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BIODIVERSITY RESEARCH

Spatial, environmental and human influences on the distribution of otter (*Lutra lutra*) in the Spanish provinces

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Abstract. In a previous survey of otters (*Lutra lutra* L. 1758) in Spain, different causes were invoked to explain the frequency of the species in each province. To find common causes of the distribution of the otter in Spain, we recorded a number of spatial, environmental and human variables in each Spanish province. We then performed a stepwise linear multiple regression of the proportion of positive sites of otter in the Spanish provinces separately on each of the three groups of variables. Geographic longitude, January air humidity, soil permeability and highway density were the variables selected. A linear regression of the proportion of otter presence on these variables explained 62.4% of the variance. We then used the selected variables in a partial regression analysis to specify which proportions of the variation are explained exclusively by spatial, environmental and human factors, and which proportions are attributable to interactions between these components. Pure environmental effects accounted for only 5.5% of the variation, while pure spatial and pure human effects explained 18% and 9.7%, respectively. Shared variation among the components totalled 29.2%, of which 10.9% was explained by the interaction between environmental and spatial factors. Human factors explained globally less variance than spatial and environmental ones, but the pure human influence was higher than the pure environmental one. We concluded that most of the variation in the proportion of occurrences of otter in Spanish provinces is spatially structured, and that environmental factors have more influence on otter presence than human ones; however, the human influence on otter distribution is less structured in space, and thus can be more disruptive. This effect of large infrastructures on wild populations must be taken into account when planning large-scale conservation policies.

Key words. Environmental influences, human influence, otter distribution, Spain, spatial structure, variation partitioning.

INTRODUCTION

The Eurasian otter (*Lutra lutra* L. 1758) is a semi-aquatic mammal (Carnivora: Mustelidae) which feeds mainly on aquatic vertebrates and large aquatic invertebrates and whose habitat is linked to the existence of fresh water, available shelter (vegetation, rocky structures and others), and abundant prey (Ruiz-Olmo & Delibes, 1998; Trindade *et al.*, 1998). This species, once widespread in Europe, has shown a sharp decline in distribution in the last few decades (Elliot, 1983; MacDonald, 1983), although in recent years a general recovery has been noted (Ruiz-Olmo & Delibes, 1998). Thus, the assessment of the human impact on wild populations of otters is very important to establish effective conservation strategies. However, the relative importance of environmental and human influences on otter distribution has not been assessed on a large scale.

Several environmental and human factors, including drought, loss of riparian vegetation, water contamination, direct human disturbance and habitat fragmentation by dams, have been suggested as causes of the regression of otter populations (see, for example, MacDonald & Mason, 1983; Jiménez & Delibes, 1990; Trindade *et al.*, 1998). However, statistical analyses made on this subject do not usually measure the autocorrelation both in the distribution of the otter and in the environmental and human factors that affect this distribution. Conversely, studies on the amount of spatial structuring in species' (or groups of species') distributions and in species richness patterns have been conducted on plants (Borcard *et al.*, 1992; Heikkinen & Birks, 1996) as well as on animals (Borcard *et al.*, 1992; Borcard & Legendre, 1994; Mandrak, 1995; O'Connor *et al.*, 1996; Vaughn & Taylor, 2000), but these studies do not take into account the relative influence of variables related to human (anthropogenic) factors. Spatial autocorrelation in the distribution of the species may result from the influence of environmental and human factors that are also spatially autocorrelated (Legendre & Fortin, 1989; Borcard *et al.*, 1992), or from processes that are inherent to its own population dynamics (e.g. contagious biotic processes such as reproduction, migration and mortality), which generate variation not explainable by environmental or human variables (Legendre, 1993). Therefore, to explain the distribution of the otter it is necessary to assess the relative influences of spatial, environmental and human factors.

Spain is situated on the western edge of the otter's distribution range and is environmentally diverse enough to allow assessment of the influence of different environmental conditions on the otter's range. A National Otter Survey (Ruiz-Olmo & Delibes, 1998) was carried out in continental Spain between 1994 and 1996. In this survey 4316 sites, distributed among the 47 administrative provinces, were checked for signs of otter such as footprints, paths along the vegetation, meal remains, holts and spraints (excrement) which are deposited in visible spots to mark the territory. The survey revealed that otter distribution in Spain is irregular. However, the authors in charge of the survey in each province suggested different causes for the scarcity or abundance of otter, and factors held responsible for the absence of otters in some areas do not seem to have an effect on otter presence in others.

In the present study we aim to explain the different proportions of positive sites of otter (areas where otter presence was confirmed) in the Spanish provinces by assessing the relative importance of spatial, environmental and human factors in the distribution of the otter in this country.

METHODS

Study area

Continental Spain, situated in south-western Europe, covers an area of 493 518 km^2. The main rivers of Spain flow longitudinally to the west (Miño, Duero, Tagus, Guadiana, Guadalquivir) and to the east (Ebro, Turia, Júcar, Segura). The Mediterranean watershed is narrow and most of its rivers have a seasonal regimen, whereas the Atlantic watershed is wider and its rivers have a more abundant and permanent flow. Within the Atlantic watershed, the rivers that flow to the Cantabrian Sea are shorter and flow latitudinally (Vilà, 1989).

The climate of Spain is heterogeneous, with a mainly longitudinal gradient of precipitation and a mainly latitudinal gradient of both precipitation and temperature. Spain may be divided into three climatic areas: Atlantic, Mediterranean and Interior. The Atlantic area is characterized by mild winters and cool summers, and by abundant and regular precipitation. The Mediterranean area has hot summers and mild winters, with scarce precipitation that occurs mainly during spring and autumn. In the Interior area the temperatures are high in summer and low in winter, and precipitation is irregular and scarce (Capel, 1981).

Variables

Data on the proportion of positive sites of otter in each province (P) were obtained from Ruiz-Olmo & Delibes (1998).

For each province, we recorded the longitude and latitude, 24 environmental variables — related to environmental energy, water availability, vegetation and orography — and 12 human variables, related to human density, transportation, tourism, agriculture and livestock (Table 1).

The relative maximum precipitation was obtained dividing the maximum precipitation in 24 h by the mean annual precipitation in order to obtain a measure of the severity of flooding (Real *et al.*, 1993). The annual actual evapotranspiration was obtained by subtracting the mean annual run-off from the mean annual precipitation. The absolute

Table 1 Environmental, human, and spatial variables recorded for each Spanish province and used in the stepwise regression procedure to select, in each group, the variables that best explain the distribution of the otter in Spain. The variables selected and used in the variance partitioning procedure are in bold type

Spatial variables	
Mean longitude (′W)[1]	Mean latitude (′N)[1]
Environmental variables	
Mean relative air humidity in January (%)[2]	Mean annual precipitation (mm)[2]
Mean relative air humidity in July (%)[2]	Maximum precipitation in 24 h (mm)[2]
Annual relative air humidity range (%)[2]	Relative maximum precipitation (mm)[2]
Mean annual insolation (hours/year)[2]	Pluviometric irregularity[3]
Mean daily solar radiation (Kwh/m^2/day)[2]	**Soil permeability**[4]
Annual potential evapotranspiration (mm)[2]	Mean annual run-off (mm)[4]
Annual actual evapotranspiration (mm)[2]	Number of bioclimatic belts[5]
Mean temperature in January (°C)[2]	Number of phytogeographic sectors[5]
Mean temperature in July (°C)[2]	Relative woodland area[6]
Mean annual temperature (°C)[2]	Minimum altitude (m)[1]
Annual temperature range (°C)[2]	Mean altitude (m)[1]
Annual days of precipitation[2]	Maximum altitude (m)[1]
	Altitude range (m)[1]
Human variables	
Population density (inhabitants/km^2)[7]	Hotels per km^2[6]
Vehicles per km^2[8]	Vacancies in tourist apartments per km^2[9]
Highway density (m/km^2)[6]	Vacancies in camping sites per km^2[9]
National road density (m/km^2)[6]	Total tourist vacancies per km^2[9]
Secondary road density (m/km^2)[6]	Relative cropland area (%)[9]
Total highway and roads density (m/km^2)[6]	Relative pasture area (%)[9]

Sources [1] maps by the Servicio Geográfico del Ejército (1975–77); [2] Font (1983); [3] Montero de Burgos & González-Rebollar (1984); [4] Instituto Geológico y Minero de España (1979); [5] Rivas-Martínez (1985); [6] Instituto Nacional de Estadística (1999); [7] http//http//www.ine.es; [8] Dirección General de Tráfico (1996); [9] Instituto Nacional de Estadística (1996).

values of woodland area and of the human variables were divided by the total surface area of each province (obtained from Instituto Nacional de Estadística, 1996) to obtain relative values and eliminate the biases caused by the differences in size between provinces. The values of longitude to the east of the Greenwich meridian were converted into minutes west by making the values negative.

Statistical analyses

We performed a stepwise linear multiple regression of P on each of the three groups of variables (spatial, environmental and human) to find, for each group, a minimal subset of statistically significant variables useful to account for the proportion of positive sites of otter. The resulting subsets represent, respectively, the spatial, the environmental and the human significant influences on otter distribution in Spain. As the purely spatial influences are interpreted here in terms of the population dynamics of the species, we used a linear trend surface equation. A third-degree polynomial of spatial terms would allow the modelling of more complex spatial trends (Borcard *et al.*, 1992), but they could hardly be attributed to the dynamics of the otter populations.

Interactions between factors often result in an overlaid effect in space (Borcard *et al.*, 1992), hence the sum of the amounts of variation explained by each of the three subsets of variables is higher than the total amount explained by the three subsets together. A linear multiple regression of the proportion of positive sites on all the selected variables was then carried out to determine the total amount of the variance in otter distribution that is explained by those variables altogether; we considered this to be the variation due to the overall action of spatial situation, environment and human activity (R^2_{EHS}).

We then used the selected variables in the variance partitioning procedure called partial regression analysis (Legendre, 1993), modified for the use of three groups of variables. The aim of this analysis is to specify which proportion of the variance in otter distribution is due to each of the three factors exclusively, and which proportions are due to interactions between pairs of factors and between the three factors together.

Each of the selected environmental variables was regressed on both subsets of human and spatial variables; the residuals, which represent the part of the variation in the environmental conditions that is independent of human influence and spatial situation, were retained. The proportion of positive sites of otter was then regressed on those residuals, thus yielding the part of the variation in otter distribution that is due exclusively to environmental factors (R^2_E). Similarly, the strictly spatial (R^2_S) and the strictly human-caused variation (R^2_H) in otter distribution were obtained. The variation due to the action of environmental and spatial causes together (R^2_{SE}) is the result of regressing the proportion of positive sites on the residuals of both the environmental and the spatial variables; the variation due only to the interaction (or simultaneous influence) of environmental and spatial factors (*SE*) was obtained subtracting from R^2_{SE} the R^2_E (strictly environmental) and the R^2_S (strictly spatial variation in the proportion of positive sites). The amounts of variation due to the interaction between the other pairs of factors (*SH* and *HE*) were calculated in a similar way. The variation due to the interaction between the three factors together (*SEH*) is $R^2_{SEH} - (R^2_S + R^2_E + R^2_H + SE + SH + EH)$. The amount of unexplained variation is $1 - R^2_{EHS}$.

The variance decomposition aims therefore to yield eight additive components of the total variation in the proportion of positive sites of otter in the 47 provinces of continental Spain, namely:

- variation explained strictly by spatial variables, independently of environmental factors and human activity (R^2_S);
- variation explained exclusively by environmental variables, independently of any spatial structuring and human activity (R^2_E);
- variation explained strictly by human (anthropogenic) variables, independently of environmental factors and geographical coordinates (R^2_H);
- variation due to environmental variables that are structured in space (*SE*);
- variation due to human activity also structured in space (*SH*);
- variation explained by environmental and human variables acting simultaneously (*EH*);
- variation explained by the interaction of environment, human activity, and space (*SEH*); and
- variation which is not explained by any of the variables selected ($1 - R^2_{SEH}$).

RESULTS

The proportion of positive sites in relation to the total number of sites checked in each province varied from zero to more than 95% (Fig. 1).

The regression equations of *P* on each subset and on the whole set of selected variables and the percentages of variance explained by them are shown in Table 2.

The stepwise regression of *P* on the spatial variables selected the geographical longitude (*Lo*), positively related with *P*, so that the proportion of positive sites increases towards the West, explaining 45.6% of the variance in otter distribution.

The environmental variables selected were, in this order, the relative air humidity in January (*HJa*), which explains 16.8% of the variance of *P*, and the soil permeability (*Per*), which explains 14.7% more. The air humidity in January is related positively with *P*, whereas soil permeability is negatively related with it.

The regression on the human variables detected only the negative influence of the highway density (*Hi*) on the proportion of positive sites of otter, explaining 28.1% of its variance.

The linear regression of the proportion of positive sites of otter on all the selected variables explains 62.4% of the variance.

The results of variance partitioning are as follows: (Fig. 2):

- strictly spatial variation (R^2_S): 18%;
- strictly environmental variation (R^2_E): 5.5%;
- strictly human-caused variation (R^2_H): 9.7%;
- spatially structured environmental variation (*SE*): 10.9%;

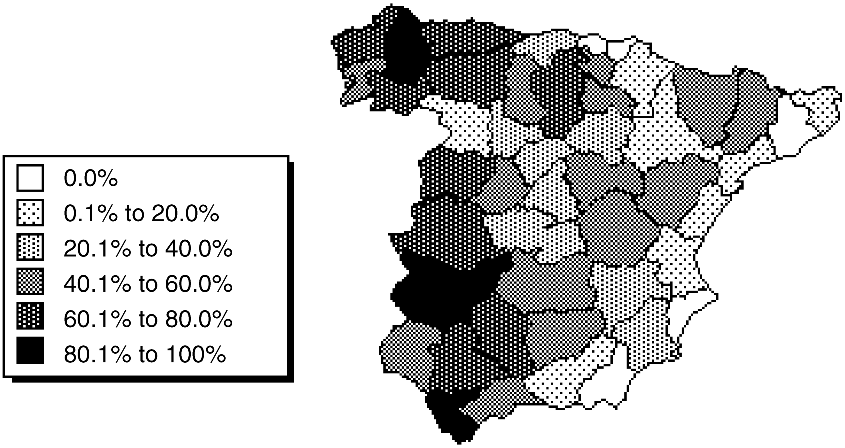

Fig. 1 Proportions of positive sites of otter *Lutra lutra* L. 1758 (areas where otter presence was confirmed) in the provinces of continental Spain.

Table 2 Regression equations and R^2 for each subset and for the whole set of selected variables. *P*: proportion of positive sites of otter (*Lutra lutra* L. 1758); *Hja*: mean relative air humidity in January; *Per*: soil permeability; *Hi*: highway density; *Lo*: mean longitude. Significance (*P*) < 0.001 in all cases

Environmental variables	
	$P = -151.729 + 2.34HJa - 22.97Per$
	$R^2 = 0.315$
Human variables	
	$P = 59.10 - 0.90Hi$
	$R^2 = 0.281$
Spatial variables	
	$P = 18.77 + 0.11Lo$
	$R^2 = 0.456$
Total	
	$P = 45.24 + 0.085Lo + 0.22HJa - 0.580Hi - 14.48Per$
	$R^2 = 0.624$

- spatially structured human-caused variation (*SH*): 3.3%;
- variation due to environmental and human causes acting simultaneously (*EH*): 1.7%;
- variation due to interaction between spatial, environmental, and human causes (*SEH*): 13.3%; and
- unexplained variation ($1 - R^2_{SEH}$): 37.6%.

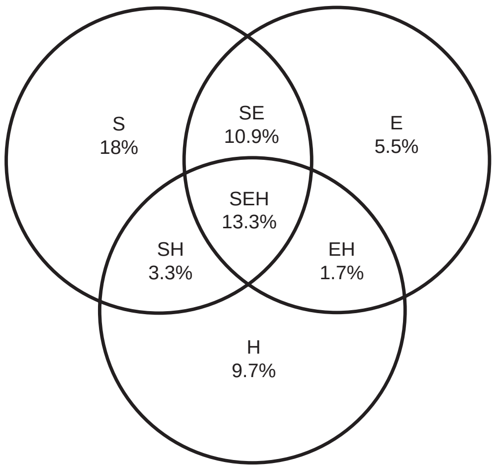

Fig. 2 Results of the variance partitioning using partial regression analysis. Values shown in the diagram are the percentages of variation in the proportion of positive sites of otter (*Lutra lutra* L. 1758) explained by spatial structure (S), environment (E), human factors (H) and by the interactions between these components (SE, SH, EH, SEH). Total explained variation: 62.4%. Unexplained variation: 37.6%.

DISCUSSION

The role of the selected factors

The positive relation of longitude with the proportion of positive sites indicates that there is a longitudinal gradient in otter distribution in which the species becomes more common towards the west. Elliot (1983) surveyed 176 sites throughout Spain and found a higher proportion of positive sites of otter in the north-western and south-western quarters than in the north-eastern and south-eastern quarters of the country. Delibes & Rodríguez (1990) analysed the results of another survey performed in 1984 on nearly the same locations used in the present study, and found a significant difference between the number of localities with otter in the western and in the eastern halves of Spain. The trend continues towards Portugal, where the otter is present in nearly 90% of the UTM 10×10-km squares (Trindade *et al.*, 1998). This may be because most of the large Iberian rivers (Miño, Duero, Tajo, Guadiana, Guadalquivir, Ebro, Júcar, Segura) flow longitudinally, thus contributing to the longitudinal spatial structuring of the climate and the population dynamics of the otter.

Since causal relationships among variables revealed by statistical regression are not necessarily direct, a variable included in a regression equation can be an indicator, or a surrogate for, a third unmeasured variable that does have a direct influence on the dependent variable analysed (Smith, 1994; Tabachnick & Fidell, 1996). The relative air humidity in January is linked to the size and form of river basins and the flow of the rivers. In Spain, a thermal inversion occurs during the night in winter, which leads to the formation of morning mists in the low areas around the rivers (Capel, 1981). In large basins, with broad valleys and a high volume of water, these mists affect much greater areas than in the shorter and narrower basins. In consequence, the mean air humidity in January is greater in provinces included in larger river basins, and its positive relation with the proportion of positive sites of otter indicates that this species is more common in these types of provinces. The relative air humidity in January has already been associated with the distribution of other organisms related to Iberian rivers; Vargas *et al*. (1998) found that air humidity in January characterizes a biotic boundary for freshwater fishes in the Iberian Peninsula, which separates the Atlantic basins from the Mediterranean ones, and interpreted this variable as indicative of the size of the basins and the flow of the rivers.

The negative relation of the soil permeability with the proportion of positive sites of otter points to the importance of water availability in the distribution of this species. Delibes & Rodríguez (1990) suggested that the distribution of otters in Spain was related to the mean annual precipitation. Precipitation could be a predictor of primary productivity (Rosenzweig, 1968). However, part of the precipitation water is filtered into the subsoil when the soil is permeable. The two variables, precipitation and soil permeability, have been included in our analysis and the fact that only soil permeability is significantly associated with the frequency of otter indicates that superficial water availability is more important than primary productivity in determining the distribution of this species in the Spanish provinces. At a more local scale, Nores *et al*. (1991) also attributed the different proportion of otter presences between the sites located on permeable and impermeable substrate in Asturias (N Spain) to the difference in superficial fresh water availability. Water availability could affect the otter not only by conditioning the habitat (Ruiz-Olmo & Delibes, 1998) but also by affecting food availability.

Regarding the human factor, the inclusion of highway density does not imply that the killing of animals by traffic is what most affects the otter, but rather that highways are probably the best indicator of the human influence on its distribution. A high highway density generally indicates higher economic development of the province and a higher level of disturbances of various kinds such as, for example, being run over, air and water pollution, noise, habitat destruction and fragmentation or artificial lighting (Spellerberg, 1998).

The influence of spatial, environmental and human factors

Part of the unexplained variation may be due to factors related to food availability, such as distribution and local abundance of prey, to human factors not included in the analysis, such as industry and the amount of pesticides used in agriculture, and to the heterogeneity in the survey, since not all provinces were sampled in the same season, under similar weather conditions or with the same sampling effort.

The 18% of purely spatial variation in the proportion of positive sites of otter seems to indicate that there is spatial autocorrelation in the distribution of this species due to processes inherent to its own dynamics. In fact, an expansion in the distribution of an otter population can only affect its surrounding area; on the other hand, areas with adequate conditions for the species cannot be naturally occupied if there are no otters nearby. For example, Ruiz-Olmo & Delibes (1998) attributed, in part, the occurrence of otters in areas with apparently inappropriate conditions in the provinces of western Spain to the high abundance of the species in this region, which forces many individuals to occupy suboptimal habitats that would otherwise not be used. On the other hand, areas that seem to offer good conditions for the species, as does part of the province of Gerona (NE Spain), are not naturally recolonized because there are no otters living in sufficiently close areas (Ruiz-Olmo & Delibes, 1998).

The proportion of purely spatial variation in otter distribution is relatively low compared to those obtained by Borcard *et al.* (1992) for oribatid mites and forest vegetation and by Vaughn & Taylor (2000) for freshwater mussels. However, these authors did not consider the human component in the spatial structure of the species. When we take into account the variation in otter distribution that is explained by the spatial structure independently of the environmental conditions, then the values are higher than those obtained for other studied organisms. The amount of non-environmental spatial variation in otter distribution, which corresponds to the sum of purely spatial and spatially structured human variation ($R^2_S + SH = 18\% + 3.3\% = 21.3\%$), is higher than that found by Borcard *et al.* (1992) for oribatid mites in Canada (12.2%), Heikkinen & Birks (1996) for subarctic plants in Finland (2.4%), Borcard *et al.* (1992) for forest vegetation in Canada (18.1%) and by Vaughn & Taylor (2000) for freshwater mussels in South Central USA (16.1%). In this way, our results seem to indicate that the population dynamics of the otter affect its distribution to a higher extent than do the population dynamics of other organisms. This could be related to the fact that otters are territorial, and the spatial configuration of potential territories could be a major determinant of the European otter distribution.

Only 5.5% of the variance is of strictly environmental origin, and even if we add the variation due to the interaction between environmental and human factors ($R^2_E + EH = 5.5\% + 1.7\% = 7.2\%$), the non-spatial environmental variation in otter distribution is lower than that found by other authors for forest vegetation (10.8%), for oribatid mites (13.7%) (Borcard *et al.*, 1992), for subarctic plants (12.6%; Heikkinen & Birks, 1996) and for freshwater mussels (7.8%; Vaughn & Taylor, 2000).

The largest proportion of the variance in otter distribution is due to the interaction between environmental and spatial variables, which means that the environmental factors that affect otter distribution are also structured in space, varying according to a longitudinal gradient. The longitudinal direction of the main Spanish mountain ranges determines the longitudinal gradient in the climatic characteristics of Spain (Capel, 1981). This common spatial structure of otter distribution and environmental variables may indicate a biogeographical response of otters to spatially varying environmental conditions. The obtained proportion of spatially structured environmental variation ($SE + SEH = 10.9\% + 13.3\% = 24.2\%$) is higher than that found by other authors for forest vegetation (7.8%; Borcard *et al.*, 1992), for subarctic plants (6.4%; Heikkinen & Birks, 1996) and for freshwater mussels (3.2%; Vaughn & Taylor, 2000), but lower than that found by Borcard *et al.* (1992) for oribatid mites (31.0%).

On the other hand, the purely human variation is higher than the purely environmental one. This may indicate that, although human variables have less influence on otter distribution than do environmental variables, they can lead to changes that are not in accordance with the spatial structure of otter populations. In this way, the human influence might be more disruptive than the influence of the environmental factors; that is, the proportion of positive sites in an area with high highway density can be lower than one could expect considering its geographical situation and environmental conditions. This type of large-scale impact of national infrastructures on wild populations should be taken into account when designing specific conservation programmes.

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