

Z. Säugetierkunde 57 (1992) 169–175
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ISSN 0044-3468

Distribution patterns of small mammal fauna along gradients of latitude and altitude in Northern Spain

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Receipt of Ms. 19. 8. 1991

Acceptance of Ms. 5. 12. 1991

Investigated the influence of geographical factors (latitude and altitude) on the distribution of small mammal fauna. We analysed approximately 3000 Barn Owl pellets collected from 20 different localities in Northern Spain. These pellets contained the remains of 9744 small mammals belonging to 17 species. Three groups of species were found: 1. one group associated with latitude (*Sorex coronatus*, *Neomys fodiens*, *Clethrionomys glareolus*, *Microtus pyrenaicus*, *Apodemus sylvaticus*, *Mus spretus*), 2. another group related to altitude (*Suncus etruscus*, *Crocidura russula*, *Microtus agrestis*), and 3. a third group whose distribution was not affected by latitude or altitude (*Sorex minutus*, *Eliomys quercinus*, *Microtus cabreræ*, *M. nivalis*, *M. duodecimcostatus*, *Arvicola sapidus*, *Rattus rattus*, *R. norvegicus*).

The distribution of these species is discussed in relation to geographical and climatic factors. Our data demonstrate that latitude is the most important factor in determining the presence of a species at the southern limit of their range.

Introduction

Distribution and diversity of small mammals are affected by geographical factors of which latitude and altitude are the main variables used in zoogeographical studies (PIANKA 1966; BOND et al. 1980; FONS et al. 1980; BRUNET-LECOMTE and DELIBES 1984; DELIBES 1985; ALCÁNTARA 1989; BRÜNNER and NEET 1991).

In Western Europe the number of small mammalian species decreases from north to south (HERRERA 1974). It has also been demonstrated that when altitude increases the diversity of small mammals decreases (ABE 1982; DELIBES 1985; ALCÁNTARA 1989). Variation in altitude may reproduce variation in latitude, so that in this study both gradients are investigated. The aim of the present study was to determine, within a medium altitudinal range, the influence of these two geographical variables on the distribution of small mammals, and at the southern limit the presence of certain species (CORBET 1978).

Material and methods

The study was conducted in the province of Huesca (42°45'–42°05' N, 00°45'–00°17' W). Although the latitudinal range is restricted, the orography varies markedly. Altitude ranges from 420 and 987 m above sea level with three distinct geographical regions (see Figure): Ebro Valley (Mediterranean lowlands), pre-Pyrenees (Atlantic lower montane area), and Pyrenees (alpine high mountain area).

The sampling method was the analysis of Barn Owl pellets. In spite of the limitations of this sampling procedure (SAINT-GIRONS and SPITZ 1966), it is valid for biogeographical studies of small mammals (HEIM DE BALSAC and BEAUFORT 1966; HERRERA 1974; BRUNET-LECOMTE and DELIBES 1984). We analysed about 3000 Barn Owl pellets collected from 20 different localities (Fig. and Tab. 1) which contained 9744 small mammals. The data gathered are most likely heterogeneous since pellets were collected at different times of the year and pooled together, and although the Barn Owl's diet shows monthly changes (SAINT-GIRONS 1968; MARTI 1973; WEBSTER 1973; HERRERA 1973), the effect of seasonal changes on the results should be buffered since, of the 20 analyses studied, 12 exceeded 300 prey items (see HERRERA 1974 for a similar approach).

Temperature and precipitation data were taken from ELÍAS and RUÍZ (1977) for the points nearest to sampling sites.



Situation of the localities from which Barn Owl pellets were taken. Numbers correspond to the localities as numbered in Table 1

Simple correlation analysis was performed to test for an effect of latitude, altitude, temperature, and precipitation on the geographical distribution of small mammals in the study area. Stepwise multiple regression analyses (SOKAL and ROHLF 1981), with the relative abundance of the different taxa as dependent variables, were performed to show which geographical variable (latitude, altitude) primarily affected the distribution of small mammals. Small mammal diversity was calculated using the Shannon-Weaver Index and richness was taken as the number of species in each locality.

Results

In the study area latitude and altitude are highly correlated ($r = 0.767$, $p < 0.001$) however, they do not show the same relation to small mammal distribution, with latitude being more highly correlated for most species.

The raw data are shown in Table 1 where the richness index for each locality is also included. Five insectivorous and 12 rodent species were found. Stepwise multiple regression analyses distinguished three groups of species (Table 2):

1. Species whose distribution is primarily related to latitude (*Sorex coronatus*, *Neomys fodiens*, *Clethrionomys glareolus*, *Microtus (Pitymys) pyrenaicus*, *Apodemus sylvaticus*, and *Mus spretus*).
2. Species whose distribution is primarily related to altitude (*Suncus etruscus*, *Crocidura russula*, and *Microtus agrestis*).
3. Species whose distribution is not related to either altitude or latitude (*Sorex minutus*, *Eliomys quercinus*, *Microtus cabrerai*, *M. nivalis*, *Microtus (Pitymys) duodecimcostatus*, *Arvicola sapidus*, *Rattus rattus*, and *R. norvegicus*).

When species were grouped in Orders, latitude was the first variable selected by the stepwise regression analysis (Table 2), being positively correlated with the abundance of Insectivora and inversely correlated with the abundance of Rodentia.

Table 1. Localities from which pellets were taken and percentages of prey

LOC	N	ALT	LAT	SM	SC	NF	SE	CR	EQ	CG	MA	MC	MN	MP	MD	AS	APS	MSP	RR	RN	R
1 Hecho	941	843	42° 45'	0.32	7.55	0.11		37.73	0.21	0.43	2.44			2.66	14.13		34.33	0.11			11
2 Navasa	347	987	42° 32'		4.32		0.58	44.96			4.61				17.29	0.29	17.29	9.80	0.86		9
3 Lavelilla	1196	710	42° 34'		0.67		1.34	23.49	0.08	0.08	0.08		0.42		21.82	0.17	47.91	3.68	0.25		12
4 Puente de Fanlo	42	750	42° 30'		2.38		2.38	61.90	2.38			2.38			4.76		16.67	7.14			8
5 Arto	396	800	42° 27'		4.29		0.76	37.12	0.25		2.53	0.25			12.63		28.03	14.14			9
6 Orma de Gállego	52	769	42° 27'		1.92			30.77			3.85	1.92			32.69		23.08	5.77			7
7 Javierrelatre	326	709	42° 24'		13.80		2.15	46.93			3.99	2.15			2.15		18.10	10.74			8
8 Aquilué	171	689	42° 22'	0.58	11.11			21.64	2.34		0.58				17.54		38.60	7.60			8
9 San Vicente	272	802	42° 21'		7.72		0.74	40.81			1.84				12.50		30.15	6.25			7
10 Arascues	442	673	42° 14'				0.45	21.72			0.23				8.37		10.41	58.82			6
11 Igríes	719	601	42° 12'				1.53	14.46	0.14		0.14				27.96		10.99	44.37	0.42		8
12 Sta. Eulalia la Mayor	465	867	42° 12'		0.22		0.43	27.96	0.22						16.34		23.87	30.97			7
13 Castilsabás	964	722	42° 11'	0.10			1.68	20.44	0.10						19.18	0.52	16.88	40.88	0.21		9
14 Otrera	242	462	42° 09'				0.41	4.13							23.97		5.37	66.12			5
15 Aller	1723	500	42° 09'				4.99	14.74							19.04	0.23	9.81	51.19			6
16 Huerríos	377	487	42° 08'				4.51	28.65							11.67	0.27	13.53	41.11		0.7	7
17 Banarics	198	472	42° 08'				15.15	17.68							9.60		4.55	53.03			5
18 Torres Secas	217	490	42° 08'				0.92	20.28	0.46						23.50	2.30	19.35	33.18			7
19 Pompenillo	128	420	42° 05'				4.69	10.94							1.56		9.38	72.66	0.78		6
20 Monflorite	515	436	42° 05'				1.17	13.98	0.19						43.69	0.19	10.10	30.49	0.19		8

Abbreviations: N = number of prey, ALT = altitude (m a.s.l.), LAT = latitude, SM = *S. minutus*, SC = *S. coronatus*, NF = *N. fodiens*, SE = *S. etruscus*, CR = *C. russula*, EQ = *E. quercinus*, CG = *C. glareolus*, MA = *M. agrestis*, MC = *M. cabrerac*, MN = *M. nivialis*, MP = *M. pyrenaeus*, MD = *M. dhodencostatus*, AS = *A. sapidus*, APS = *A. sylvaticus*, MSP = *Mus spretus*, RR = *R. rattus*, RN = *R. norvegicus*, R = Richness.

Table 2. Stepwise multiple regression analyses of species distribution showing the first selected variable, the partial correlation coefficient (r) and the significance level (p)

Species	Variable	r	p
<i>S. minutus</i>	—	—	—
<i>S. coronatus</i>	latitude	0.55	0.05
<i>N. fodiens</i>	latitude	0.55	0.05
<i>S. etruscus</i>	altitude	-0.47	0.05
<i>C. russula</i>	altitude	0.70	0.01
<i>E. quercinus</i>	—	—	—
<i>C. glareolus</i>	latitude	0.61	0.01
<i>M. agrestis</i>	altitude	0.64	0.01
<i>M. cabreræ</i>	—	—	—
<i>M. nivalis</i>	—	—	—
<i>M. pyrenaicus</i>	latitude	0.55	0.05
<i>M. duodecimcostatus</i>	—	—	—
<i>A. sapidus</i>	—	—	—
<i>A. sylvaticus</i>	latitude	0.70	0.01
<i>R. rattus</i>	—	—	—
<i>R. norvegicus</i>	—	—	—
<i>Mus spretus</i>	latitude	-0.82	0.01
Insectivora	latitude	0.66	0.01
Rodentia	latitude	-0.64	0.01
Richness	latitude	0.73	0.01
H'	altitude	0.57	0.01

Richness and diversity (H') were positively correlated with both geographical variables, but the former was primarily related to latitude and the latter to altitude.

Discussion

In the present study three geographical zones could be differentiated: Pyrenees, pre-Pyrenees, and Ebro Valley. These important physiographic variations are accompanied by parallel variation in temperature, precipitation (ELÍAS and RUFZ 1977), and vegetation (PEINADO and RIVAS-MARTÍNEZ 1987). All of these factors highly affected the distribution of small mammals in this area.

The distributions of *S. coronatus*, *N. fodiens*, *C. glareolus*, *M. pyrenaicus*, *A. sylvaticus* and *Mus spretus* are primarily related to latitude. All these species, except *A. sylvaticus* and *Mus spretus*, have Eurosiberian distributions (SAINT-GIRONS 1973; AMORI et al. 1984; HAUSER et al. 1985) and the south slope of the Pyrenees constitutes the southern limit of their distribution. As expected, they show a positive correlation with latitude, increasing in abundance from the Mediterranean to the Eurosiberian region. In spite of the few individuals found for some species (i.e., *N. fodiens* and *C. glareolus*), the positive correlation with precipitation ($p < 0.01$ in all cases) and negative with temperature ($p < 0.01$ in *N. fodiens* and *C. glareolus*; $p = 0.06$ in *S. coronatus*) seems to indicate that a general trend exists in these species for inhabiting areas with a balanced Atlantic climate.

The distributions of *A. sylvaticus* and *Mus spretus* are also primarily related to latitude, the former being directly correlated and the latter inversely. In France and Spain *Mus spretus* shows an increase in abundance to the south (SAINT-GIRONS and VESCO 1974; BRUNET-LECOMTE and DELIBES 1984). It appears from this study that *Mus spretus* requires Mediterranean conditions, as its distribution is positively correlated with temperature and negatively correlated with precipitation ($p < 0.01$ in both cases; see also THALER et al. 1981). *A. sylvaticus*, however, shows a clear positive gradient northwards, with its

distribution directly correlated with precipitation ($p < 0.01$) but unrelated to temperature ($p = 0.2$). ALCÁNTARA (1989) pointed out that the distribution of this species is related to habitat structural features. Given the latitudinal variation of vegetation in the study area (PEINADO and RIVAS-MARTÍNEZ 1987), our results may reflect such variation in habitats.

The distribution of *C. russula*, *S. etruscus*, and *M. agrestis* is related to altitude. *Crociodura russula* increases with altitude. The general trend for Crocidurinae is, on the contrary, to inhabit temperate lowland areas (ABE 1982; ALCÁNTARA 1989; BRÜNNER and NEET 1991). This apparent contradiction to general findings might be explained by considering the unusual kind of habitat preference exhibited by *C. russula* in the mountain areas of western Europe, where its presence is restricted to the vicinity of human dwellings (CHURCHFIELD 1990) rather than being influenced by any geographical factors. *S. etruscus* decreases with altitude, in accordance with the general distribution of European Crocidurinae (CHURCHFIELD 1990). *M. agrestis* increases at higher altitudes, following the general trend shown for this species in Spain (DUEÑAS and PERIS 1985; DELIBES 1985).

The distributions of *S. minutus*, *E. quercinus*, *M. cabreræ*, *M. nivalis*, *A. sapidus*, *M. duodecimcostatus*, *R. rattus*, and *R. norvegicus* are not affected by either altitude or latitude. *S. minutus* has been shown as a species inhabiting altitudes above 1000 m a.s.l. in the Pyrenees (VERICAD 1970; GOSÁLBEZ and LÓPEZ-FUSTER 1985); however, in our study area, where all sites are lower, its distribution is not affected by altitude. DELIBES (1981) did not find any correlation between altitude and the distribution of this species in the eastern Cantabric Mountains (North of Spain). In spite of the small number of individuals found in our study, the results seem to suggest that the main factor affecting the distribution of this species is humidity, rather than altitude, since its distribution is positively correlated with precipitation ($p = 0.02$; see GOSÁLBEZ 1976 for a similar result).

Arvicola sapidus, *E. quercinus*, *R. rattus*, and *R. norvegicus* are widely distributed in Spain. Their distribution does not seem to be related to geographical factors, but (with the exception of *E. quercinus*) to the presence of water-bodies or human habitation (GOSÁLBEZ and LÓPEZ-FUSTER 1985).

In Spain, *M. duodecimcostatus* has a typical Mediterranean distribution (SANS-COMA et al. 1973). Absence of relatedness with all variables considered in this study supports the suggestion of GOSÁLBEZ et al. (1985) that *M. duodecimcostatus* is distributed according to the nature of the ground rather than on any geographical factor.

The distribution of *M. cabreræ* and *M. nivalis* is not related to latitude or altitude, but is likely to be restricted to localised habitats in Spain (GOSÁLBEZ and LÓPEZ-FUSTER 1985), e.g. rockslides for *M. nivalis* and rush for *M. cabreræ*.

Insectivora increase with latitude while Rodentia decrease. These results agree with those by HERRERA (1973), CHEYLAN (1976), and BRUNET-LECOMTE and DELIBES (1984), who found a decline in the proportion of Insectivora southwards in Europe. This trend may be explained by the boreal origin of most of these species (HAUSSER et al. 1985).

Generally, diversity decreases with altitude (e.g. MARTÍN and VERICAD 1977; BLONDEL et al. 1978; ABE 1982; ALCÁNTARA 1989) since high mountains have an island effect (MCARTHUR 1972). Our results, however, are in contradiction to this general trend in that diversity increases with altitude. Such disagreement may be explained by the altitudinal range of the study area, which probably represents an ecotone (HOFFMANN 1984); i.e., the lowest limit for high altitude species and the highest limit for low altitude species (see DUEÑAS and PERIS 1985 for a similar result).

Latitudinal gradients in richness are well known, with species numbers decreasing as latitude increases (HERRERA 1974; MCCOY and CONNOR 1980). Our results, however, show an increase in richness as latitude increases. Similar to the trend in diversity, it could be argued that such an increase is the consequence of the border effect (MCARTHUR 1972), due to the Eurosiberian distribution of the species.

Acknowledgements

The authors thank M. ALCÁNTARA for helpful comments on the manuscript. R. JOHNSTON corrected the language.

Zusammenfassung

Verteilung der Kleinsäugerfauna entlang von Breiten- und Höhen-Gradienten in Nordspanien

Es wurde der Einfluß der geographischen Breite und der Höhe über NN auf die Verbreitung von Kleinsäufern untersucht. Annähernd 3000 Schleiereulengewölle von 20 verschiedenen Orten Nordspaniens wurden untersucht. Diese Gewölle enthielten Überreste von 9744 Kleinsäufern aus 17 Arten. Diese Arten konnten drei Gruppen zugeordnet werden: 1. Beziehung zur geographischen Breite (*Sorex coronatus*, *Neomys fodiens*, *Clethrionomys glareolus*, *Microtus pyrenaicus*, *Apodemus sylvaticus*, *Mus spretus*), 2. Beziehung zur Höhe über NN (*Suncus etruscus*, *Crocidura russula*, *Microtus agrestis*), 3. Keine Beziehungen zu geographischer Breite und Höhe über NN (*Sorex minutus*, *Eliomys quercinus*, *Microtus cabreræ*, *M. nivalis*, *M. doudecimcostatus*, *Arvicola sapidus*, *Rattus rattus*, *R. norvegicus*).

Die Verteilung der Arten wird in Beziehung zu geographischen und klimatischen Faktoren gesetzt. Unsere Daten zeigen, daß die geographische Breite der für das Auftreten von Arten nahe ihrer südlichen Verbreitungsgrenze bedeutendste Faktor ist.

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Zeitschrift/Journal: [Mammalian Biology \(früher Zeitschrift für Säugetierkunde\)](#)

Jahr/Year: 1992

Band/Volume: [57](#)

Autor(en)/Author(s): Moreno Eulalia, Barbosa Andrés

Artikel/Article: [Distribution patterns of small mammal fauna along gradients of latitude and altitude in Northern Spain 169-175](#)