rate of some 11 km year^{-1} for an otter population recolonizing the Cévennes National Park in southern France, as well as similar rates for other expanding populations in France and Denmark. Delibes *et al.* (2009) reported the rapid recolonization of over 60 km of the Guadiamar River (in western Andalusia) only 1 year after a massive mine spill. A reintroduced otter population in the north-east Iberian Peninsula followed a similarly rapid expansion, with 23 liberated animals occupying more than 300 km of rivers and streams only 2 years after being released (Saavedra, 2002). Rapid spread of otters in newly colonized areas and areas of reintroduction can be related to the availability of high-quality habitats but also to the release from intra-specific interactions, which play a major role in the use of space by otters (see Ó Néill *et al.*, 2009). Therefore, our results strongly suggest that the expansion rates recorded in Andalusia are well below the species' potential and are probably due to habitat constraints limiting colonization events.

There was a clear difference in the degree of human influence on the landscape between subcatchments with permanent otter presence and those in which the species remained absent in two consecutive surveys (Fig. 3). Colonized subcatchments had values along human gradients that fell between those where otters were absent and those where they maintained a population. This indicates that otter expansion was directed towards areas that are more impacted by humans than those occupied by stable populations. In fact, otters are currently present in some big cities in Andalusia and other Spanish areas (Jiménez *et al.*, 2008) and are also colonizing urbanized areas in southern Italy, although there they do not seem to be occupying intensively cultivated lands (Marcelli & Fusillo, 2009). Occupation of human-perturbed areas by otters can be potentially explained by two different, though non-mutually exclusive, mechanisms. First, the previously poor environmental status in human-dominated landscapes could have improved to the point that otters are currently able to live in areas that were otherwise unfavourable for the species two decades ago. Second, the occupation of perturbed areas could depend on source-sink population dynamics, with saturated populations present in natural habitat patches acting as sources from which dispersed individuals may form new population nuclei in suboptimal habitats (e.g. Delibes *et al.*, 2009).

Among the possible changes that could have occurred in human-perturbed landscapes in Andalusia in recent times, the reduction of urban and industrial pollution of water courses is one of the main things to have had a positive effect, whether

direct or indirect, on otter populations. Following the implementation of European Union (EU) directives, many water treatment plants were constructed across Spain from the mid 1990s. This led to a general improvement in water quality, even though pollution, especially of urban origin, can still be considered a widespread problem in Andalusia (Prenda *et al.*, 2006). Levels of PCBs from otter tissues were high in Spain in the 1980s and early 1990s. Peak values recorded in Andalusia surpassed by approximately 20 times the concentrations estimated to cause reproductive failure (Ruiz-Olmo *et al.*, 2000). However, these levels were notably lower in the late 1990s, when they rarely exceeded strong toxicity thresholds (Jiménez *et al.*, 2008). A reduction in the level of pollution could also have induced increases in the populations of potential otter prey, especially those of fish. This would have allowed the sequential colonization of fish and otter in areas which were in the past too polluted to sustain either prey or predator populations. Unfortunately, we cannot support this hypothesis with real evidence, because there are no clear data on the trends of fish availability in Andalusia or other Iberian areas from the last 20 years.

Recent additions of new trophic resources may have also favoured otter expansion. For example, since its establishment in southern Spain in the mid 1970s and subsequent explosive expansion, the invasive red swamp crayfish (*Procambarus clarkii*) has become a frequent food item of otter and other carnivore and avian predators (Beja, 1996; Correia, 2001). Otters have been shown to occupy habitats where fish are scarce or absent provided that crayfish populations are abundant (Ruiz-Olmo & Clavero, 2008). The red swamp crayfish usually occupies low- to middle-elevation water bodies in the Iberian Peninsula and becomes rare or completely absent in otter diet at elevations over 600 m (Clavero *et al.*, 2008). The species has also been shown to be relatively resistant to organic pollution, being able to thrive in degraded fluvial habitats (e.g. Torreblanca *et al.*, 1989; Barbaresi & Gherardi, 2000). These features fit well with the recent colonization by otters of lowland, degraded habitats. It had already been proposed that the spread of red swamp crayfish has favoured otter recovery (e.g. Jiménez *et al.*, 2008; Ruiz-Olmo & Clavero, 2008), but our results also suggest that variations of crayfish availability along landscape gradients can also influence the characteristics of areas colonized by otters.

On the other hand, the improvement of previously unfavourable habitats, described above, may not be enough to fully explain otter expansion in Andalusia over the last few decades. In fact, otters seem to be unable to colonize most anthropized landscapes (Fig. 3) and expansion rates have been much slower than those recorded in other newly occupied areas. This suggests that the colonization of new areas by otters also relies on the role of saturated areas acting as sources. Therefore, the question arises: why have otter populations in favourable habitats reached a supposedly saturated state and begun to spread over the last 20 years?

Recent expansion of otter populations, in Andalusia and elsewhere, could be related to processes operating at large

spatial scales. If PCBs and DDT were the main cause of large-scale otter declines throughout Europe, it is plausible that these pollutants were also affecting other populations inhabiting areas where declines were not as evident, perhaps by reducing their biological performance. As previously mentioned, the process of otter recovery in Spain coincides with a clear reduction in the concentration of chlorinated pollutants found in otter carcasses (Jiménez *et al.*, 2008). An attenuation of the negative effects of these compounds could have favoured increased reproductive success and/or reduced mortality among remaining otter populations, with these acting as a source of individuals occupying newly colonized areas. Further, human-impacted landscapes could then be acting as sinks, receiving otter individuals from the more natural source areas. In suboptimal habitats, otter populations are likely to be limited by reduced prey availability, the poor development of riparian vegetation (thus offering little refuge) and/or the direct sublethal effects of pollutants.

CONCLUSIONS

Our results show that otter distribution dynamics are related to both environmental and spatial variables and provide important insights for the conservation of the species. Otter distribution is clearly limited by the level of human influence on landscape characteristics. Therefore, reintroduction projects would only be justifiable in well-conserved areas where natural recolonization is highly improbable due to the presence of strong limitations to species dispersal. A number of otter reintroduction projects have been developed in Europe over the past few decades, and some of them have succeeded in establishing free-ranging wild populations (e.g. Saavedra, 2002; Copp & Roche, 2003). However, most of these reintroduced populations have also received naturally dispersing individuals (Copp & Roche, 2003; Ferrando *et al.*, 2008), revealing that reintroduction areas would probably have been recolonized without otter releases, although the releases may have accelerated the process. Based on our results, we believe that the future management of otter populations should concentrate on the conservation and improvement of aquatic and riparian habitats. These measures would favour the further expansion of the species distribution and would also produce a more general benefit to the aquatic environment than that of species-specific management actions.

ACKNOWLEDGEMENTS

We gratefully acknowledge the huge and mainly voluntary work of all those people who made possible the compilation of large-scale otter distribution data in Spain in three different surveys. Special thanks are due to the SECEM (Spanish Society for the Conservation and Study of Mammals) and particularly to Chema López-Martín, Juan Jiménez and Jordi Ruiz-Olmo for the impetus given to Spanish otter surveys, as well as to José Prenda and Luís Javier Palomo, who coordinated the last survey in Andalusia and kindly allowed us to use those data.

This latter survey received financial support from the Water Agency of the Andalusian Government. Núria Roura-Pascual read and improved the manuscript and Carlos Camino helped us with GIS-based calculations. Stephani Januchwski and Fraser Hartley helped us to improve the English. M.C. benefited from a Juan de la Cierva post-doctoral contract granted by the Spanish Ministry of Education and Science. This work has received financial support from the projects Consolider Montes CSD2008-00040 granted by the Spanish Ministry of Education and Science (MEC) and the European granted FP7 project 226852 SCALES.

REFERENCES

- Barbaresi, S. & Gherardi, F. (2000) The invasion of the alien crayfish *Procambarus clarkii* in Europe, with particular reference to Italy. *Biological Invasions*, **2**, 259–264.
- 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 modelling at two resolution scales suited to conservation planning in the Iberian Peninsula. *Biological Conservation*, **114**, 377–387.
- Beja, P.R. (1996) An analysis on otter *Lutra lutra* predation on introduced American crayfish *Procambarus clarkii* in Iberian streams. *Journal of Applied Ecology*, **33**, 1156–1170.
- Bottrill, M., Joseph, L.N., Carwardine, J., Bode, M.C., Cook, C., Game, E.T., Grantham, H., Kark, S., Linke, S., McDonald-Madden, E., Pressey, R.L., Walker, S., Wilson, K.A. & Possingham, H.P. (2009) Finite conservation funds mean triage is unavoidable. *Trends in Ecology and Evolution*, **24**, 183–184.
- Brotos, L., Thuiller, W., Araújo, M.B. & Hirtzel, A.H. (2004) Presence-absence versus presence-only modelling methods for predicting bird habitat suitability. *Ecography*, **27**, 437–448.
- Brotos, L., Herrando, S. & Pons, P. (2008) Wildfires and the expansion of threatened farmland birds: the ortolan bunting, *Emberiza hortulana*, in Mediterranean landscapes. *Journal of Applied Ecology*, **45**, 1059–1066.
- Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multimodel inference: a practical information-theoretical approach*, 2nd edn. Springer-Verlag, New York.
- Clavero, M., Prenda, J. & Delibes, M. (2003) Trophic diversity of the otter (*Lutra lutra* L.) in temperate and Mediterranean freshwater habitats. *Journal of Biogeography*, **30**, 761–769.
- Clavero, M., Ruiz-Olmo, J., Sales-Luis, T., Blanco-Garrido, F., Romero, R., Pedrosa, N.M., Prenda, J., Santos-Reis, M., Narváez, M. & Delibes, M. (2008) Lo que comen las nutrias Ibéricas [What Iberian otters eat]. *La nutria en España. Veinte años de seguimiento de un mamífero amenazado* (ed. by J.M. López-Martín and J. Jiménez), pp. 345–367. SECEM, Málaga (in Spanish).
- CMA (1999) *Mapa de usos y coberturas vegetales de Andalucía*, 1:25,000. Junta de Andalucía, Sevilla.
- Copp, G.H. & Roche, K. (2003) Range and diet of Eurasian otters *Lutra lutra* (L.) in the catchment of the River Lee (south-east England) since re-introduction. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **13**, 65–76.
- Correia, A.M. (2001) Seasonal and interspecific evaluation of predation by mammals and birds on the introduced red swamp crayfish *Procambarus clarkii* (Crustacea, Cambaridae) in a freshwater marsh (Portugal). *Journal of Zoology, London*, **255**, 533–541.
- Cote, J., Clobert, J. & Fitze, P.S. (2007) Mother-offspring competition promotes colonization success. *Proceedings of the National Academy of Sciences USA*, **104**, 9703–9708.
- Davies, Z.G., Wilson, R.J., Brereton, T.M. & Thomas, C.D. (2005) The re-expansion and improving status of the silverspotted skipper butterfly (*Hesperia comma*) in Britain: a metapopulation success story. *Biological Conservation*, **124**, 189–198.
- Delibes, M. (1990) *La nutria en España [The otter in Spain]*. ICONA, Serie Técnica, Madrid (in Spanish).
- Delibes, M., Cabezas, S., Jiménez, B. & González, M.J. (2009) Animal decisions and conservation: the recolonization of a severely polluted river by the Eurasian otter. *Animal Conservation*, **12**, 400–407.
- Ferrando, A., Lecis, R., Domingo-Roura, X. & Ponsà, M. (2008) Genetic diversity and individual identification of reintroduced otters in north-eastern Spain by DNA genotyping of spraints. *Conservation Genetics*, **9**, 129–139.
- Ferreras, P., Delibes, M., Palomares, F., Fedriani, J.M., Calzada, J. & Revilla, E. (2004) Proximate and ultimate causes of dispersal in the Iberian lynx *Lynx pardinus*. *Behavioural Ecology*, **15**, 31–40.
- García-Berthou, E. & Moreno-Amich, R. (1993) Multivariate analysis of covariance in morphometric studies of the reproductive cycle. *Canadian Journal of Fisheries and Aquatic Sciences*, **50**, 1394–1399.
- Gasith, A. & Resh, V.H. (1999) Streams in Mediterranean climate regions: abiotic influences and biotic responses to predictable seasonal events. *Annual Review of Ecology and Systematics*, **30**, 51–81.
- Hengeveld, R. (1989) *Dynamics of biological invasions*. Chapman and Hall, London.
- IUCN (1998) *Guidelines for re-introductions*. Prepared by the IUCN/SSC Re-introduction Specialist Group, IUCN, Gland and Cambridge, UK. Available at: <http://www.iucnsscrsg.org/download/English.pdf>
- Janssens, X., Defourny, P., Kermabon, J. & Baret, P.V. (2006) The recovery of the otter in the Cevennes (France): a GIS-based model. *Hystrix*, **17**, 5–14.
- Jiménez, J., López-Martín, J.M., Ruiz-Olmo, J. & Delibes, M. (2008) Por qué se está recuperando la nutria en España? [Why is the otter recovering in Spain?]. *La nutria en España. Veinte años de seguimiento de un mamífero amenazado* (ed. by J.M. López-Martín and J. Jiménez), pp. 273–304. SECEM, Málaga (in Spanish).

- Klar, N., Fernández, N., Kramer-Schadt, S., Herrmann, M., Trinzen, M., Büttner, I. & Niemitz, C. (2008) Habitat selection models for European wildcat conservation. *Biological Conservation*, **141**, 308–319.
- Kruuk, H. (2006) *Otters: ecology, behaviour and conservation*. Oxford University Press, Oxford.
- Lenton, E.J., Chanin, P.R.F. & Jefferies, D.J. (1980) *Otter survey of England 1977–79*. Nature Conservancy Council, London.
- Linke, S., Pressey, R.L., Bailey, R.C. & Norris, R.H. (2007) Management options for river conservation planning: condition and conservation re-visited. *Freshwater Biology*, **52**, 918–938.
- López-Martín, J.M. & Jiménez, J. (eds) (2008) *La nutria en España. Veinte años de seguimiento de un mamífero amenazado [The otter in Spain. Twenty years of monitoring of a threatened mammal]*. SECEM, Málaga (in Spanish).
- Macdonald, S.M. & Mason, C.F. (1990) Action plan for European otters. *Otters: an action plan for their conservation* (compiled by P. Foster-Turley, S. Macdonald and C. Mason), pp. 29–40. IUCN/SSC Otter Specialist Group, Gland.
- Macdonald, S.M. & Mason, C.F. (1994) *Status and conservation needs of the otter (Lutra lutra) in the Western Palearctic*. Nature Environment 67. Council of Europe, Strasbourg.
- Magalhães, M.F., Beja, P.R., Canas, C. & Collares-Pereira, M.J. (2002) Functional heterogeneity of dry-season fish refugia across a Mediterranean catchment: the role of habitat and predation. *Freshwater Biology*, **47**, 1919–1934.
- Maidment, D.R. (2002) *Arc Hydro: GIS for water resources*. ESRI Press, Redlands, CA.
- Marcelli, M. & Fusillo, R. (2009) Assessing range re-expansion and recolonization of human-impacted landscapes by threatened species: a case study of the otter (*Lutra lutra*) in Italy. *Biodiversity and Conservation*, **18**, 2941–2959.
- Mason, C.F. & Macdonald, S.M. (1986) *Otters: ecology and conservation*. Cambridge University Press, Cambridge.
- Matthews, W.A. (1998) *Patterns in freshwater fish ecology*. Chapman and Hall, New York.
- McGarigal, K., Cushman, S. & Stafford, S. (2000) *Multivariate statistics for wildlife and ecology research*. Springer, New York.
- Naves, J., Wiegand, T., Revilla, E. & Delibes, M. (2003) Endangered species constrained by natural and human factors: the case of brown bears in northern Spain. *Conservation Biology*, **17**, 1276–1289.
- Ó Néill, L., Veldhuizen, T., Jongh, A. & Rochford, J. (2009) Ranging behaviour and socio-biology of Eurasian otters (*Lutra lutra*) on lowland mesotrophic river systems. *European Journal of Wildlife Research*, **55**, 363–370.
- Ottaviani, D., Panzacchi, M., Jona Lasinio, G., Genovesi, P. & Boitani, L. (2009) Modelling semi-aquatic vertebrates' distribution at the drainage basin scale: the case of the otter *Lutra lutra* in Italy. *Ecological Modelling*, **220**, 111–121.
- Prenda, J. & Granado-Lorencio, C. (1996) The relative influence of riparian habitat structure and fish availability on otter *Lutra lutra* L. sprainting activity in a small Mediterranean catchment. *Biological Conservation*, **76**, 9–15.
- Prenda, J. & Palomo, L.J. (2008) La nutria en Andalucía [The otter in Andalusia]. *La nutria en España. Veinte años de seguimiento de un mamífero amenazado* (ed. by J.M. López-Martín and J. Jiménez), pp. 47–69. SECEM, Málaga (in Spanish).
- Prenda, J., López-Nieves, P. & Bravo, R. (2001) Conservation of otter *Lutra lutra* in a Mediterranean area: the importance of habitat quality and temporal variation in water availability. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **11**, 343–355.
- Prenda, J., Clavero, M., Blanco-Garrido, F., Menor, A. & Hermoso, V. (2006) Threats to the conservation of biotic integrity in Iberian fluvial ecosystems. *Limnetica*, **25**, 377–388.
- Remonti, L., Prigioni, C., Balestrieri, A., Sgrosso, S. & Priore, G. (2008) Distribution of a recolonising species may not reflect habitat suitability alone: the case of the Eurasian otter (*Lutra lutra*) in southern Italy. *Wildlife Research*, **35**, 798–805.
- Reuther, C., Dolch, D., Green, R., Jahrl, J., Jefferies, D.J., Krekemeyer, A., Kucerova, M., Madsen, A.B., Romanowski, J., Roche, K., Ruiz-Olmo, J., Teubner, J. & Trindade, A. (2000) Surveying and monitoring distribution and population trends of the Eurasian otter (*Lutra lutra*). Guidelines and evaluation of the standard method for surveys as recommended by the European section of the IUCN/SSC Otter Specialist Group. *Habitat*, **12**, 1–152.
- Rivas-Martínez, S., Asensi, A., Díez-Garretas, B., Molero, J. & Valle, F. (1997) Biogeographical synthesis of Andalusia (southern Spain). *Journal of Biogeography*, **24**, 915–928.
- Robitaille, J.F. & Laurence, S. (2002) Otter, *Lutra lutra*, occurrence in Europe and in France in relation to landscape characteristics. *Animal Conservation*, **5**, 337–344.
- Rodríguez, A. & Delibes, M. (2002) Internal structure and patterns of contraction in the geographic range of the Iberian lynx. *Ecography*, **25**, 314–328.
- Roos, A., Greyerz, E., Olsson, M. & Sandegren, F. (2001) The otter (*Lutra lutra*) in Sweden – population trends in relation to sigma DDT and total PCB concentrations during 1968–99. *Environmental Pollution*, **111**, 457–469.
- Roura-Pascual, N., Bas, J.M. & Hui, C. (2010) The spread of the Argentine ant: environmental determinants and impacts on native ant communities. *Biological Invasions*, **12**, 2399–2412.
- Ruiz-Olmo, J. (1998) Influence of altitude on the distribution, abundance and ecology of the otter (*Lutra lutra*). *Behaviour and ecology of riparian mammals* (ed. by N. Dunstone and M.L. Gorman), pp. 159–176. Cambridge University Press, Cambridge.
- Ruiz-Olmo, J. & Clavero, M. (2008) Los cangrejos en la ecología y recuperación de la nutria en la Península Ibérica [Role of crayfish in the ecology and recovery of the otter in the Iberian Peninsula]. *La nutria en España. Veinte años de seguimiento de un mamífero amenazado* (ed. by J.M. López-Martín and J. Jiménez), pp. 369–396. SECEM, Málaga (in Spanish).

- Ruiz-Olmo, J. & Delibes, M. (eds) (1998) *La nutria en España ante el horizonte del año 2000 [The otter in Spain facing the year 2000 horizon]*. SECEM, Málaga (in Spanish).
- Ruiz-Olmo, J. & Jiménez, J. (2008) Ecología de la nutria en los ambientes mediterráneos de la Península Ibérica [Otter ecology in Mediterranean environments in the Iberian Peninsula]. *La nutria en España. Veinte años de seguimiento de un mamífero amenazado* (ed. by J.M. López-Martín and J. Jiménez), pp. 305–343. SECEM, Málaga (in Spanish).
- Ruiz-Olmo, J. & Jiménez, J. (2009) Diet diversity and breeding of top predators are determined by habitat stability and structure: a case study with the Eurasian otter (*Lutra lutra* L.). *European Journal of Wildlife Research*, **55**, 133–144.
- Ruiz-Olmo, J., Lafontaine, L., Prignioni, C., López-Martín, J.M. & Santos-Reis, M. (2000) Pollution and its effects on otter populations in south-western Europe. *Proceedings of the First Otter Toxicology Conference, Isle of Skye, September 2000* (ed. by J.W.H. Conroy, P. Yoxon and A.C. Gutleb), pp. 63–82. International Otter Survival Fund, Broadford, Scotland, UK.
- Ruiz-Olmo, J., López-Martín, J.M. & Palazón, S. (2001) The influence of fish abundance on the otter (*Lutra lutra*) populations in Iberian Mediterranean habitats. *Journal of Zoology, London*, **254**, 325–336.
- Ruiz-Olmo, J., Olmo-Vidal, J.M., Mañas, F. & Batet, A. (2002) The influence of resource seasonality on the breeding patterns of the Eurasian otter (*Lutra lutra*) in Mediterranean habitats. *Canadian Journal of Zoology*, **80**, 2178–2189.
- Ruiz-Olmo, J., Jiménez, J. & Chacón, W. (2007) The importance of ponds for the otter (*Lutra lutra*) during drought periods in Mediterranean ecosystems: a case study in Bergantes River. *Mammalia*, **71**, 16–24.
- Saavedra, D. (2002) *Reintroduction of the Eurasian otter (Lutra lutra) in Muga and Fluvià basins (north-eastern Spain): viability, development, monitoring and trends of the new population*. PhD Thesis, Universitat de Girona, Girona.
- Sax, D.F., Stachowicz, J.J. & Gaines, S.D. (2005) *Species invasions: insights into ecology, evolution and biogeography*. Sinauer Press, Sunderland, MA.
- Sol, D., Lefebvre, L. & Rodriguez-Teijeiro, J.D. (2005) Brain size, innovative propensity and migratory behaviour in temperate Palaearctic birds. *Proceedings of the Royal Society B: Biological Sciences*, **272**, 1433–1441.
- Suter, W., Bollman, K. & Holderegger, R. (2009) Landscape permeability: from individual dispersal to population persistence. *A changing world. Challenges for landscape research* (ed. by F. Kienast, O. Wildi and S. Ghosh), pp. 157–174. Landscape Series. Springer, Dordrecht.
- Torreblanca, A., Ramo, J. & Díaz-Mayans, J. (1989) Gill ATPase activity in *Procambarus clarkii* as an indicator of heavy metal pollution. *Bulletin of Environmental Contamination and Toxicology*, **42**, 829–834.
- White, P.C.L., Gregory, K.W., Lindley, P.J. & Richards, G. (1997) Economic values of threatened mammals in Britain: a case study of the otter (*Lutra lutra*) and the water vole (*Arvicola terrestris*). *Biological Conservation*, **82**, 345–354.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Estimation of otter detectability based on multiple surveys in specific subcatchments.

Appendix S2 Main gradients in land uses in 1991 and 1999.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials are peer-reviewed and may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.

BIOSKETCH

Miguel Clavero is a post-doctoral researcher at the Centre Tecnològic Forestal de Catalunya (CTFC). He is interested in the influences of environmental gradients on the ecology of populations and communities in Mediterranean ecosystems, including invasive species and their impacts on biodiversity. He has worked with freshwater fish, birds and semi-aquatic mammals.

Author contributions: All four authors conceived and discussed the initial ideas; M.C. and V.H. gathered the data; M.C. analysed the data and led the writing, which was actively participated in by the rest of the authors.

Editor: Jon Sadler