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# Species richness, rarity and endemicity of European mammals: a biogeographical approach

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Abstract. This paper investigates the distribution of species richness, rarity and endemicity of European land mammals (bats and introduced species excluded). The highest level of species richness was in Central Europe, while Southern areas had the highest rarity and endemicity scores. The distribution of richness was affected by the location of sampling points in islands and peninsulas. After excluding these sampling points, richness continued to decrease Westward suggesting the existence of a large-scale peninsular effect on mammal distribution. These patterns of continental distribution of richness, rarity and endemicity could be the result of the distribution of refuge areas in the southern Mediterranean peninsulas, and the Pleistocene advances and retreats of mammals throughout the Western Palearctic. Thus, European mammal distribution can be interpreted on the basis of two different patterns of abundance distribution in which Palearctic species reduce their abundance from central-Europe outwards, while endemic, rare species show a similar depletion in the North. It should be useful to evaluate the role of the different regions in Europe in conserving the demographic interactions between central and peripheral populations of mammal species. Given the restricted distribution and potential small size of population, these endemic species are most likely to be susceptible to anthropogenic environmental degradation.

Key words: conservation, endemicity, European mammals, geographical distribution, rarity, species richness

### Introduction

The study of the species richness, endemicity and rarity across geographical areas is essential to select the best places for conserving biodiversity (Scott et al. 1993; Conroy and Noon 1996; Kerr 1997; Williams et al. 1996). Assigning priority to areas for conservation is usually approached from different, albeit interdependent, geographical scales, given the fact that the arguments used to assign conservation values at local scales are frequently determined by guidelines derived from regional or continental scales (Conroy and Noon 1996; Collins and Glenn 1997). On account of the usefulness of large scale approaches to interpret the conservation value of sectors under evaluation, it is interesting to analyse the different geographical patterns of richness, rarity and endemicity indices in those groups of conservation concern

(e.g. Huntley 1993; Mönkkönen 1994; Ceballos and Brown 1995; Blackburn and Gaston 1996; Oberdorff et al. 1997; Fraser 1998). It is also important to analyse the historical processes that have affected the observed patterns in order to design, over sound theoretical bases, management decisions focused to protect the biogeographical processes affecting the distribution of endangered species (Kerr 1997; Arita et al. 1997).

Despite the large amount of information on the biology, distribution and taxonomic status of mammals in this region (Niethamer and Krapp 1978, 1982, 1986, 1993; Corbet 1978; Wilson and Reeder 1993), and the development of specific strategies to conserve the more endangered species (e.g. Council of Europe 1979, 1993), few studies have attempted to summarise and interpret the importance of the different European regions for mammal conservation on a large scale. There is, nevertheless, sound knowledge of the biogeographical processes that have affected the current distribution of European mammals and this can be used to suggest some guide-line directed to conserve key processes affecting the survival of European mammal fauna.

Mammal fauna in Europe is poorly diversified compared to other sectors in the Northern Hemisphere. Western North America is the richest region with 14% and 44% more species than eastern Asia and Europe, respectively (Mönkkönen and Viro 1997). This pattern, common to other taxonomic groups (Huntley 1993; Blondel and Mouver-Chauviré 1998; Mönkkönen 1994; Mönkkönen and Viro 1997; Oberdorff et al. 1997), supports the view that Europe is a macropeninsula in the western extreme of the Palearctic where species richness decrease Westward ('peninsula effect', Simpson 1964). This peninsula effect could be a consequence of several complementary processes. On the one hand, if the bulk of the European land mammal fauna is composed of species adapted to the environmental conditions of central Palearctic, increasing distances from this core area will produce a gradual depletion of habitat suitability and a concomitant reduction of species richness (Brown 1984; Lawton 1993). On the other hand, nonvolant mammals are weak dispersers. Therefore their reduced ability to colonise, totally or partially, sectors surrounded by sea has been proposed as one of the main responsible factor for the richness depletion (Lomolino 1986).

These proposed trends in species richness could be blurred, however, by the latitudinal distribution of species. Southern sectors in the Western Palearctic were important refuge areas for many mammals during the coldest periods of the Pleistocene, from where they migrated northwards after the recession of glaciations (Zeuner 1959; Hewitt 1996; Taberlet et al. 1998; Avise and Walker 1998). This historical background has possibly played an important role in shaping the latitudinal distribution of the species richness, specially of endemic species refuged in Southern Europe during the Pleistocene (Hewitt 1996; Blondel and Vigne 1993; see, however, Currie 1991 and Kerr and Packer 1997 for mammals richness in North America). If endemic species represent an important percentage of the mammal

fauna in some Southern European regions, the distribution of species richness will result in a balance between the distribution of this group and the distribution of non-endemic mammals. As endemic species are frequently restricted to smaller areas and show smaller populations (Thomas 1991), their distribution will also affect the geographical patterns of rarity scores (Arita et al. 1997). From a conservation perspective, these hypothetical trends predict different distribution of richness, especially of non-endemic mammals, with respect to endemicity and rarity scores throughout Europe and a concomitant different role of European regions from the perspective of mammal conservation.

### Methods

### Study area and sources of data

We defined 289 sampling points distributed evenly throughout Europe (islands smaller than Mallorca were not considered; Figure 1a). Using species distribution maps, we counted the number of geographical ranges of terrestrial mammals (113 species, after excluding bats and introduced species; see Appendix) coinciding in each sampling point (Niethamer et al. 1978, 1982, 1986, 1993; Heptner and Sludskii 1992; Arnold 1993; Mitchell-Jones et al. 1999). We assumed that the species distribution was known and that errors were simply too small to affect the results reported here (see, however, Conroy and Noon 1996, for the effects of sampling effort). Each sampling point was assigned to one geographical co-ordinate (Lambert projection), classified according to its location in both Northern-Southern (as an index of the effect of latitude) and East–West Europe (longitude), defined by two lines crossing Europe (Figure 1b). It was also classified according to its position in a continent, a peninsula or an island (as an index of *isolation*). We divided Europe into 11 sectors to summarise the regional distribution of the mean richness, rarity and endemicity scores and to evaluate their conservation role (Figure1b).

### Richness, rarity and endemicity indices

We estimated species richness as the total number of species' range present in each sampling point, and endemicity by recording in each sample point the number of those mammal species whose worldwide distribution is restricted to Europe (see Appendix). As the distribution range of species has been used as a criterion of rarity for conservation purposes (Rabinowitz et al. 1986; Arita et al. 1997), we also calculated in each sampling point, the following index of rarity (R):

$$R = \sum (1/c_i) \quad \{i: c_i \neq 0, \ 1 \le i \le S\}$$



*Figure 1.* (a) Distribution of sampling points (N = 289) throughout Europe. (b) Geographic sectors delimited in this study: 1 = Scandinavian Peninsula, 2 = Iceland, 3 = Atlantic islands, 4 = Iberian Peninsula, 5 = Mediterranean islands, 6 = Italian Peninsula, 7 = Balkan Peninsula, 8 = South-eastern continent, 9 = North-eastern continent, 10 = North-western continent, 11 = South-western continent. The horizontal and vertical line crossing Central Europe, separates North–South and West–East sectors delimited in this paper.

where  $c_i$  is the number of sampling points occupied by the species *i* (area of occupancy, Gaston 1996), and *S* is the species richness in the sampling point (Williams et al. 1996; Kerr 1997; Arita et al. 1997). Thus species with very narrow distributions have higher rarity scores, while the most restricted species (occurring in one sampling point only) scored 1.0. This measure provides an estimation of the geographical distribution of rarity (Kerr 1997).

### Analyses

Inter-regional differences in richness, rarity and endemicity, and the effects of latitude and isolation on their scores, were analysed by means of ANOVA and AN-COVA. It should be noted that data are spatially autocorrelated (that is, two points close to each other in Europe will be less independent of each other than two points located at a larger distance from each other, see Legendre 1990; Borcard et al. 1992). This would lead to a pseudoreplication problem (Hurlbert 1984) if each point were to be considered as an independent unit (Hurlbert 1984; Borcard et al. 1992; Fortin and Gurevitch 1993). Multiple regression procedures allow for the generation of models for conditioning on the contribution of spatial distributions of sampling units to the variation in the studied variables (Borcard et al. 1992). In this paper, the interest of these regression models is twofold. First, they will allow us to model the spatial distribution of richness, rarity and endemicity of mammals in Europe. Second, the role of the two factors under analysis (latitude and isolation) in shaping the final distribution of the studied indices will be properly approached only after conditioning on the spatial structure of these variables (Borcard et al. 1992; Fortin and Gurevitch 1993). Thereby, we analysed the spatial structure of the log-transformed indexes (richness, rarity and endemicity:  $Z_i$ ) from the matrix of two-dimensional geographical co-ordinates ( $X_i$ : longitude,  $Y_i$ : latitude) by generating all terms for a cubic trend surface regression (Legendre 1990), in which  $X_i$ and  $Y_i$  were centered to mean 0 (ranges of longest axis from -1 to +1; Neter et al. 1985; Burrough 1995). These terms described the linear gradient as well as more complex features, such as patches or gaps, which require the quadratic and cubic terms of the co-ordinates and their interactions to be described accurately (Borcard et al. 1992). A multiple regression (Akaike's Information Criterion, smallest AIC for the best subset, Burnham and Anderson 1992) was carried out for each richness, rarity and endemicity indices. The residuals of the reduced model of each regression were used to assess, by means of ANOVA and ANCOVA, the effects of geographical location on richness, rarity and endemicity, after conditioning of their spatial structure. Schematic views of variations in patterns of richness, rarity and endemicity scores were produced by means of surface plot graphics, in which hump-shaped planes (adjusted to each index's distribution by least-squares fit, see StatSoft 1996) are used to represent graphically the variation in each index throughout Europe.

# Results

### Species composition

Species endemic to Europe accounted for 34.5% (39 out 113) of the total pool of mammals considered in this study. However, the mean percentage of endemic on the total richness in each sample point dropped to 11.36% (SE = 0.35, n = 289). This low mean percentage of endemic species in the sampling points can be explained by their restricted distribution to some small sectors and a concomitant high turnover of endemic species throughout the continent (Figure 2; Appendix). It is also relevant to point out that the less distributed non-endemic species were mostly represented by some mammals common to the middle East that penetrate South-eastern Europe, where they show a restricted distribution (e.g. *Apodemus mystacinus, A. microps, A. agrarius, Criceturus migratorius, Microtus guentteri, M. majori, Erinaceus concolor, Capra aegregus* and *Canis aureus* which represent 41% of the 17 non-endemic species occupying less than 20 sampling points; Figure 2, Appendix).

### Patterns of richness, rarity and endemicity

The mean scores of species richness, rarity and endemicity differed among regions and were related to latitude and isolation, with decreasing scores in northern areas and isolated (e.g. islands) sectors (Table 1). The species richness was highest in Central Europe, and decreased towards the borders. However, the highest rarity and



*Figure 2.* Distribution of the number of sampling points in which endemic (white bars) and non-endemic species (black bars) were recorded.

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Ν	Richness Mean $\pm$ SE (m–M)	Rarity Mean $\pm$ SE (m–M)	Endemicity Mean ± SE (m–M)
56	23.64 ± 0.52 (16–31)	0.27 ± 0.02 (0.13-0.64)	2.29 ± 0.12 (1-4)
9	$5.00 \pm 0.00$ (5–5)	$0.47 \pm 0.00 \ (0.05 - 0.05)$	$1.00 \pm 0.00$ (1–1)
20	19.55 ± 5.01 (26-13)	$0.11 \pm 0.03 \ (0.14 - 0.07)$	$1.00 \pm 0.86$ (2–0)
38	$29.95 \pm 0.94$ (22–43)	$0.50 \pm 0.02 \ (0.23 - 0.85)$	$5.71 \pm 0.37$ (2–10)
16	$17.56 \pm 0.47 (12 - 20)$	$0.32 \pm 0.09 \ (0.12 - 1.31)$	$0.81 \pm 0.19$ (0–2)
14	31.93 ± 0.93 (25–36)	$0.45 \pm 0.03 \; (0.21 - 0.61)$	$3.71 \pm 0.46$ (1–7)
23	32.61 ± 1.51 (21-44)	$0.64 \pm 0.08 \ (0.22 - 1.87)$	$4.65 \pm 0.60 (1-10)$
20	$41.85 \pm 0.50$ (38–46)	$0.62 \pm 0.07 \ (0.34 - 1.69)$	$5.40 \pm 0.27$ (4–7)
42	$33.33 \pm 1.23 (13-42)$	$0.42 \pm 0.03$ (0.17–1.12)	$2.71 \pm 0.19$ (1–6)
21	32.95 ± 0.69 (28-40)	$0.24 \pm 0.01$ (0.17–0.33)	$3.43 \pm 0.29$ (2–5)
30	$37.20 \pm 0.59~(3244)$	$0.46 \pm 0.05 \; (0.23  1.62)$	$5.47 \pm 0.36 \ \text{(310)}$
	N 56 9 20 38 16 14 23 20 42 21 30	RichnessNMean $\pm$ SE (m–M)5623.64 $\pm$ 0.52 (16–31)95.00 $\pm$ 0.00 (5–5)2019.55 $\pm$ 5.01 (26–13)3829.95 $\pm$ 0.94 (22–43)1617.56 $\pm$ 0.47 (12–20)1431.93 $\pm$ 0.93 (25–36)2332.61 $\pm$ 1.51 (21–44)2041.85 $\pm$ 0.50 (38–46)4233.33 $\pm$ 1.23 (13–42)2132.95 $\pm$ 0.69 (28–40)3037.20 $\pm$ 0.59 (32–44)	$\begin{array}{c cccc} Richness & Rarity \\ N & Mean \pm SE (m-M) & Mean \pm SE (m-M) \\ \hline \\ 56 & 23.64 \pm 0.52 (16-31) & 0.27 \pm 0.02 (0.13-0.64) \\ 9 & 5.00 \pm 0.00 (5-5) & 0.47 \pm 0.00 (0.05-0.05) \\ 20 & 19.55 \pm 5.01 (26-13) & 0.11 \pm 0.03 (0.14-0.07) \\ 38 & 29.95 \pm 0.94 (22-43) & 0.50 \pm 0.02 (0.23-0.85) \\ 16 & 17.56 \pm 0.47 (12-20) & 0.32 \pm 0.09 (0.12-1.31) \\ 14 & 31.93 \pm 0.93 (25-36) & 0.45 \pm 0.03 (0.21-0.61) \\ 23 & 32.61 \pm 1.51 (21-44) & 0.64 \pm 0.08 (0.22-1.87) \\ 20 & 41.85 \pm 0.50 (38-46) & 0.62 \pm 0.07 (0.34-1.69) \\ 42 & 33.33 \pm 1.23 (13-42) & 0.42 \pm 0.03 (0.17-1.12) \\ 21 & 32.95 \pm 0.69 (28-40) & 0.24 \pm 0.01 (0.17-0.33) \\ 30 & 37.20 \pm 0.59 (32-44) & 0.46 \pm 0.05 (0.23-1.62) \\ \end{array}$

*Table 1.* Species richness, rarity and endemicity values for the 11 European sectors in Figure 1. Sample size, means  $\pm$  standard errors and ranges (in brackets) are shown.

endemicity scores were in the southern sectors (Figure 3). This can be explained by the presence in Southern Europe of the bulk of endemic species and by the entrance of some Asian mammals into this area from the Southeast. Despite these different patterns, richness correlated to rarity and endemicity (Pearson correlation, rarity: r = 0.749, P < 0.001, endemicity, r = 0.669, P < 0.001, n = 289) supporting the view that richness, rarity and endemicity are all positively correlated. As this pattern could reflect an artefactual effect of richness on the others indices, we will control richness in further analyses.

### Effects of latitude, isolation and peninsular effect

After ruling out the effect of the geographical position of each sampling point (see models in Table 2), the distribution of the residuals of the species richness, rarity and endemicity were affected by isolation but not by latitude, although it is important to underline their significant interaction (Table 3). To illustrate the existence of a peninsular effect on richness, after ruling out the observed effect of islands and peninsulas, we analysed the patterns of richness distribution in continental Europe (sectors 8, 9, 10 and 11 in Figure 1a). Results were similar to those observed in the whole studied area. A two-way ANOVA in which latitude (North–South) and longitude (West–East) were used as factors, reflected strong effect of longitude on the evolution of richness (Table 4).

To emphasise the opposite trends of distribution of species according to their European status, we plotted the distribution of non-endemic (total species less endemic species) and endemic species on continental sectors. Results showed a sharp decrease of richness Westwards and a clear, opposite pattern of distribution in all groups of mammal species (Table 4; Figure 3).



*Figure 3.* Three-dimensional surface plots representing the study indices according to gradients of latitude and longitude. (a), (b) and (c) The distribution pattern of richness, rarity and endemicity for whole study area. (d) The distribution of the richness of non-endemic species for continental Europe.

### Discussion

### Biogeographical patterns

The decreasing number of species from East-central sectors outwards is consistent with a peninsular effect on the distribution of land mammal fauna in Europe. This pattern can be partially explained by the effect of the decreasing land area towards coastal areas, as shown by the sharp reduction in the number of species from continent to peninsulas and islands. However, after removing the effects of these geographical features on species richness, it is possible to detect again a peninsular effect for continental Europe. This can be the result of an array of environmental and historical factors affecting mammal distribution. The loss of species richness with latitude has

*Table 2.* AIC multiple regression models of richness, rarity, endemicity and non-endemic species (see text for details) distribution throughout Europe. *X* refers to the transformed longitude and *Y* to the transformed latitude. All models were significant at P < 0.0001.

Model bu	ding	AIC
Richness $X, Y, X^2,$ Rarity $X, Y, X^2,$ Endemicity $X, Y, X^2,$ No. Non-endemic species $X, Y, X^2,$	$Y^2, Y^3, XY, X^2Y, XY^2$ $Y^2, Y^3, X^2Y, XY^2$ $Y^3, XY, X^2Y, XY^2$ $Y^2, Y^3, XY, X^2Y, XY^2$	-694.717 -150.491 -156.986 -780.854

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Richness Endemicity Rarity ANOVA  $F_{1.283} = 1.43^{\text{NS}}$  $F_{1.283} = 0.002^{\text{NS}}$  $F_{1.283} = 0.003^{\text{NS}}$ A: Latitude  $F_{2.283} = 33.48^{***}$  $F_{2.283} = 23.02^{***}$  $F_{2.283} = 34.70^{***}$ B: Isolation  $F_{2,283} = 10.66^{***}$  $\mathbf{A} \times \mathbf{B}$  $F_{2,283} = 8.12^{**}$  $F_{2,283} = 4.73^*$ ANCOVA A: Latitude  $F_{1.282} = 0.22^{\text{NS}}$  $F_{1.282} = 0.35^{\text{NS}}$  $F_{2.282} = 10.16^{***}$  $F_{2.282} = 20.47^{***}$ B: Isolation  $F_{2.282} = 5.14^*$  $F_{2.282} = 11.48^{***}$  $\mathbf{A}\times\mathbf{B}$  $F_{1.282} = 1.46^{\text{NS}}$  $F_{1.282} = 2.36^{\text{NS}}$ Covariate (Richness)

*Table 3.* Results of a two-way ANOVA of the residual richness, rarity and endemicity and a two-way ANCOVA of the residual rarity and endemicity, in which logrichness has been used as the covariate. Factors: latitude (North vs. South) and isolation (continent, peninsula or island).

NS = non-significant, \*P < 0.01, \*\*P < 0.001, \*\*P < 0.001.

*Table 4.* Result of a two-way ANOVA on the residual richness and richness without endemicity in continental Europe (sectors 8, 9, 10 and 11 in Figure 1). Factors: latitude (North vs. South) and longitude (East vs West).

	Richness	Richness-Endemicity
A: Latitude	$F_{1.109} = 1.27^{\text{NS}}$	$F_{1.109} = 0.001^{\text{NS}}$
B: Longitude	$F_{1.109} = 30.32^{***}$	$F_{1.109} = 25.57^{***}$
A × B	$F_{1.109} = 0.05^{\text{NS}}$	$F_{1.109} = 0.08^{\text{NS}}$

NS = non-significant, \*\*\* P < 0.0001.

been related, for instance, to the difficulties of southern organisms in colonising the hard northern habitats (McCoy and Connor 1980; Rohde 1992; Kerr 1999). The Westward reduction in species richness has been explained by the effects of the marked palaeo-environmental fluctuations of the Western Palearctic during the Quaternary (Huntley 1993; Mönkkönen 1994). The loss of suitable habitats for mammals during the glacial periods, together with concomitant population bottlenecks, could have increased extinction rates of mammal population in Western Europe, which would have then lost more species than other Eastern sectors (Huntley 1993; Bennett et al. 1991; Mönkkönen 1994; Hewitt 1996; Klicka and Zink 1997; Avise and Walker 1998). The depletion of mammal diversity in the Southernmost sectors of the Palearctic can also be ascribed to the effects of severe and ancient (Neolithic) human pressures, such as habitat modifications. The climatic vegetation of most of the Mediterranean European region would have not been shrubs, but different types of forests, if humans had not systematically destroyed the Mediterranean forest. The present abundance of shrubs is a modern and secondary feature caused by human deforestation, which was continuous after the early Neolithic (Blondel and Vigne 1993). Animal husbandry and hunting have probably contributed to the modification of natural distribution patterns and caused the retreat of the previous rich fauna to the North. (Cheylan 1991; Blondel and Vigne 1993). This was probably accentuated by the reduced exchange of mammal species between Europe and Africa because of the barrier effect of the Strait of Gibraltar and the Sahara desert (Jaeger et al. 1987; Huntley 1993). This is not the case, however, with the East and South-eastern sectors, where several immigration waves brought new fauna elements from temperate Asia (Cheylan 1991).

Endemic species tended to be more abundant in Southern Europe. The Iberian Peninsula is the sector with more endemic species, followed by the Southwest and Southeast continental sectors, the Balkan Peninsula and the Italian Peninsula (Table 1). The Iberian Peninsula has frequently been regarded as a peripheral area in which populations of several vertebrates evolved in isolation from the main European stocks during the Pleistocene (Baker 1992; Helbig et al. 1995; Merilä et al. 1996), and from where some groups have colonised the northernmost sectors (Taberlet and Bouvet 1994). Recent investigations however, suggest that isolation during glaciations was not responsible for faunal diversification at the species level, since speciation processes began earlier (Klicka and Zink 1997; Avise and Walker 1998; Blondel and Mourer-Chauviré 1998). Therefore, the observed patterns of endemicity should reflect the presence of relict Tertiary species, quartered on the warmest Mediterranean sectors during successive glaciation events. Nevertheless, in the case of some diverse small mammal taxa (e.g., Microtus, Sorex; Appendix), with limited dispersal ability and large local populations, it could be postulated some allopatric speciation and other evolutionary processes which would have enlarged species richness in these areas during the Pleistocene (Chaline and Mein 1979; Hewitt 1996; Feduccia 1995; Mönkkönen and Viro 1997).

The patterns of species richness, rarity and endemicity of land mammals in Europe can thus be explained as a result of two different biogeographical processes that acted in different ways throughout the continent. Widely distributed Palearctic mammals were eliminated by glaciations and human interference in southern Europe areas, retreating to central sectors (Blondel and Vigne 1993). On the other hand, endemic species were concentrated in southern areas, with a slight entry into Northern Europe. From this it follows that Central Europe lodges a rich mammal fauna, especially in the Eastern continental sectors where the bulk of the Palearctic taxons reside; southeastern sectors have many rare species because of the abundance of Asian species and European endemics; and, finally, southern peninsulas lodge many endemic mammals resulting from Pleistocene events.

#### Implications for conservation

One fundamental assumption of most models on the geographic patterns of abundance distribution is that a positive correlation exists between the regional abundance and the number of sites occupied by the species (Hengeveld and Haeck 1982; Hanski 1982, 1991; Brown 1984). This is the reason why species with small ranges are usually more prone to extinction than widespread forms, so that special conservation value has usually been given to taxa with restricted distributions (Arita et al. 1997 for review). The frequency distribution of range sizes of European mammals is right-skewed in both endemic and non-endemic species (see also Lechter and Harvey 1994; Gaston 1996), but the number of mammals with restricted distribution is particularly important in the case of the endemic ones (see Greuter 1991, for a similar result with plant species). This restricted distribution in Southern Mediterranean countries, the potential small size of their populations and their worldwide distribution restricted to southern Europe increases very much the need for improving local and regional protection of endemic mammals.

A second proposal refers to the consequences of the different patterns of European distribution of endemic and non-endemic species in the design of large-scale conservation strategies. For the sake of simplicity, we can interpret the current distribution of European mammal fauna as the result of an opposite pattern of abundance distribution in which populations of Palearctic species reduce their regional abundance from central-Europe outwards while endemic, rare species show a similar abundance in depletion to the North. The ability of peripheral populations to survive, of both endemic and non-endemic species, will probably decrease as habitat suitability decreases in the species' border (Brown 1988, 1995), and their ability to cope with increasing extinction risk will come down because of their increasing isolation from larger source populations in core areas (Brown and Kodric-Brown 1977; Hanski 1991; Lawton 1993). From this meta-population perspective, sectors in central Europe and southern Mediterranean areas could be viewed as eventual source areas for non-endemic and endemic mammals, respectively. But they can also be considered as regions that maintain scarce populations of endemic and non-endemic species which need specific conservation management. It should be very useful to investigate, in the context of some large-scale guide-lines directed to improve the protection of European wildlife (e.g. Council of Europe 1979, 1993, 1996), the role of different regions in conserving the connectivity of these central and peripheral populations of mammals.

Finally, it would be of use to improve our knowledge of the intra-specific variation of central and peripheral populations of European mammal species. It has been proposed that the decreasing abundance of peripheral populations in the range border is the result of a decreased fitness of individuals due to the effects of the asymmetric gene flow from central, densely populated sectors which hinder any adaptation to local conditions (Holt and Gomulkiewicz 1997; Kirkpatric and Barton 1997). But these peripheral populations can however, show some morphological and ecological adaptations to local conditions because of genetic isolation, as has probably occurred with some northern species in southern Mediterranean areas (Hewitt 1996). It follows then, that the main objective of the management strategies for mammal conservation at the scale of Europe should be to evaluate the taxonomic status of peripheral populations in order to define isolated, endemic populations on which to design proper conservation strategies (Lesica and Allendorf 1995).

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# Appendix

Mammal species considered in this study. Each one has been labelled according to its status in the Western Palearctic region. N is the number of sampling point where the species was recorded.

1					
Species name	Status	Ν	Species name	Status	Ν
Acomys minous	Е	3	Eliomys quercinus	Р	135
Alces alces	Р	81	Erinaceus europaeus	Р	169
Alopex lagopus	Р	33	Erinaceus concolor	А	73
Arvicola sapidus	Е	59	Felis silvestris	Р	144
Arvicola terrestris	Р	215	Galemys pyrenaicus	Е	14
Atelerix algirus	Р	4	Genetta genetta	Р	60
Apodemus agrarius	А	69	Glis glis	Р	115
Apodemus flavicollis	Р	139	Gulo gulo	Р	44
Apodemus microps	А	15	Herpestes ichneumon	Р	7
Apodemus mystacinus	А	20	Hytrix cristata	Р	17
Apodemus sylvaticus	Р	233	Lemmus lemmus	Е	34
Bison bonasus	Е	123	Lepus timidus	Р	101
Canis lupus	Р	84	Lutra lutra	Р	271
Canis aureus	А	27	Lynx lynx	Р	71
Capra aegegrus	А	2	Lynx pardina	Е	5
Capra ibex	Р	7	Marmota marmota	Е	9
Capra pyrenaica	Е	8	Martes foina	Р	175
Capreolus capreolus	Р	169	Martes martes	Р	233
Cervus elaphus	Р	87	Meles meles	Р	240
Citellus citellus	Е	10	Mesocricetus newtoni	Е	1
Citellus suslicius	Р	5	Micromys minutus	Р	137
Clethrionomys glareolus	Е	212	Micropalax leucodon	Е	23
Clethrionomys rufocanus	Р	35	Microtus agrestis	Р	168
Clethrionomys rutilus	Р	35	Microtus arvalis	Р	113
Cricetus cricetus	Р	28	Microtus babaricus	Е	1
Cricetulus migratorius	А	18	Microtus cabrerae	Е	5
Crocidura leucodon	Р	87	Microtus duodecimcostatus	Е	36
Crocidura russula	Р	78	Microtus epiroticus	Р	12
Crocidura suaveolens	Р	110	Microtus felteni	Е	2
Crocidura zimmermanni	Е	3	Microtus guentheri	А	7
Dama dama	Р	99	Microtus lusitanicus	Е	13
Dinaromys bogdanovi	Е	6	Microtus majori	А	3
Dryomys nitedula	Р	60	Microtus multiplex	Е	12

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appendia, continued.
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Species name	Status	Ν	Species name	Status	Ν
Microtus nivalis	Е	27	Rupicapra rupicapra	Е	33
Microtus oeconomus	Р	55	Sciurus vulgaris	Р	252
Microtus pyrenaicus	Е	7	Sicista subtilis	Р	12
Microtus savii	Р	26	Sicista betulina	Р	38
Microtus subterraneus	Р	68	Sorex alpinus	Е	28
Microtus tatricus	Е	2	Sorex araneus	Р	188
Microtus thomasi	Е	8	Sorex caecutiens	А	57
Mus musculus	Р	293	Sorex coronatus	Е	36
Mus spretus	Р	34	Sorex granarius	Е	11
Muscardinus avellanarius	Р	132	Sorex isodon	Е	18
Mustela erminea	Р	200	Sorex minutus	Р	244
Mustela lutreola	Е	67	Sorex minutissimus	Р	35
Mustela nivalis	Р	278	Sorex sammiticus	Е	12
Mustela putorius	Р	182	Spalax polonicus	Е	3
Myomimus roachi	Е	5	Suncus etruscus	Р	69
Myopus schisticolor	Е	31	Sus scrofa	Р	193
Neomys anomalus	Е	90	Talpa caeca	Е	15
Neomys fodiens	Р	195	Talpa europaea	Р	151
Ovibos moschatus	Р	7	Talpa occidentalis	Е	27
Oryctolagus cunniculus	Р	165	Talpa romana	Е	11
Pteromys volans	Р	11	Talpa stankovici	Е	3
Rangifer tarandus	Р	25	Ursus arctos	Р	76
Rattus rattus	Р	109	Vulpes vulpes	Р	280
Rattus norvegicus	Р	89	* *		

E: European endemics; P: typical West Palaeartic species; A: typical Asian species with marginal distribution in the Western Palaeartic.

## References

- Arita HT, Figueroa F, Frisch A, Rodríguez P and Santos-del-Prado K (1997) Geographical range size and the conservation of Mexican mammals. Conservation Biology 11(1): 92–100
- Arnold HR (1993) Atlas of mammals in Britain. Natural Environment Research Council. HMSO, London Avise JC and Walker DW (1998) Pleistocene phylogeographic effects on avian populations and the speciation process. Proceeding of Royal Society of London B 265: 457–463
- Baker AJ (1992) Genetic and morphometric divergence in ancestral European and descendent New Zealand populations of Chaffinches (*Fringilla coelebs*). Evolution 46: 1784–1800
- Bennett KD, Tzedakis PC and Willis KJ (1991) Quaternary refugia of north European trees. Journal of Biogeography 18: 103–115
- Blackburn TM and Gaston KJ (1996) Spatial patterns in the species richness of birds in the New World. Ecography 19: 369–376
- Blondel J and Mouver-Chauviré C (1998) Evolution and history of the Western Palearctic avifauna. Trends in Ecology and Evolution 13: 488–492
- Blondel J and Vigne JD (1993) Space, time, and man as determinants of diversity of birds and mammals in the Mediterranean region. In: Ricklefs RE and Schluter D (eds) Species Diversity in Ecological Communities, pp 135–146. University of Chicago Press, Chicago and London
- Borcard D, Legendre P and Drapeau P (1992) Partialling out the spatial component of ecological variation. Ecology 73(3): 1045–1055
- Brown JH (1984) On the relationship between abundance and distribution of species. American Naturalist 124: 253–279

- Brown JH (1988) Species diversity. In: Myers A and Giller PS (eds) Analytical Biogeography, pp 57–89. Chapman & Hall, London
- Brown JH (1995) Macroecology. University of Chicago Press, Chicago/London
- Brown JH and Kodric-Brown A (1977) Turnover rates in insular biogeography. Effect of immigration on extinction. Ecology 58: 445–449
- Burnham KP and Anderson DR (1992) Data-based selection of an appropriate biological model: the key to modern data analysis. In: McCullogh DR and Barret RH (eds) Wildlife 2001: Populations, pp 16–30. Elsevier Science Publishers, London
- Burrough PA (1995) Spatial aspects of ecological data. In: Jongman RHG, Ter Braak CJF and Van Tongeren OFR (eds) Data Analysis in Community and Landscape Ecology, pp 213–251. Cambride University Press, London
- Ceballos G and Brown JH (1995) Global patterns of mammalian diversity, endemism, and endangerment. Conservation Biology 9(3): 559–568
- Chaline J and Mein P (1979) Les rongeurs et l'Évolution. Doin Éditeurs. Paris
- Cheylan G (1991) Patterns of Pleistocene turnover, current distribution and speciation among Mediterranean mammals. In: Groves RH and di Castri F (eds) Biogeography of Mediterranean Invasions, pp 227–262. Cambridge University Press, Cambridge/New York
- Collins SL and Glenn SM (1997) Effects of organismal and distance scalling on analysis of species distribution and abundance. Ecological Application 7(2): 543–551
- Conroy MJ and Noon BR (1996) Mapping of richness for conservation of biological diversity: conceptual and methodological issues. Ecological Application 6(3): 763–773
- Council of Europe (1979) Bern Convention The Convention on the Conservation of the European Wildlife and Natural Habitats. Council of Europe Press, Strasbourg
- Council of Europe (1993) Convention on the Conservation of European Wildlife and Natural Habitat. Council of Europe Press, Strasbourg
- Council of Europe (1996) The Pan-European Biological and Landscape Diversity Strategy. Council of Europe, Strasbourg
- Corbet GB (1978) The Mammals of the Palearctic Region: A Taxonomic Review. British Museum (Natural History). Cornell University Press, London
- Currie DJ (1991) Energy and large-scale patterns of animal and plant-species richness. American Naturalist 137: 27–49
- Feduccia A (1995) Explosive evolution in Tertiary birds and mammals. Science 267: 637-638
- Fraser RH (1998) Vertebrate species richness at the mesoscale: relative roles of energy and heterogeneity. Global Ecology and Biogeography Letters 7: 215–220
- Fortin MJ and Gurevitch J (1993) In: Scheiner SM and Gurevitch J (eds) Mantel Test: Spatial Structure in Field Experiments. Design and Analysis of Ecological Experiments, pp 342–359. Chapman & Hall, London
- Gaston KJ (1996) Species-range-size distributions: patterns, mechanisms and implications. Trends in Ecology and Evolution 11(5): 197–201
- Greuter W (1991) Botanical diversity, endemism, rarity, and extinction in the Mediterranean area: an analysis based on the published volumes of Med-Checklist. Bot Chron 10: 63–79
- Hanski I (1982) Dynamics of regional distribution: the core and satellite species hypothesis. Oikos 38: 210–221
- Hanski I (1991) Single-species metapopulation dynamics: concepts, models and conservations. Biological Journal of Linnean Society 42: 17–38
- Helbig AJ, Martens J, Seibold Y, Henning F, Schottler B and Wink M (1995) Phylogeny and species limits in the Palaearctic chiffchaff *Phylloscopus collybita* complex: mitochondrial genetic differentiation and bioacoustic evidence. Ibis 138: 650–666
- Hengeveld R and Haeck J (1982) The distribution of abundance. I. Measurement. Journal of Biogeography 9: 303–316
- Heptner VG and Sludskii AA (eds) (1992) Mammals of the Soviet Union. Volume II, Part 2. Carnivora (Hyaenas and Cats) E.J. Brill Leiden, New York, Kobenhavn and Köln
- Hewitt GM (1996) Some genetic consequences of ice ages, and their role in divergence and speciation. Biological Journal of Linnean Society 58: 247–276

- Holt RD and Gomulkiewicz R (1997) How does immigration influence local adaptation? A reexamination of a familiar paradigm. American Naturalist 149: 563–572
- Huntley B (1993) Species-richness in north-temperate zone forests. Journal of Biogeography 20: 163–180
  Hurlbert SH (1984) Pseudoreplication and the design of ecological field experiments. Ecological Monograph 54(2): 187–211
- Jaeger JJ, Coiffait B, Tong H and Denys C (1987) Rodent extinctions following Mesinian faunal exchanges between western Europe and northern Africa. Memories de la Société Geologique de France 150: 153–158
- Kerr JT and Packer L (1997) Habitat heterogeneity as a determinant of mammal species richness in high-energy regions. Trends in Ecology and Evolution 16: 252–254
- Kerr JT (1997) Species richness, endemism, and the choice of areas for conservation. Conservation Biology 11(5): 1094–1100
- Kerr JT (1999) Weal links: 'Rapoport's rule' and large-scale species richness patterns. Global Ecology and Biogeography 8: 47–54
- Kirkipatric M and Barton NH (1997) Evolution of a species' range. American Naturalist 150: 1-23
- Klicka J and Zink RM (1997) The importance of recent ice ages in speciation: a failed paradigm. Science 277: 1666–1669
- Lawton JH (1993) Range, population abundance and conservation. Trends in Ecology and Evolution 8 (11): 409-413
- Lechter A and Harvey PH (1994) Variation in geographical range size among mammals of the Palearctic. American Naturalist 144: 30–42
- Legendre P (1990) Quantitative methods and biogeographic analysis. In: Garbary DJ and South RR (eds) Evolutionary Biogeography of the Marine Algae of the North Atlantic, pp 9–34. NATO ASI Series, Volume G 22. Springer-Verlag, Berlin
- Lesica P and Allendorf FW (1995) When are peripheral populations valuable for conservation? Conservation Biology 9: 753–760
- Lomolino MV (1986) Mammalian community structure on islands: the importance of inmigration, extinction and interactive effects. In: Heaney LR and Patterson BD (eds) Island Biogeography of Mammals, pp 1–21. Academic Press, London
- Mitchell-Jones AJ, Amori G, Bogdanowicz W, Kryštufek B, Reijnders PJH, Spitzenberger F, Stubbe M, Thissen JBM, Vohralík V and Zima J (1999) The atlas of european mammals. T & AD Poyser, London
- McCoy ED and Connor EF (1980) Latiduninal gradients in the species diversity of North American mammals. Evolution 34: 193–203
- Merilä J, Björklund M and Baker AJ (1996) Genetic population structure and gradual northward decline in genetic variability in the Greenfich (*Carduelis chloris*) Evolution 50: 2548–2557
- Mönkkönen M (1994) Diversity patterns in Palaearctic and Nearctic forest bird assemblages. Journal of Biogeography 21: 183–195
- Mönkkönen M and Viro P (1997) Taxonomic diversity of the terrestrial bird and mammal fauna in temperate and boreal biomes of the northern hemisphere. Journal of Biogeography 24: 603– 612
- Neter J, Waserman W and Kutner MH (1985) Applied linear statistical models, 2nd ed. Irwin Homewood, Illinois
- Niethamer H von J and Krapp F (1978) Handbuch der Säugetiere Europas. Band 1. Nagetiere I. Akademische Verlagsgesellschaft, Wiesbaden
- Niethamer H von J and Krapp F (1982) Handbuch der Säugetiere Europas. Band 2/I. Nagetiere II. Akademische Verlagsgesellschaft, Wiesbaden
- Niethamer H von J and Krapp F (1986) Handbuch der Säugetiere Europas. Band 2/II. Paarhufer. Akademische Verlagsgesellschaft, Wiesbaden
- Niethamer H von J and Krapp F (1993) Handbuch der Säugetiere Europas. Band 5. Raubsäeger. Akademische Verlagsgesellschaft, Wiesbaden
- Oberdorff T, Hugueny B and Guégan JF (1997) Is these an influence of historical events on contemporary fish species richness in rivers? Comparisions between Western Europe and North America. Journal of Biogeography 24: 461–467

- Rabinowitz D, Cairns S and Dillon T (1986) Seven forms of rarity and their frequency in the flora of the British Isles. In: Soulé ME (ed) Conservation Biology: The Science of Scarcity and Diversity, pp 182–204. Sinauer Associates, Sunderland, Massachusetts
- Rohde K (1992) Latitudinal gradients in species diversity: the search for the primary cause. Oikos 65: 514–527
- Scott JM, Davis F, Csuti B, Noss R, Butterfield B, Groves C, Anderson H, Caicoo S, D'Erchia F, Edwars TC Jr, Ulliman J and Wright RG (1993) Gap analysis: a geographic approach to protection of biological diversity. Wildlife Monographs 123
- Simpson GG (1964) Species density of North American recent mammals. Systematica Zoologica 12: 57-73
- Statsoft, Inc (1996) STATISTICA for Windows (computer program manual). Statsoft, Inc., Tulsa
- Taberlet P and Bouvet J (1994) Mitochondrial DNA polymorphism, phylogeography, and conservation genetic of the brown bear (*Ursus arctos*) in Europe. Proceeding of Royal Society of London B 255: 195–200
- Taberlet P, Fumagalli L, Wust-Saucy AG and Cossons JF (1998) Comparative phylogeography and postglacial colonization routes in Europe. Molecular Ecology 7: 453–464
- Thomas CD (1991) Habitat use and geographic ranges of butterflies from the wet lowlands of Costa Rica. Biological Conservation 55: 269–281
- Williams P, Gibbons D, Margules C, Anthony R, Humphires C and Pressey R (1996) A comparision of richness hotsplots, rarity hotspots, and complementary areas for conserving diversity of british birds. Conservation Biology 10(1): 155–174
- Wilson DE and Reeder DM (eds) (1993) Mammals Species of the World. A taxonomic and Geographic reference. 2nd edition. Smithsonian Institution Press, Washington/London
- Zeuner FE (1959) The Pleistocene periods: its climate, chronology and faunal successions. Hutchinson, London