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Quantitative palaeoclimatic inference based on terrestrial mammal faunas

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ABSTRACT

Aim The main goal of this paper is to propose a new tool, in the form of Quantitative Bioclimatic Models (QnBMs), for reconstructing past climates based on fossil mammal associations. As a case study, European climatic conditions during the basal early Pleistocene will be inferred using QnBMs.

Location The study uses faunas throughout the world to develop a quantitative bioclimatic model, which is then applied to Quaternary faunas from Eurasia.

Methods The models were constructed by applying multivariate linear regression to modern mammal faunas and climates from all over the world. The models were validated with a second group of modern faunas, which includes several from transitional zones between different climates (ecotones). To test the reliability of the method when applied to fossil associations, the results obtained for the Pleistocene have been compared with those obtained from palynology.

Results Validation of the models shows that as many as 11 climatic factors can be inferred with high reliability using the regression models developed in this work. Comparisons of results in the late Pleistocene–Holocene of Barová (Czech Republic) between a palynological study and the quantitative bioclimatic analysis show a high degree of similarity. The results for the early Pleistocene show colder and drier climatic conditions for Europe than today.

Main conclusions The application of the quantitative bioclimatic models to present day as well as Quaternary mammal faunas proves to be a useful tool for palaeoclimatic reconstruction during the Quaternary and probably most of the Neogene. Transfer functions are presented for a complete set of climatic factors, allowing a precise estimation of the climate in a locality from its mammal fauna.

Keywords

Bioclimatology, Europe, Mammalia, mammalian communities, methodology, multiple regression analysis, palaeoclimatology, Pleistocene, Rodentia.

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INTRODUCTION

Palaeoclimate reconstructions are important both for providing reliable boundary conditions for climate models, and for evaluating the results obtained from climatic models that simulate the very different climates of the past. Therefore, a large amount of data on past climatic conditions is needed to assess the results of diverse climatic models (Kohfeld & Harrison, 2000). Palaeoclimatic databases usually include a large amount of palaeoenvironmental data from marine plankton, lake levels, isotope records and, mainly, palynology (CLIMAP, 1976; COHMAP, 1988; PRISM,

1995; Prentice & Webb, 1998; Kohfeld & Harrison, 2000; Prentice *et al.*, 2000; CAPE, 2003). Nevertheless, the continental record is quite discontinuous and thus these data can seldom be obtained for particular periods or regions, and due to the scarcity of palaeoclimate proxies, in terms of spatial and temporal distribution, the palaeoclimatic history of the continents is not yet well established. There is, however, a large amount of fossil mammal data containing unique information, which complements that from other disciplines, that has been scantily used in palaeoclimatic databases. Mammals are highly responsive to climate (e.g. Fleming, 1973; FAUNMAP, 1996; Hernández Fernández, 2001a)

and they are abundant in a wide range of continental sedimentary environments, thus allowing a high temporal and spatial resolution as well as a relatively continuous record for climate reconstructions.

Several attempts to reconstruct ancient environments based on mammal faunas have been made, of which the most widely used are the analysis of ecological diversity (Andrews *et al.*, 1979) and the use of cenograms (Legendre, 1986). Andrews *et al.* (1979) proposed the use of the distribution of body size, locomotion, taxonomy and diet of African mammal fossil faunas to deduce the environment in which they lived. Legendre's (1986) method infers past environmental conditions based on the distributions of body mass (for a criticism of this methodology see Rodríguez, 1999). Recently, Hernández Fernández (2001a) developed the bioclimatic analysis, which is based on the relationship between climate and mammalian biogeographical distributions. In order to apply it to palaeoclimatic inference, Hernández Fernández & Peláez-Campomanes (2003) developed a series of Qualitative Bioclimatic Models (QIBMs), by which qualitative climatic data could be obtained from mammalian faunas. This methodology allows inference of the type of climate in a locality, according to Walter's (1970) climatic classification, from the study of its terrestrial mammal association. Nevertheless, all these qualitative methodologies have the same weakness; there are extensive ecotones between climate zones that are not properly recognized by a qualitative analysis.

In this work, we propose a new method of palaeoclimatic inference, which produces quantitative climatic estimates based on mammal associations. In this way, bioclimatic analysis (Hernández Fernández, 2001a; Hernández Fernández & Peláez-Campomanes, 2003) is refined for application in ecotone areas between two climate zones. In these situations Quantitative Bioclimatic Models (QnBMs) are able to offer more precise results than qualitative analyses. Certain climatic factors vary widely within a climate zone, so the development of a quantitative methodology offers a much higher precision than any qualitative methodology.

Mammal assemblages as a climatic data source could provide valuable information on the temporal as well as geographical distribution of climatic conditions, comparable to estimates obtained by the use of other kind of records. As an example, the developed model will be applied to mammal associations from fossil sites with a parallel palaeovegetation record. The interpretations obtained from mammal assemblages will be compared with those based on palynological data.

In addition, we apply the QnBMs to several Eurasian rodent faunas from the basal early Pleistocene. The QIBM has already been applied to these fossil faunas (Hernández Fernández & Peláez-Campomanes, 2003), so the results of our qualitative and quantitative analyses will be compared. The study will indicate the general characteristics of the European climate during that period, which has not been studied in depth using other palaeobiological records. This kind of spatially extensive data is of key importance for the understanding of climatic mechanisms because climate change is always spatially variable.

MATERIALS AND METHODS

Quantitative bioclimatic models (QnBMs)

Localities

The QnBMs are constructed from a database generated by Hernández Fernández (2001a), who determined the biome occupation of 1392 mammal species described from 50 localities distributed all over the world. The database includes 3226 presence records of those species in the studied localities and 3171 presence records in the studied biomes. The 50 localities studied, for which there is information available on both fauna and climate, were selected in a way that they cover all the climate zones (according to Walter, 1970), they are as widely scattered as possible, and they represent the average climatic conditions within their corresponding climate zone. In order to have comparable data for all the biomes, the database contains five localities from each of the 10 considered biomes. Information on the studied localities and references used to obtain the faunal lists can be consulted in Hernández Fernández (2001a).

Bioclimatic spectra

For every locality a species-by-climate matrix is constructed. The value assigned to each of the species in each climate zone is 0 when the species does not live in that climate zone or $1/n$ (called the Climatic Restriction Index, CRI; Hernández Fernández, 2001a) when it does live on it, n being the number of climates in which the species is present. See Hernández Fernández (2001a) for a more detailed description of the determination of the climate zones inhabited by a species.

Hernández Fernández (2001a) introduced the Bioclimatic Component (BC) term, which is the representation in a specific locality of each of the 10 existing climates. Ten BC values for each locality are calculated according to the formula:

$$BC_i = (\sum CRI_i)100/S$$

in which i is climate zone i , and S is the number of species in the locality. Each BC value may be understood as the percentage of the faunal assemblage that is characteristic of the corresponding climate. The 10 BC values of a locality constitute its bioclimatic spectrum, which is used in the multivariate analysis. The bioclimatic spectra calculated for the whole faunas, rodent faunas, macromammal faunas and whole faunas without bats of the 50 recent faunas are available in Hernández Fernández & Peláez-Campomanes (2003).

Climatic variables

In order to provide precise climate reconstructions, we have considered as many climatic parameters and indexes as possible. The selection criteria for these variables have been that they must be well suited for characterizing the specific climate in an area and that they be the most generally used in various climate classifications

Table 1 Climatic variables studied in this work

Abbr.	Climatic factor	Explanation	Units	References	
1	T	Annual mean temperature	Average of the mean monthly temperatures (t).	°C	
2	Tp	Annual positive temperature	Sum of the monthly mean temperature of those months whose average temperature is higher than 0 °C in tenths of °Celsius.	0.1 °C	Rivas Martínez (1994)
3	Tmax	Mean temperature of the warmest month		°C	
4	Tmin	Mean temperature of the coldest month		°C	
5	Mta	Mean annual thermal amplitude	A simple continentality index. Mta is the number expressing the range between the average temperatures of the warmest and coldest months of the year ($Mta = Tmax - Tmin$).	°C	Rivas Martínez (1994)
6	It	Thermicity index	An index that measures the intensity of winter cold ($It = 10(T + 2Tmin)$).	0.1 °C	Rivas Martínez (1994)
7	Itc	Compensated thermicity index	An index designed to equilibrate the cold 'excess' that occurs during winter in the continental climates (average temperature of the coldest month of the year), or the excessively mild winter in the marked oceanic regions, so that these index values can be significantly compared. It is derived from It: If $Mta < 9 \Rightarrow Itc = It - 10(9 - Mta)$ If $9 \leq Mta \leq 18 \Rightarrow Itc = It$ If $18 < Mta \leq 21 \Rightarrow Itc = It + 5(Mta - 18)$ If $21 < Mta \leq 27 \Rightarrow Itc = It + (15 + 10(Mta - 21))$ If $27 < Mta \leq 46 \Rightarrow Itc = It + (15 + 60 + 20(Mta - 27))$ If $46 < Mta \Rightarrow Itc = It + (15 + 60 + 380 + 30(Mta - 46))$	0.1 °C	Rivas Martínez (1994)
8	W	Winter length	Period in which $t < 0$ °C.	months	
9	VAP	Vegetative activity period	Period in which $t > 7$ °C. This index estimates the length of plants' winter dormancy and spring–summer growing periods.	months	Fernández González (1997)
10	FVAP	Free vegetative activity period	Since vegetation growth stops during the dry season, this index gives the length of the period in which both the temperature and the humidity allow the normal growing of vegetation ($FVAP = VAP - D$).	months	
11	Io	Ombrothermic index	An index that shows the relation between temperature and environmental humidity. Since no environmental humidity exists if the monthly mean temperature is below 0 °C, it is the quotient of the sum of mean precipitation (in mm) in months when $t > 0$ °C (Pp) and the sum (in °C) of t in those months ($Io = 10Pp/Tp$).		Rivas Martínez (1994)
12	P	Annual total precipitation		mm	
13	D	Drought length	Period in which $P < 2T$. This index estimates the length of the dry period.	months	Walter (1970); Rivas Martínez (1987)

(Köppen, 1931; Walter, 1970; Strahler & Strahler, 1987; Rivas Martínez, 1994). Some climatic indexes have been selected because they show closer relationships with vegetation distribution (Rivas Martínez, 1994) than more commonly employed climatic parameters such as annual precipitation or mean annual temperature. Values of 13 climatic variables related to temperature, precipitation and their seasonality have been compiled from each locality (Table 1). The values for each climatic factor in each locality are given in Appendix 1.

Predictive equations

The predictive equations for each of the studied climatic variables were obtained from a standard multiple linear regression

using the *enter* method of the Statistical program SPSS 11.0 (SPSS, 2001). For the analyses, we introduced the 10 untransformed BC_i as the independent variables and the climatic variable as the dependent one. Although some of the variables introduced in the model do not always contribute significantly to the predictive equations, we prefer to use the *enter* method instead of the *stepwise* one, since some of the excluded variables in the latter contribute significantly in the *enter* method. In addition, since all BC_i represent equivalent parts of the bioclimatic spectrum without any meaning on their own, we prefer to include them all. For each climatic variable, we performed four multiple linear regressions and obtained four regression models, one for each of the groups of bioclimatic spectra considered (whole faunas, rodent faunas, macromammal faunas and whole faunas without bats).

Model validation

To validate the models, we applied them to 13 new recent faunas. These 13 localities were studied by Hernández Fernández & Peláez-Campomanes (2003), providing additional information about new 120 species. For more information on these localities, see Hernández Fernández & Peláez-Campomanes (2003). Special emphasis was put on including in the test mammal faunas from areas other than the 50 previously used and from a wide range of climatic conditions. Some of these localities, distributed throughout the world, are located within ecotones between climate zones. In this way, the reliability of the predictive equations was tested for faunas without a clear climatic characterization.

Bioclimatic spectra of whole faunas, rodent faunas, macro-mammal faunas and whole faunas without bats of these 13 new localities are given in Hernández Fernández & Peláez-Campomanes (2003). These bioclimatic spectra were used to infer the values of the studied climatic variables using the multiple regression functions previously developed in this work.

To test the accuracy of the regression models, coefficients of determination between the observed (Appendix 2) and predicted values for the 13 new localities (r_p^2) were calculated. These r_p^2 were compared to the coefficient of determination of the corresponding calculated multiple regressions (r_r^2) in order to determine the degree of decrease in goodness of fit. Due to sample chance, small decreases in goodness of fit are expected even within accurate models. Thus, we consider in a somewhat arbitrary way, that a decrease of 10% in goodness of fit is the threshold to consider a model as inaccurate. Therefore, if $r_r^2 - r_p^2$ was larger than $r_r^2/10$ the model was considered inaccurate and thus rejected. In addition, if $r_r^2 - r_p^2$ was between $r_r^2/10$ and $r_r^2/20$ the model was considered accurate; and if it was lower than $r_r^2/20$, very accurate.

Application of the QnBMs to palaeoclimatic reconstruction

Fossil localities

As pointed out above, the purpose of the QnBMs is to analyse fossil faunas bioclimatically and compare past faunal and climatic variations through time and geography. As an example of the results that can be obtained and their reliability when compared with other sources of palaeoclimatic data and interpretations, we studied two late Pleistocene–Holocene superposed levels from the Barová Cave (Czech Republic), where faunal and palynological data are available (Svoboda *et al.*, 2000). In addition, 12 basal Pleistocene fossil mammal assemblages from Eurasia were analysed by the method developed in this study (Table 2).

The ages of these associations have usually been determined by means of biochronological analyses (Chaline & Michaux, 1974; Jánossy, 1986; Nadachowski, 1990; Rekovets & Nadachowski, 1995; Terzea, 1996; Alexeeva, 1998; von Koenigswald & Heinrich, 1999; Hernández Fernández, 2001b) and they belong to the earliest Pleistocene (approximately 1.8 million years before present). Since most of these reported assemblages comprise exclusively small mammals, we will use the models developed for rodent

Table 2 Eurasian early Pleistocene sites used in this work.

Additional information and references on these localities can be consulted in Hernández Fernández & Peláez-Campomanes (2003)

N	Fossil site	Country
1	Quibas	Spain
2	Bagur 2	Spain
3	Mas Rambault 1	France
4	Les Valerots	France
5	Neuleiningen 5	Germany
6	Monte Peglia A	Italy
7	Chlum 6	Czech Republic
8	Villany 5	Hungary
9	Kamyk	Poland
10	Betfia 9a	Rumania
11	Tiligul	Ukraine
12	Dodogol 1	Russia

faunas. These fossil sites were selected because all of them have supplied more than 100 fossils of first and second upper and lower rodent molars, providing a minimum sample size of rodent fossils adequate to obtain accurate palaeoclimatic inferences (van de Weerd & Daams, 1978; Daams *et al.*, 1999). Most of these localities have a karstic origin; only two of them (Tiligul, Dodogol 1) come from alluvial deposits. One question usually raised is the potential influence of site characteristics on faunal compositions, which may alter the palaeoecological interpretation of the mammalian associations. Faunal assemblages from karstic sites are generally considered as indicating more arid environments than those from fossil sites with alluvial origin (van de Weerd & Daams, 1978). Nevertheless, Aguilar *et al.* (1999) have not found a difference between the two kinds of faunas and thus there is no indication that karst infills systematically give a picture of drier environments. Therefore, we do not think the differences in sedimentary environment among our assemblages influence the results of the bioclimatic analysis.

Qualitative bioclimatic analysis was already applied to those localities and the bioclimatic spectra of their rodent associations are given in Hernández Fernández & Peláez-Campomanes (2003). For each locality and each predicted climatic factor a 95% confidence interval of the mean prediction is calculated using the Statistical program SPSS 11.0 (SPSS, 2001).

RESULTS AND DISCUSSION OF THE QUANTITATIVE BIOCLIMATIC MODELS

Predictive equations

Tables 3–6 show the results for each regression analysis. In order to avoid collinearity, SPSS excluded one of the 10 bioclimatic components in each of the regression models (BC I). Most of these transfer functions have high significance levels and very high coefficients of determination, indicating that an important amount of the variability of the climatic factors can be explained by the distribution of bioclimatic values.

Table 3 Multiple linear regressions for each studied climatic factor (see Table 1) as a function of the bioclimatic components from the whole fauna ($N = 50$). The statistical significance is: (ns) $P > 0.05$, non significant; (*) $0.05 > P > 0.01$; (**) $0.01 > P > 0.001$; (***) $P < 0.001$. b, intercept; aII–IX, slopes of the different bioclimatic components (see Hernández Fernández, 2001a); r^2 , determination coefficient; ES standard error of the estimate. See Supplementary Material (a) for the significance of the coefficients for each independent variable

Climatic factor	b	aII	aII/III	aIII	aIV	aV	aVI	aVII	aVIII	aIX	r^2	ES	F (sig.)
T (°C)	24.296	0.159	-0.103	0.032	-0.038	-0.145	-0.110	-0.217	-0.372	-0.451	0.939	3.386	68.763 (***)
Tp (0.1 °C)	2920.208	18.761	-12.514	2.845	-5.054	-14.783	-21.896	-21.833	-26.537	-35.444	0.914	356.156	47.112 (***)
Tmax (°C)	23.635	0.187	-0.030	0.051	0.072	-0.039	-0.099	-0.004	-0.058	-0.358	0.745	4.772	12.954 (***)
Tmin (°C)	25.655	0.115	-0.201	-0.007	-0.132	-0.258	-0.107	-0.460	-0.717	-0.523	0.943	4.656	73.050 (***)
Mta (°C)	-2.020	0.072	0.171	0.058	0.203	0.218	0.008	0.456	0.659	0.165	0.780	6.392	15.756 (***)
It (0.1 °C)	756.064	3.886	-5.047	0.180	-3.018	-6.582	-3.242	-11.375	-18.065	-14.957	0.949	118.351	82.392 (***)
Itc (0.1 °C)	655.351	4.591	-4.331	0.434	-1.831	-4.425	-5.719	-6.958	-9.651	-15.534	0.952	90.466	88.516 (***)
W (months)	-0.163	0.011	-0.011	0.004	-0.017	0.007	-0.036	0.066	0.109	0.120	0.938	0.861	67.657 (***)
VAP (months)	12.205	-0.010	-0.006	-0.004	0.027	0.038	-0.077	-0.081	-0.091	-0.175	0.947	1.037	78.873 (***)
FVAP (months)	15.078	-0.054	-0.207	-0.238	-0.109	0.072	-0.056	-0.148	-0.110	-0.197	0.898	1.495	38.984 (***)
Io	10.957	-0.138	-0.042	-0.121	-0.197	0.002	0.191	-0.128	-0.189	0.236	0.367	6.847	2.576 (*)
P (mm)	3240.416	-19.414	-37.247	-37.435	-38.442	-7.015	-5.144	-32.647	-35.223	-30.164	0.674	533.236	9.208 (***)
D (months)	-2.882	0.045	0.200	0.235	0.137	-0.035	-0.023	0.070	0.020	0.022	0.906	1.472	42.680 (***)

Table 4 Multiple linear regressions for each studied climatic factor (see Table 1) as a function of the bioclimatic components from the rodent fauna ($N = 50$). The statistical significance is: (ns) $P > 0.05$, non significant; (*) $0.05 > P > 0.01$; (**) $0.01 > P > 0.001$; (***) $P < 0.001$. b, intercept; aII–IX, slopes of the different bioclimatic components (see Hernández Fernández, 2001a); r^2 , determination coefficient; ES standard error of the estimate. See Supplementary Material (b) for the significance of the coefficients for each independent variable

Climatic factor	b	aII	aII/III	aIII	aIV	aV	aVI	aVII	aVIII	aIX	r^2	ES	F (sig.)
T (°C)	26.686	0.024	-0.029	-0.024	-0.074	-0.120	-0.135	-0.217	-0.404	-0.386	0.930	3.637	59.028 (***)
Tp (0.1 °C)	3205.394	2.657	-3.408	-3.762	-8.691	-12.934	-23.194	-22.625	-30.897	-32.036	0.911	362.682	45.273 (***)
Tmax (°C)	26.219	0.070	0.021	0.020	0.031	-0.032	-0.113	-0.037	-0.121	-0.287	0.746	4.754	13.086 (***)
Tmin (°C)	27.538	-0.033	-0.096	-0.080	-0.175	-0.212	-0.141	-0.418	-0.710	-0.465	0.932	5.081	60.622 (***)
Mta (°C)	-1.319	0.103	0.117	0.100	0.206	0.180	0.027	0.381	0.589	0.178	0.779	6.408	15.656 (***)
It (0.1 °C)	817.614	-0.421	-2.199	-1.846	-4.242	-5.435	-4.163	-10.533	-18.235	-13.165	0.938	130.569	66.901 (***)
Itc (0.1 °C)	726.156	0.267	-1.497	-1.583	-2.949	-3.973	-5.752	-7.092	-11.409	-13.014	0.948	94.587	80.593 (***)
W (months)	-0.013	0.002	-0.004	-0.006	-0.004	0.006	-0.034	0.049	0.110	0.090	0.920	0.980	51.292 (***)
VAP (months)	12.075	-0.007	0.002	0.003	0.010	0.027	-0.055	-0.066	-0.107	-0.131	0.955	0.949	95.055 (***)
FVAP (months)	13.137	-0.050	-0.139	-0.187	-0.099	0.055	-0.030	-0.117	-0.114	-0.146	0.918	1.337	49.826 (***)
Io	9.635	-0.092	-0.062	-0.109	-0.137	-0.005	0.179	-0.092	-0.156	0.191	0.418	6.565	3.194 (**)
P (mm)	2978.195	-21.237	-27.563	-33.050	-32.648	-6.678	-5.076	-28.400	-33.109	-25.980	0.746	470.615	13.083 (***)
D (months)	-1.064	0.043	0.141	0.189	0.110	-0.027	-0.027	0.053	0.006	0.014	0.926	1.306	55.454 (***)

In general, the results obtained for each of the studied faunal groups are similar. The different transfer functions for each climatic variable have similar coefficients of determination in all groups but large mammals, the ability of which to predict variables depending on precipitation is appreciably lower (lower r^2 in P, D, and FVAP). The standard errors for each climatic variable are also similar in the four faunal groups.

Focusing on the three groups with the best results (whole fauna, rodents and whole fauna without bats), nine out of 13 variables (T, Tp, Tmin, It, Itc, W, VAP, FVAP, and D) show coefficients of determination higher than 0.9, while Tmax and Mta have r^2 around 0.75 and P around 0.7 (for rodents 0.75). For the

macromammal data, only seven variables (T, Tp, Tmin, It, Itc, W and VAP) have r^2 equal to or higher than 0.9. Less than 50% of the variance in the ombrothermic index (Io) is explained by the regression models in the four analyses and therefore we will not consider this climatic factor in the subsequent discussion.

The results of the four analyses (whole fauna, rodent fauna, macromammal fauna and whole fauna without bats) indicate that, on average, the bioclimatic spectra of the rodent faunas produce somewhat better predictions than the others, particularly for variables depending on precipitation. Nevertheless, the whole fauna and the whole faunas without bats also offer very good results and the macromammal faunas present acceptable predictions.

Table 5 Multiple linear regressions for each studied climatic factor (see Table 1) as a function of the bioclimatic components from the mammalian fauna ($N = 50$). The statistical significance is: (ns) $P > 0.05$, non significant; (*) $0.05 > P > 0.01$; (**) $0.01 > P > 0.001$; (***) $P < 0.001$. b, intercept; aII-IX, slopes of the different bioclimatic components (see Hernández Fernández, 2001a); r^2 , determination coefficient; ES standard error of the estimate. See Supplementary Material (c) for the significance of the coefficients for each independent variable

Climatic factor	b	aII	aII/III	aIII	aIV	aV	aVI	aVII	aVIII	aIX	r^2	ES	F (sig.)
T (°C)	25.177	0.206	-0.193	0.153	-0.014	-0.203	-0.061	-0.265	-0.420	-0.529	0.926	3.751	55.237 (***)
Tp (0.1 °C)	2996.526	24.048	-22.393	17.208	-6.285	-18.484	-23.082	-24.433	-27.894	-41.069	0.910	364.183	44.864 (***)
Tmax (°C)	24.611	0.232	-0.162	0.177	0.064	-0.028	-0.193	0.009	-0.006	-0.462	0.749	4.730	13.260 (***)
Tmin (°C)	26.441	0.153	-0.243	0.081	-0.044	-0.371	0.068	-0.586	-0.853	-0.578	0.920	5.491	51.251 (***)
Mta (°C)	-1.830	0.079	0.081	0.095	0.108	0.343	-0.261	0.595	0.848	0.115	0.758	6.704	13.920 (***)
It (0.1 °C)	780.596	5.126	-6.788	3.158	-1.016	-9.446	0.747	-14.365	-21.261	-16.841	0.928	140.066	57.555 (***)
Itc (0.1 °C)	672.737	5.832	-6.520	3.591	-1.111	-5.724	-5.072	-7.975	-10.229	-18.176	0.940	100.927	70.245 (***)
W (months)	-0.208	0.002	-0.005	0.003	-0.042	0.038	-0.116	0.103	0.149	0.135	0.928	0.930	57.446 (***)
VAP (months)	12.253	-0.005	-0.013	0.009	0.033	0.022	-0.045	-0.094	-0.108	-0.200	0.896	1.448	38.279 (***)
FVAP (months)	13.726	-0.038	-0.212	-0.239	-0.103	0.079	0.026	-0.155	-0.124	-0.189	0.769	2.243	14.837 (***)
Io	9.252	-0.054	-0.029	-0.107	-0.219	-0.166	0.596	-0.206	-0.423	0.415	0.429	6.501	3.344 (**)
P (mm)	2927.258	-8.227	-39.211	-35.020	-35.597	-19.727	30.365	-37.819	-49.564	-21.422	0.643	558.709	7.991 (***)
D (months)	-1.479	0.033	0.199	0.249	0.136	-0.057	-0.073	0.064	0.016	-0.010	0.772	2.287	15.085 (***)

Table 6 Multiple linear regressions for each studied climatic factor (see Table 1) as a function of the bioclimatic components from the whole fauna without Chiroptera ($N = 50$). The statistical significance is: (ns) $P > 0.05$, non significant; (*) $0.05 > P > 0.01$; (**) $0.01 > P > 0.001$; (***) $P < 0.001$. b, intercept; aII-IX, slopes of the different bioclimatic components (see Hernández Fernández, 2001a); r^2 , determination coefficient; ES standard error of the estimate. See Supplementary Material (d) for the significance of the coefficients for each independent variable

Climatic factor	b	aII	aII/III	aIII	aIV	aV	aVI	aVII	aVIII	aIX	r^2	ES	F (sig.)
T (°C)	25.429	0.119	-0.099	0.063	-0.059	-0.139	-0.118	-0.227	-0.370	-0.473	0.934	3.539	62.591 (***)
Tp (0.1 °C)	3054.674	13.664	-11.670	6.240	-7.752	-14.180	-23.161	-23.104	-27.162	-37.431	0.910	362.958	45.198 (***)
Tmax (°C)	24.887	0.161	-0.052	0.094	0.040	-0.041	-0.113	-0.016	-0.060	-0.378	0.747	4.750	13.115 (***)
Tmin (°C)	26.512	0.059	-0.164	0.008	-0.144	-0.239	-0.109	-0.465	-0.707	-0.547	0.934	4.984	63.161 (***)
Mta (°C)	-1.625	0.103	0.112	0.085	0.184	0.198	-0.004	0.448	0.646	0.169	0.774	6.483	15.194 (***)
It (0.1 °C)	784.534	2.357	-4.265	0.795	-3.472	-6.175	-3.364	-11.564	-17.837	-15.669	0.941	127.119	70.826 (***)
Itc (0.1 °C)	687.416	3.078	-3.656	0.984	-2.390	-4.225	-5.891	-7.273	-9.712	-16.089	0.948	94.778	80.251 (***)
W (months)	-0.131	0.007	-0.007	-0.002	-0.014	0.009	-0.043	0.064	0.106	0.122	0.932	0.907	60.508 (***)
VAP (months)	12.231	-0.013	-0.003	0.000	0.023	0.035	-0.071	-0.079	-0.090	-0.177	0.945	1.054	76.232 (***)
FVAP (months)	13.796	-0.050	-0.177	-0.220	-0.096	0.073	-0.035	-0.135	-0.101	-0.183	0.910	1.405	44.726 (***)
Io	10.044	-0.112	-0.054	-0.114	-0.174	0.000	0.214	-0.122	-0.186	0.247	0.386	6.741	2.799 (*)
P (mm)	3061.537	-19.503	-33.374	-34.677	-35.418	-6.073	-1.824	-31.420	-34.000	-28.287	0.715	498.552	11.174 (***)
D (months)	-1.572	0.038	0.174	0.220	0.119	-0.038	-0.037	0.059	0.011	0.006	0.915	1.395	47.999 (***)

Validation

Table 7 shows the results obtained from comparing the coefficient of determination of the QnBMs (r_r^2) and the determination coefficient of the regression between the observed and predicted values (r_p^2). Of the 12 climatic variables studied, five show very accurate results ($r_r^2 - r_p^2 < r_r^2/20$) for all the study groups. These variables are T, Tp, Tmax, Itc and D. In addition, FVAP and P show very accurate results for all groups but mammals and rodents; their models are merely accurate ($r_r^2/20 < r_r^2 - r_p^2 < r_r^2/10$). The models for the other five variables show different results depending on the study group. Whole fauna and whole fauna without bats have similar results: Tmin, It

and VAP models are accurate and Mta and W models are not accurate ($r_r^2 - r_p^2 > r_r^2/10$). Mammals show the worst results: the It model is accurate but Tmin, Mta, W and VAP models are not accurate. The best results are those from the rodent faunas, for which the models for most variables are very accurate except for VAP and W, which are accurate and inaccurate, respectively. Thus the latter rodent model was rejected.

Discussion

The results show that three climatic variables (Tmax, Mta and P) have low determination coefficients for the four mammalian groups (Tables 3–6). These results are not surprising since Tmax

Table 7 Validation results for the four kind of models. r_r^2 , coefficient of determination of the quantitative bioclimatic models; r_p^2 , determination coefficient of the regression between the observed and predicted values. The values of the validation test are in bold for the rejected models ($r_r^2 - r_p^2 > r_r^2/10$), italics for the accurate models ($r_r^2/20 < r_r^2 - r_p^2 < r_r^2/10$), and plain for the very accurate models ($r_r^2 - r_p^2 < r_r^2/20$)

Climatic factor	Whole faunas			Rodent faunas		
	r_p^2	r_r^2	$r_r^2 - r_p^2$	r_p^2	r_r^2	$r_r^2 - r_p^2$
T	0.937	0.939	0.002	0.955	0.930	-0.025
Tp	0.957	0.914	-0.043	0.963	0.911	-0.052
Tmax	0.874	0.745	-0.129	0.847	0.746	-0.101
Tmin	0.851	0.943	0.092	0.899	0.932	0.033
Mta	0.658	0.780	0.122	0.745	0.779	0.034
It	0.878	0.949	0.071	0.919	0.938	0.019
Itc	0.947	0.952	0.005	0.958	0.948	-0.010
W	0.780	0.938	0.158	0.827	0.920	0.093
VAP	0.873	0.947	0.074	0.888	0.955	0.067
FVAP	0.908	0.898	-0.010	0.928	0.918	-0.010
P	0.732	0.674	-0.058	0.704	0.746	0.042
D	0.955	0.906	-0.049	0.967	0.926	-0.041

Climatic factor	Macromammal faunas			Whole faunas without bats		
	r_p^2	r_r^2	$r_r^2 - r_p^2$	r_p^2	r_r^2	$r_r^2 - r_p^2$
T	0.917	0.926	0.009	0.943	0.934	-0.009
Tp	0.927	0.910	-0.017	0.955	0.910	-0.045
Tmax	0.750	0.749	-0.001	0.850	0.747	-0.103
Tmin	0.819	0.920	0.101	0.863	0.934	0.071
Mta	0.558	0.758	0.200	0.668	0.774	0.106
It	0.852	0.928	0.076	0.889	0.941	0.052
Itc	0.933	0.940	0.007	0.954	0.948	-0.006
W	0.654	0.928	0.274	0.793	0.932	0.139
VAP	0.758	0.896	0.138	0.857	0.945	0.088
FVAP	0.699	0.769	0.070	0.927	0.910	-0.017
P	0.589	0.643	0.054	0.741	0.715	-0.026
D	0.765	0.772	0.007	0.967	0.915	-0.052

is not a strong limiting factor for mammal distribution and thus neither is Mta which is dependent on it. Annual precipitation (P) does not have a direct influence on mammal faunas, since it operates through vegetation used by mammals as food resources or refuge, and precipitation also varies seasonally as a function of the presence or absence of a dry period. For example, in tropical areas, flowering and fruiting of different plants depend on the presence of drought more than on the volume of precipitation (Walter & Breckle, 1986). In the same way, the forest canopy gradually becomes sparser from the rain forest to the desert with the increasing drought length (Walter, 1970). Drought also determines the fall of leaves in woody species from tropical forests and savannas (Walter & Breckle, 1986). Nevertheless, the amount of precipitation also influences those processes, this influence being stronger when the drought is longer (Walter, 1970; Walter & Breckle, 1986). Other factors can also influence these processes, in particular the capacity of soil for retaining water (Walter & Breckle, 1986). Therefore, within the subset of climatic factors dependent on precipitation, it makes sense that variables related to drought length (D and FVAP) obtain better predictions than the absolute rainfall amount (P).

Among the climatic factors dependent exclusively on temperature, the difference between absolute variables and durations of favourable periods is not observed so clearly (i.e. the coefficients of determination are similar). Both kinds of factors influence the phenology of the dominant vegetation. For example, the photoperiod, which is closely correlated with temperature, determines the fall of leaves in nemoral broadleaf-deciduous forests (Walter, 1970). On the other hand, when the vegetative activity period (VAP) is too short, these forests are replaced by boreal forests (Walter, 1970). Therefore, both groups of temperature variables (absolute and periods) influence mammal life histories.

The differences observed in accuracy and goodness of fit between the four faunal groups could be explained by the existence of physiological differences among taxa. Small-bodied species have a higher ratio of surface area and body size than large-bodied mammals, and therefore heat loss through their body surface is faster and they are more influenced by external temperature. This may affect their ability to inhabit different climate regimes. In addition, several species hibernate and this process is governed by the existence of predictable long winter periods during which temperatures are too cold for activity or food supply. There are

also ecological reasons that could help to explain the differences among groups, such as extent of home range and migration ability, which allow several species to occupy some climate zones only when the environmental conditions are adequate (e.g. the reindeer that inhabit the taiga during the winter but migrate to the tundra in spring). Dispersal capabilities of mammals are directly related to home range area (Bowman *et al.*, 2002), which is positively correlated with body size (McNab, 1963; Harestad & Bunnell, 1979; Lindstedt *et al.*, 1986; Swihart *et al.*, 1988). So, in general, large-bodied mammal species have larger home ranges and longer dispersal distances than small-bodied species. Thus, micromammals are restricted to a smaller part of the landscape during their life time than macromammals, which in addition have longer life cycles (Kelt & Brown, 1998). This, together with differences in body size, might be responsible for the differences in scale of landscape perception between both groups. While small mammals can find a greater variety of appropriate microhabitats, macromammals have a more restricted range of habitats because of their large body size (Hutchinson & MacArthur, 1959; May, 1986, 1988; Lawton, 1990; Fenichel, 1993). Therefore, macromammals have to inhabit large regions where patches of their required habitats are available and likely must deal satisfactorily with different climates. Thus, micromammals can be more adapted than macromammals to particular climatic conditions because their microhabitats are easily available in smaller areas and consequently they are not as constrained by habitat requirements as the large mammals. Large mammals can also travel long distances seasonally looking for adequate environmental conditions, which can be understood as an opportunist species character (Margalef, 1977). Perhaps for all these reasons the rodents are more influenced by climate than large mammals, and therefore provide better climatic inferences.

APPLYING THE QUANTITATIVE BIOCLIMATIC MODEL TO RODENT FAUNAS FROM THE QUATERNARY OF EURASIA

Barová cave (late Pleistocene–Holocene)

The bioclimatic spectra of the rodent associations from the Barová Cave fossil site are given in Hernández Fernández & Peláez-Campomanes (2003). The results obtained from the QnBMs are shown in Table 8. They show a considerable increase in temperature and precipitation from Barová 12 to Barová 9–10c–10b and the climatic values inferred for these levels agree with the vegetation recorded at them (Svobodová, 1992). The bioclimatic horizon (*sensu* Rivas Martínez, 1994) assumed for Barová 12 as a function of the climatic values inferred from the application of the QnBMs to its rodent fauna is Mesoboreal. This is consistent with a vegetation dominated by *Pinus*, *Picea*, *Juniperus* and *Salix*, as has been documented by palynological analysis. The bioclimatic horizon inferred for Barová 9–10c–10b is Montane–Subalpine (the thermotype assignation varies depending on the use of T_p or I_{tc}), which is consistent with a vegetation dominated by *Corylus* and *Betula*, as shown by the pollen record.

Table 8 Values for the different climatic factors (see Table 1) estimated by applying the quantitative bioclimatic models to two layers from the Barová Cave fossil site (\pm 95% confidence interval of mean prediction)

Climatic factor	Barová 12	Barová 9–10c–10b
T (°C)	-2.0 ± 1.9	5.6 ± 3.9
T_p (0.1 °C)	599.3 ± 193.0	807.4 ± 390.5
T_{max} (°C)	12.9 ± 2.5	16.1 ± 5.1
T_{min} (°C)	-16.8 ± 2.7	-4.3 ± 5.5
M_{ta} (°C)	29.7 ± 3.4	20.4 ± 6.9
I_t (0.1 °C)	-357.1 ± 69.4	-30.5 ± 140.5
I_{tc} (0.1 °C)	-191.7 ± 50.3	1.4 ± 101.8
VAP (months)	3.5 ± 0.5	5.5 ± 1.0
FVAP (months)	2.9 ± 0.7	6.2 ± 1.4
P (mm)	503.6 ± 250.3	1247.1 ± 506.5
D (months)	0.6 ± 0.7	-0.8 ± 1.4

Comparison with the qualitative analysis of Hernández Fernández & Peláez-Campomanes (2003) shows that the results offered by both qualitative model and quantitative models are consistent and robust. The QnBMs provide climatic data that, according to the scheme of Walter (1970) and Allué Andrade (1990), places Barová 12 in climate zone VIII and Barová 9–10c–10b in the climate zone VI, which are the climate zones inferred by the qualitative bioclimatic model for these fossil assemblages.

Eurasian earliest Pleistocene

Table 9 shows the estimates obtained for each climatic factor from selected basal Pleistocene fossil sites from Eurasia, which were obtained by applying QnBMs to the bioclimatic spectra of the rodent associations studied in Hernández Fernández & Peláez-Campomanes (2003). Table 10 shows the differences between the inferred early Pleistocene climate and the present climate at localities close to the fossil sites.

Climatic variables related to temperatures (T, T_p , T_{min} , T_{max} , I_t , I_{tc} , W, VAP)

Among the Eurasian Pleistocene sites, we see a general latitudinal gradient in temperature (Fig. 1). Temperatures increase from central Europe (Neuleiningen 5, $T = 4.0$ °C) to southern Europe (Quibas, $T = 15.4$ °C). This gradient is less clearly defined in Eastern Europe (Kamyk, $T = 8.9$ °C), which may be because the fossil sites were not exactly contemporaneous. One noteworthy issue is the presence in Europe of a slightly weakened latitudinal gradient in temperature during the earliest Pleistocene. The differences between the coldest and the warmest localities were lower in the basal Pleistocene than today.

Most of the fossil sites had lower temperatures in the early Pleistocene than today. It seems that the difference in temperature was higher in the western and southern parts of Europe than in the rest, but a clear pattern in these differences is not observed

Table 9 Values for the different climatic factors (see Table 1) estimated by applying the quantitative bioclimatic models to the earliest Pleistocene Eurasian fossil sites ($\pm 95\%$ confidence interval of mean prediction)

N	Fossil sites	T (°C)	Tp (0.1 °C)	Tmax (°C)	Tmin (°C)	Mta (°C)	It (0.1 °C)
1	Quibas	15.4 ± 2.7	2046.8 ± 270.3	26.1 ± 3.5	4.3 ± 3.8	21.8 ± 4.8	239.9 ± 97.3
2	Bagur 2	9.9 ± 2.3	1477.9 ± 231.0	23.1 ± 3.0	-3.8 ± 3.2	26.9 ± 4.1	22.3 ± 83.1
3	Mas Rambault 1	13.1 ± 2.7	1679.9 ± 265.5	23.7 ± 3.5	2.6 ± 3.7	21.1 ± 4.7	181.8 ± 95.5
4	Les Valerots	7.4 ± 1.7	1149.5 ± 171.6	19.3 ± 2.2	-4.4 ± 2.4	23.7 ± 3.0	-13.6 ± 61.8
5	Neuleiningen 5	4.0 ± 1.9	1092.4 ± 194.0	18.3 ± 2.5	-10.7 ± 2.7	29.0 ± 3.4	-174.7 ± 69.8
6	Monte Peglia A	10.1 ± 1.8	1460.9 ± 184.0	22.4 ± 2.4	-2.6 ± 2.6	25.0 ± 3.3	49.0 ± 66.2
7	Chlum 6	5.9 ± 2.3	986.1 ± 232.7	18.1 ± 3.1	-6.1 ± 3.3	24.2 ± 4.1	-63.3 ± 83.7
8	Villany 5	10.2 ± 1.9	1471.0 ± 191.6	22.5 ± 2.5	-2.3 ± 2.7	24.8 ± 3.4	55.4 ± 68.9
9	Kamyk	8.9 ± 1.9	1314.3 ± 186.1	21.2 ± 2.4	-3.8 ± 2.6	25.0 ± 3.3	12.6 ± 67.0
10	Betfia 9	7.0 ± 2.1	1101.6 ± 204.8	20.1 ± 2.7	-6.6 ± 2.9	26.7 ± 3.6	-61.5 ± 73.7
11	Tiligul	11.0 ± 2.0	1519.6 ± 195.1	23.2 ± 2.6	-1.6 ± 2.7	24.9 ± 3.4	77.5 ± 70.2
12	Dodogol 1	5.6 ± 2.4	1115.7 ± 240.8	21.3 ± 3.2	-11.1 ± 3.4	32.4 ± 4.3	-167.2 ± 86.7

N	Fossil sites	Itc (0.1 °C)	VAP (months)	FVAP (months)	P (mm)	D (months)
1	Quibas	334.1 ± 70.4	9.6 ± 0.7	4.7 ± 1.0	417.2 ± 350.6	4.9 ± 1.0
2	Bagur 2	165.6 ± 60.2	7.7 ± 0.6	3.8 ± 0.9	356.4 ± 299.7	4.0 ± 0.8
3	Mas Rambault 1	245.5 ± 69.2	8.8 ± 0.7	4.7 ± 1.0	532.3 ± 344.4	4.1 ± 1.0
4	Les Valerots	72.1 ± 44.7	7.0 ± 0.4	4.4 ± 0.6	721.5 ± 222.6	2.6 ± 0.6
5	Neuleiningen 5	-12.3 ± 50.6	5.8 ± 0.5	1.1 ± 0.7	143.3 ± 251.6	4.7 ± 0.7
6	Monte Peglia A	167.6 ± 47.9	8.7 ± 0.5	4.6 ± 0.7	539.5 ± 238.6	4.1 ± 0.7
7	Chlum 6	27.3 ± 60.7	6.0 ± 0.6	4.2 ± 0.9	777.3 ± 301.9	1.8 ± 0.8
8	Villany 5	165.3 ± 49.9	8.0 ± 0.5	2.5 ± 0.7	306.4 ± 248.6	5.6 ± 0.7
9	Kamyk	120.3 ± 48.5	7.3 ± 0.5	2.5 ± 0.7	400.2 ± 241.4	4.8 ± 0.7
10	Betfia 9	66.3 ± 53.4	6.4 ± 0.5	3.4 ± 0.8	596.3 ± 265.7	3.0 ± 0.7
11	Tiligul	190.2 ± 50.8	8.3 ± 0.5	2.7 ± 0.7	339.6 ± 253.1	5.6 ± 0.7
12	Dodogol 1	45.0 ± 62.8	6.3 ± 0.6	1.9 ± 0.9	194.7 ± 312.4	4.5 ± 0.9

Table 10 Differences between the values inferred for the different climatic factors (see Table 1) obtained by applying the quantitative bioclimatic models to the earliest Pleistocene Eurasian fossil sites and the values for the present climate in localities close to the fossil sites. Ref., References for the current climate: 1 Elías & Ruiz, 1977; 2, Meteorological Office, 1972; 3, Arlery, 1970; 4, Schüpp & Schirmer, 1977; 5, Cantu, 1977; 6, Okolowicz, 1977; 7, Lydolph, 1977

N	Fossil sites	T (°C)	Tp (0.1 °C)	Tmax (°C)	Tmin (°C)	Mta (°C)	It (0.1 °C)	Itc (0.1 °C)	VAP (months)	FVAP (months)	P (mm)	D (months)	Current climate localities	Ref.
1	Quibas	-4.2	-303.2	-1.9	-8.2	6.3	-206.1	-111.9	-2.4	2.4	114.2	-4.8	Abanilla	1
2	Bagur 2	-6.3	-467.1	-0.2	-13.8	13.6	-339.7	-196.4	-4.3	-5.3	-149.6	1.1	Bagur	1
3	Mas Rambault 1	-0.8	11.9	1.3	-3.3	4.6	-75.2	-11.5	-1.0	-2.7	-176.7	1.7	Montpellier	2
4	Les Valerots	-3.1	-110.5	-0.3	-5.7	5.4	-144.6	-60.4	-0.9	-3.5	-17.5	2.6	Dijon	3
5	Neuleiningen 5	-6.1	-116.6	-1.2	-11.5	10.3	-291.7	-132.8	-1.5	-6.2	-617.7	4.7	Karlsruhe	4
6	Monte Peglia A	-5.4	-403.1	-2.3	-9.5	7.2	-244.0	-125.4	-3.1	-4.8	-341.1	1.7	Roma	5
7	Chlum 6	-3.0	-114.9	-1.2	-3.4	2.2	-98.3	-32.7	-0.9	-2.7	250.3	1.8	Brno Turany	6
8	Villany 5	-1.3	83.0	-0.1	-1.6	1.5	-45.6	26.3	0.2	-5.3	-360.6	5.6	Pecs	6
9	Kamyk	1.5	345.3	3.0	0.3	2.7	20.6	100.3	1.1	-3.7	-243.8	4.8	Kielce	6
10	Betfia 9	-3.3	-162.4	-1.7	-3.9	2.2	-110.5	-32.7	-0.8	-3.8	12.3	3.0	Debrecen	6
11	Tiligul	1.4	311.6	1.1	1.2	0.0	37.5	96.2	1.3	-1.4	-49.4	2.7	Odessa	7
12	Dodogol 1	7.3	406.7	1.9	14.3	-12.4	357.8	139.0	1.8	-1.0	-51.3	2.9	Ulan Ude	7

because of the small number of assemblages analysed and, probably, because of the influence of topography and proximity to the coast. These differences are generally greater in the mean temperature of the coldest month (Tmin) than in the annual mean

temperature (T) or the mean temperature of the warmest month (Tmax). These low temperatures were probably associated with the Eburonian glacial period, which developed at the beginning of the Pleistocene (Kukla & Cílek, 1996).

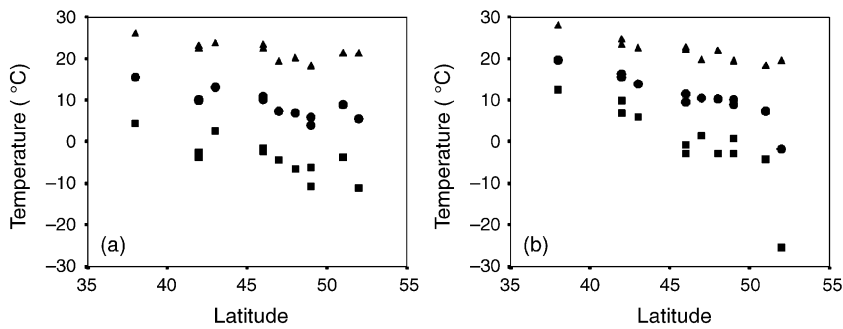


Figure 1 (a) Relation between latitude and inferred temperature in 12 basal Pleistocene fossil sites from Eurasia as estimated by applying the quantitative bioclimatic models to their rodent faunas. (b) Present day relationship between latitude and temperature in localities near these fossil sites (see Table 10). Circles, annual mean temperature; squares, mean temperature of the coldest month; triangles, mean temperature of the warmest month.

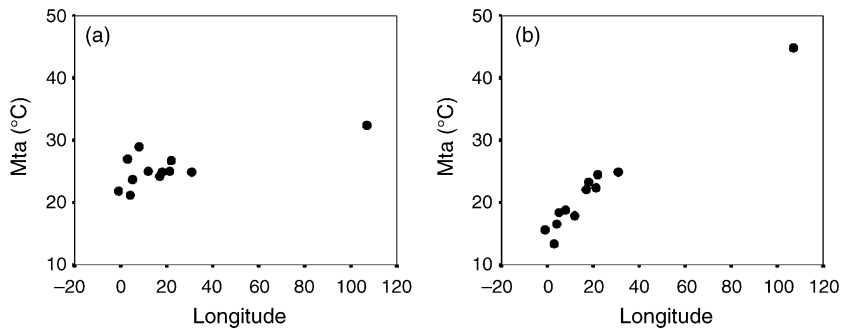


Figure 2 (a) Relationship between longitude and mean annual thermal amplitude (Mta) in 12 basal Pleistocene fossil sites from Eurasia as estimated by applying the quantitative bioclimatic models to their rodent faunas. (b) Present day relationship between longitude and mean annual thermal amplitude (Mta) in localities near these fossil sites (see Table 10).

Unsurprisingly, both thermicity indices (I_t , I_{tc}) show patterns similar to those of temperatures, since they are functions of them. Similarly, the vegetative activity period (VAP) was shorter during the earliest Pleistocene in Europe than today.

For all the analysed variables, Dodogol 1 (southern Siberia) stands out from the rest of the fossil assemblages. In particular, according to our analysis, T_{min} was 14.3 °C higher in the early Pleistocene than today. Two explanations can be suggested: first, this fossil assemblage may not be exactly contemporaneous with the others; second, during the Eburonian glacial, climatic relationships between central Asia and Europe might have been different from the present day ones, since the development of the Scandinavian glacial sheet probably had greater consequences in Europe than in central Asia because of geographical closeness to the former. These explanations are not mutually exclusive and could potentially reinforce each other.

Thermal seasonality (M_{ta})

During the early Pleistocene, mean annual thermal amplitude (M_{ta}) ranges from 21 to 29 °C in Europe, whereas in Transbaikalia (Dodogol 1) M_{ta} reaches 32.4 °C (Table 9). This shows a greater thermal seasonality in central Asia than in Europe, as today (Fig. 2). The differences between the estimated and the present values in both areas, however, show a clear longitudinal trend (Fig. 3). In all the European assemblages, the inferred M_{ta} was higher during the basal Pleistocene than today (Table 10). This increase is considerable in Western Europe and lower in Eastern Europe. Tilgul (Ukraine) shows the same M_{ta} during the Pleistocene as today. This trend culminates with the great decrease in thermal seasonality at Dodogol 1, where the M_{ta} was 12.4 °C lower in the earliest Pleistocene than today. This provides additional support for the hypothesis presented in the previous section,

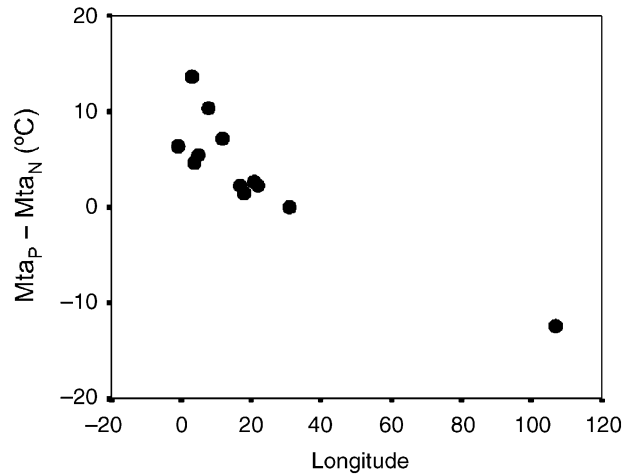


Figure 3 Relationship between longitude and the differences in mean annual thermal amplitude between basal Pleistocene (M_{ta_P}) and modern climate (M_{ta_N}) in 12 Eurasian fossil sites as estimated by applying the quantitative bioclimatic models to their rodent faunas.

according to which there was a different climatic relationship between central Asia and Europe during the Eburonian glacial.

Precipitation (P)

This variable does not show a clear gradient, either latitudinal or longitudinal, during the European earliest Pleistocene. Nevertheless, a considerable increase in the amount of rainfall was observed in the fossil sites close to the Alps (Les Valerots, Chlum 6) and Apennines (Monte Peglia A) in comparison with the other assemblages. This pattern is also observed today (Strahler &

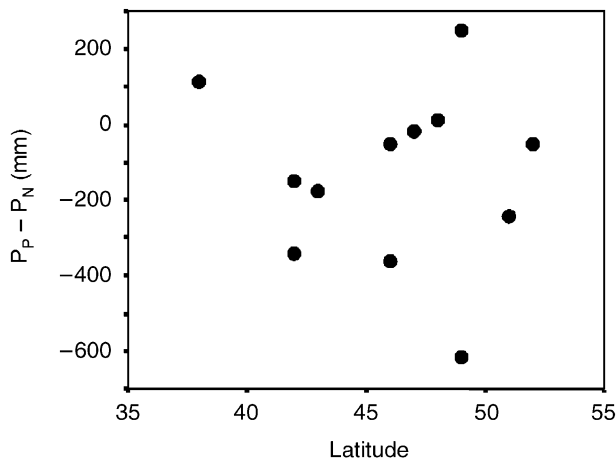


Figure 4 Relationship between latitude and the differences in annual precipitation between basal Pleistocene (P_p) and modern climate (P_n) in 12 Eurasian fossil sites as estimated by applying the quantitative bioclimatic models to their rodent faunas.

Strahler, 1987). However, the amount of annual rainfall was generally lower during the early Pleistocene than today (Fig. 4). As with temperatures, this could be related to the Eburonian glaciation. Only three faunal assemblages have higher precipitation values in the Pleistocene (Quibas, Chlum 6, Betfia 9).

Hydric seasonality (D)

This factor also shows no clear trend. As with the previous result, the fossil sites with the shortest drought lengths are Les Valerots and Chlum 6. The rest of the European assemblages have drought lengths of 4–6 months. Generally, these values are higher than present day values, except in Quibas, which had a much shorter dry period. The differences are small in Mediterranean areas but the dry period shows great lengthening during the Pleistocene in Northern and Eastern Europe (Fig. 5). Changes in rainfall seasonality and precipitation amount could be associated with changes in the atmospheric circulation due to the presence of huge polar ice sheets during the glacial periods (COHMAP, 1988; Spaulding, 1991). These changes provoke a general decrease in precipitation, which is more pronounced in central and north-western Europe than in Mediterranean areas, which can benefit from pluvial episodes (Spaulding, 1991; Prentice *et al.*, 1992).

Climatic hostility (FVAP)

Climate was much more hostile (shorter free vegetative activity period) in the northernmost fossil sites (Neuleiningen 5, Kamyk) and in some of the eastern assemblages (Villány 5, Tiligul, Dodogol 1) than in Western Europe. In the first case, there was a joint effect of low temperatures and the presence of an appreciable dry period. In the second case, the hostility is determined by the drought length, which extended for a considerable part of the year. Comparison with present values shows that, generally, the climate was more hostile during the Eburonian glacial than

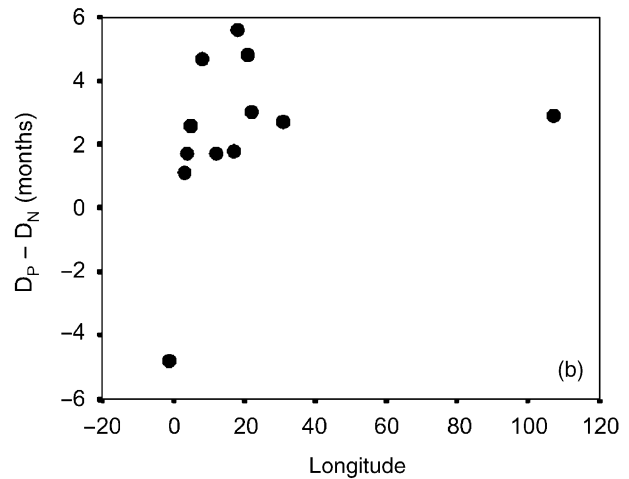
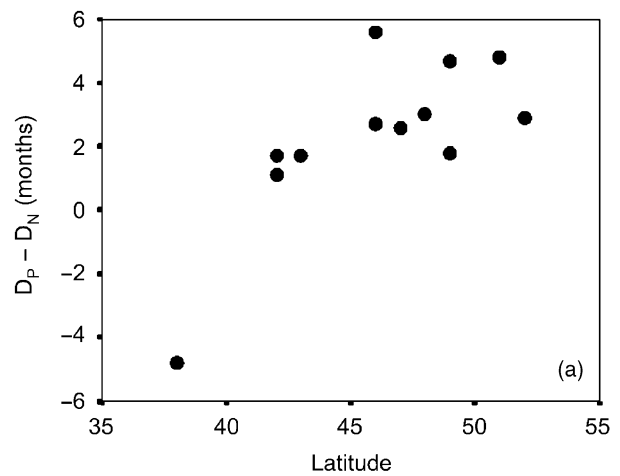


Figure 5 Relationship between latitude (a) or longitude (b) and the differences in drought length between basal Pleistocene (D_p) and modern climate (D_n) in 12 Eurasian fossil sites as estimated by applying the quantitative bioclimatic models to their rodent faunas.

today, but the shortening of free vegetative activity period does not show a clear geographical tendency (Fig. 6).

Comparison with the qualitative bioclimatic model (QIBM)

Table 11 shows the climatic assignments that can be made as a function of the climatic data inferred for each fossil site by means of the QnBMs and compares them with the results of the application of the QIBM for the rodent faunas from the Eurasian basal Pleistocene (Hernández Fernández & Peláez-Campomanes, 2003). These climatic assignments have been made using the keys provided by Allué Andrade (1990) and Walter (1970), Strahler & Strahler (1987), and Rivas Martínez (1994), and the climatic values inferred for each fossil rodent fauna to designate its climate according to, respectively, Walter's (1970), Köppen's (1931) and Rivas Martínez's (1994) climatic classifications. The use of these three major climatic typologies provides a very complete definition of one locality's climate that can be easily understood by any researcher familiarized with any of these classifications.

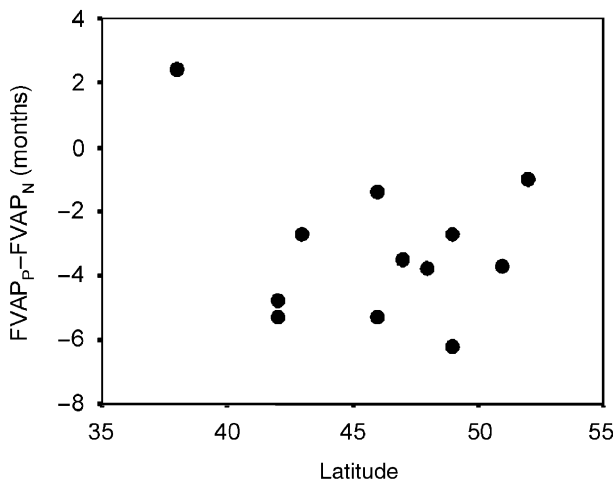


Figure 6 Relationship between latitude and the differences in climatic hostility between basal Pleistocene (FVAP_P) and modern climate (FVAP_N) in 12 Eurasian fossil sites as estimated by applying the quantitative bioclimatic models to their rodent faunas.

There is a general agreement between both quantitative and qualitative analyses, which indicates a high internal consistency of the bioclimatic analysis. The only remarkable differences are in the fossil assemblages of Monte Peglia A, Les Valerots, Neuleiningen 5 and Chlum 6. While Monte Peglia A has been classified by the qualitative analysis as belonging to the nemoral biome (VI), the quantitative results place this assemblage in the steppe biome (VII). Nevertheless, it is placed in a bioclimatic horizon (*sensu* Rivas Martínez, 1994), the Subhumid Supra-Mediterranean, of which the main vegetation is the marcescent (semideciduous)

forests with a physiognomy similar to that of the typical nemoral broadleaf-deciduous forests from climate zone VI. This kind of forest constitutes a southern latitudinal band between the nemoral deciduous forests and the more arid southern biomes (Rivas Martínez *et al.*, 1999). Les Valerots is placed in the ecotone IV/VI/VII by the quantitative bioclimatic analysis, whereas the qualitative analysis classified it as belonging to climate zone VI. Chlum 6 was classified as belonging to climate zone VI, but the short dry period inferred from the quantitative analysis, probably during the summer, places it in the ecotone VI/VII. The results from these two fossil sites show the potential of the QnBMs to produce climatic information not accessible from qualitative analysis. The quantitative analysis refers Neuleiningen 5 to the ecotone VII/VIII, while the qualitative analysis classified it in climate zone VIII, although the probability of the most probable climate zone was low ($P_1 = 0.486$), the second most probable climate zone ($P_2 = 0.339$) being the steppe biome (VII). Other fossil assemblages with relatively low values of P_1 are Bagur 2 (0.561), Kamyk (0.538) and Betfia 9 (0.570). In these cases the quantitative analysis is coincident with the classification made by the qualitative analysis and ecotonal conditions are not inferred for them according to (Walter, 1970) climatic typology. However, the climatic values inferred for these fossil sites place them in the ecotones between open lands and forests according to their bioclimatic horizons (Rivas Martínez, 1996).

These results altogether suggest not only that precise climatic information can be inferred by using the QnBMs but also that the comparison between the results of quantitative and qualitative analysis provides us with additional information on the physiognomy of the local vegetation. This indicates that rodent faunas can be indicators of vegetation physiognomy, which is in

Table 11 Results of the bioclimatic analysis of the rodent faunas from the Eurasian basal early Pleistocene. The climatic assignments were determined from climatic data estimated by the quantitative bioclimatic models. For the determination of the climates according to the climatic typologies by Walter, Köppen, and Rivas Martínez we have used, respectively, Allué Andrade (1990) and Walter (1970), Strahler & Strahler (1987), and Rivas Martínez (1994). P_1 , probability of the highest probability climate zone; P_2 , probability of the second highest probability climate zone (see Hernández Fernández & Peláez-Campomanes, 2003). IV, Mediterranean climate zone (Mediterranean biome); VI, typical temperate climate zone (nemoral biome); VII, arid-temperate climate zone (steppe biome); VIII cold-temperate climate zone (taiga biome). Mme, Meso-Mediterranean; Sme, Supra-Mediterranean; Ome; Oro-Mediterranean; Mon, Montane; Sar, Semiarid; Sec, Dry; Shu, Subhumid; Hum, Humid

N	Fossil site	Qualitative bioclimatic model			Quantitative bioclimatic models			
		Highest probability climate zone	P_1	2nd Highest probability climate zone	P_2	Walter	Köppen	Rivas Martínez
1	Quibas	IV	1.000	VI	0.000	IV	BSh	Mme-Sec
2	Bagur 2	VII	0.561	VI	0.432	VII	Bsk	Sme-Sec
3	Mas Rambault 1	IV	1.000	VI	0.000	IV	Csa	Mme-Shu
4	Les Valerots	VI	0.999	VII	0.000	IV/VI/VII	Dsb	Ome-Hum
5	Neuleiningen 5	VIII	0.486	VII	0.339	VII/VIII	Bsk	Ome
6	Monte Peglia A	VI	0.902	VII	0.097	VII	Csa	Sme-Shu
7	Chlum 6	VI	0.999	VIII	0.001	VI/VII	Dfb/Dsb	Mon-Hum
8	Villany 5	VII	0.840	IV	0.120	VII	BSh	Sme-Sar
9	Kamyk	VII	0.538	VI	0.462	VII	Dsb	Sme-Sec
10	Betfia 9	VII	0.570	VI	0.430	VII	Dsb	Ome-Shu
11	Tiligul	VII	0.999	VI	0.001	VII	BSh	Sme-Sar
12	Dodogol 1	VII	1.000	VI	0.000	VII	BSh	Ome-Sar

agreement with the results presented by Monjeau *et al.* (1997, 1998) and Schweiger *et al.* (2000).

CONCLUSIONS

This study presents transfer functions for a complete set of climatic factors, which allow a reconstruction of the climate in a locality from its mammal fauna. Most of the climatic variables used in the definition of climates can be estimated by applying multiple linear regressions based on bioclimatic spectra, using whole faunas, rodent faunas, macromammal faunas, or whole faunas without bats, from localities all around the world. This method allows increased precision over the inferences made by our previous qualitative bioclimatic analysis (Hernández Fernández, 2001a; Hernández Fernández & Peláez-Campomanes, 2003). In summary, this methodology consists of two different kinds of models (qualitative and quantitative) that are complementary and allow a parallel approach to the reconstruction of palaeoenvironmental conditions under which the faunas recorded in the fossil sites lived. While the QnBMs provide values for several important climatic variables, the QIBMs offer information on the climate regimen, specially the type of hydric seasonality (summer rain–winter rain). Comparison of the results obtained from both models can provide further information on the local vegetation physiognomy (at least in the case of rodent faunas).

The use of the rodent faunas supplies the best and most complete climatic inferences, but the other mammal groupings studied (whole faunas, whole faunas without bats, and macromammal faunas) also provided satisfactory qualitative and quantitative climatic reconstructions. This allows the combination of these different groupings to obtain climatic data from different fossil assemblages that do not represent past mammal communities fully, because of ecological and/or taphonomical processes.

The QnBMs offer statistically significant but approximate results. Therefore, it must be kept in mind that, although the obtained results are excellent, they should not be perceived as absolute numbers. Instead, when this methodology is applied to fossil assemblages, the results of quantitative bioclimatic analysis should be seen as indicators of general trends, either geographical or temporal.

The application of this methodology to the basal Pleistocene allowed us to establish the general climatic conditions in Europe during the Eburonian glaciation. The most remarkable results are the lower temperatures and the presence of a relatively long dry period all over Europe, which clearly differ from the present climate and are consistent with most reconstructions of full-glacial conditions.

The application of our method to present day as well as Quaternary mammal faunas has demonstrated that it provides a useful and robust tool for reconstructing palaeoclimate from the fossil mammal record. We think that the technique presented here can contribute to full exploitation of the potential of Neogene–Quaternary mammal assemblages for quantitative palaeoclimate analyses. The possibility of achieving greater realism in global climatic models depends not only on modelling developments *per se*, but also on the availability of key input information. In this paper, it has been shown that mammals can offer high precision climatic data. Therefore, we believe major benefits

can be obtained by using palaeoclimatic evidence provided by the mammalian fossil record in the use and validation of global climatic models.

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SUPPLEMENTARY MATERIAL

The following material is available from <http://www.blackwellpublishing.com/products/journals/suppmat/GEB/GEB125/GEB125sm.htm>

Appendix S1. Significance levels for each coefficient in the multiple linear regressions for each studied climatic factor (see Table 1 in main text) as a function of the bioclimatic components from the whole fauna (see Table 3 in main text).

Appendix S2. Significance levels for each coefficient in the multiple linear regressions for each studied climatic factor (see Table 1 in main text) as a function of the bioclimatic components from the rodent fauna (see Table 4 in main text).

Appendix S3. Significance levels for each coefficient in the multiple linear regressions for each studied climatic factor (see Table 1 in main text) as a function of the bioclimatic components from the macromammal fauna (see Table 5 in main text).

Appendix S4. Significance levels for each coefficient in the multiple linear regressions for each studied climatic factor (see Table 1 in main text) as a function of the bioclimatic components from the whole fauna without Chiroptera (see Table 6 in main text).

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BIOSKETCHES

Manuel Hernández Fernández has broad interests in the area of evolutionary biology and a wide variety of problems related to the biological and climatic evolution of the Neogene-Quaternary Earth. He is particularly interested in the interface between macroecology and palaeoclimatology and the focus of his current research is in the use of mammal faunas for high precision palaeoenvironmental inference.

Pablo Peláez-Campomanes is interested in understanding the structure of Cenozoic mammal communities by integrating evolutionary and community ecology theories into studies with a multispecies perspective. His studies also provide extensive data sets for subsequent analyses of the evolution of mammalian lineages.

Appendix 1. Values for each studied climatic variable in the localities used for the development of the quantitative bioclimatic model. N is the number assigned to each locality in Hernández Fernández (2001a). For the abbreviations see Table 1. For more information on the localities see Hernández Fernández (2001a)

N	Locality	T (°C)	Tp (0.1 °C)	Tmax (°C)	Tmin (°C)	Mta (°C)	It (0.1 °C)	Itc (0.1 °C)	W (months)	VAP (months)	FVAP (months)	Io	P (mm)	D (months)	References
1	Barrow	-12.5	78.0	3.9	-27.9	31.8	-683.0	-512.0	9.0	0.0	0.0	6.7	109.0	0.0	Hare & Hay, 1974
2	Port Harrison	-6.9	269.0	8.9	-25.3	34.2	-575.0	-356.0	8.0	2.0	2.0	7.3	395.0	0.0	Hare & Hay, 1974
3	Malye-Karmaerly	-5.7	168.0	6.4	-15.4	21.8	-365.0	-342.0	8.0	0.0	0.0	7.8	317.0	0.0	Lydolph, 1977
4	Mys Chelyuskin	-15.6	14.0	0.8	-31.1	31.9	-778.0	-605.0	10.0	0.0	0.0	39.3	232.0	0.0	Lydolph, 1977
5	Mys Schmidta	-12.1	77.0	3.6	-27.3	30.9	-667.0	-514.0	9.0	0.0	0.0	13.0	296.0	0.0	Lydolph, 1977
6	Fairbanks	-3.4	573.0	15.4	-23.9	39.3	-512.0	-191.0	7.0	4.0	4.0	3.2	287.0	0.0	Hare & Hay, 1974
7	Fort Smith	-3.2	590.0	16.2	-25.4	41.6	-540.0	-173.0	6.0	4.2	4.2	3.7	337.0	0.0	Hare & Hay, 1974
8	Kajaani	1.9	606.0	16.1	-10.6	26.7	-193.0	-121.0	5.0	4.2	4.2	6.6	564.0	0.0	Werner, 1970
9	Serov	0.0	637.0	16.7	-16.9	33.6	-338.0	-131.0	5.0	4.5	4.5	4.8	446.0	0.0	Lydolph, 1977
10	Erbogachen	-6.7	544.0	17.0	-31.2	48.2	-691.0	-170.0	7.0	3.5	3.5	3.8	323.0	0.0	Lydolph, 1977
11	Rapid City	8.2	1119.0	23.2	-5.6	28.8	-30.0	81.0	4.0	6.3	3.3	2.8	373.0	3.0	Court, 1974
12	Puerto Santa Cruz	8.5	1020.0	14.3	1.8	12.5	121.0	121.0	0.0	7.5	0.4	2.0	200.0	7.1	Prohaska, 1976
13	Fort Schevchenko	11.1	1373.0	25.8	-3.6	29.4	39.0	162.0	3.0	7.0	0.0	0.8	130.0	7.7	Lydolph, 1977
14	Urumchi	5.3	1163.0	23.9	-15.8	39.7	-263.0	66.0	5.0	6.0	1.3	0.5	276.3	4.7	Watts, 1969
15	Paotou	6.4	1095.0	22.7	-11.8	34.5	-172.0	53.0	5.0	6.5	5.3	1.9	303.9	1.2	Watts, 1969
16	Prince Rupert	7.6	912.0	13.9	1.8	12.1	112.0	112.0	0.0	6.7	6.7	26.3	2399.0	0.0	Hare & Hay, 1974
17	Cleveland	9.4	1183.0	21.7	-2.4	24.1	46.0	92.0	3.0	6.7	6.7	6.0	897.0	0.0	Court, 1974
18	Evangelistas	6.4	768.0	8.8	4.4	4.4	152.0	106.0	0.0	5.8	5.8	33.5	2569.7	0.0	Miller, 1976
19	Vlissingen	9.9	1188.0	17.4	2.9	14.5	157.0	157.0	0.0	7.7	7.7	5.8	689.0	0.0	Arléry, 1970
20	Tsingtao	12.3	1476.0	25.1	0.1	25.0	125.0	180.0	0.0	7.9	7.9	4.4	646.6	0.0	Watts, 1969
21	New Orleans	21.3	2556.0	28.6	13.3	15.3	479.0	479.0	0.0	12.0	12.0	6.3	1613.0	0.0	Court, 1974
22	Puerto Montt	11.1	1332.0	15.2	7.6	7.6	263.0	249.0	0.0	12.0	12.0	14.9	1981.0	0.0	Miller, 1976
23	Corrientes	21.5	2580.0	27.4	15.7	11.7	529.0	529.0	0.0	12.0	12.0	4.9	1269.0	0.0	Prohaska, 1976
24	Foochow	19.8	2376.0	28.5	10.7	17.8	412.0	412.0	0.0	12.0	12.0	5.9	1390.4	0.0	Watts, 1969
25	Kagoshima	16.8	2016.0	27.1	6.6	20.5	300.0	312.5	0.0	11.8	11.8	11.6	2337.1	0.0	Arakawa & Taga, 1969
26	Fresno	16.9	2028.0	27.0	7.5	19.5	319.0	326.5	0.0	12.0	4.9	1.4	285.0	7.1	Court, 1974
27	Santiago de Chile	14.0	1680.0	20.0	8.1	11.9	302.0	302.0	0.0	12.0	5.1	2.2	365.5	6.9	Miller, 1976
28	Sanlucar de Barrameda	16.9	2028.0	24.5	10.3	14.2	375.0	375.0	0.0	12.0	6.8	2.4	479.0	5.3	Elias & Ruiz, 1977
29	Aleppo	17.3	2076.0	28.4	6.1	22.3	295.0	323.0	0.0	11.7	4.9	1.6	340.8	6.8	Taha <i>et al.</i> , 1981
30	Esfahan	16.1	1932.0	29.4	3.6	25.8	233.0	296.0	0.0	7.8	0.4	1.6	301.0	7.4	Taha <i>et al.</i> , 1981
31	Phoenix	21.4	2568.0	32.9	10.4	22.5	422.0	452.0	0.0	12.0	0.0	0.7	184.0	12.0	Court, 1974
32	Arica	18.8	2256.0	22.3	15.8	6.5	504.0	479.0	0.0	12.0	0.0	0.0	0.7	12.0	Miller, 1976
33	Asswan	26.5	3180.0	34.1	16.1	18.0	587.0	587.0	0.0	12.0	0.0	0.0	2.0	12.0	Estienne & Godard, 1970
34	Mascate	28.5	3420.0	34.5	22.0	12.5	725.0	725.0	0.0	12.0	0.0	0.3	106.0	12.0	Taha <i>et al.</i> , 1981
35	Lüderitz Bay	15.9	1908.0	18.0	13.5	4.5	429.0	384.0	0.0	12.0	0.0	0.1	18.0	12.0	Schulze, 1972
36	Las Piedras	28.7	3444.0	30.3	26.9	3.4	825.0	769.0	0.0	12.0	3.4	1.6	541.0	8.6	Snow, 1976
37	Catamarca	20.3	2436.0	27.7	11.4	16.3	431.0	431.0	0.0	12.0	2.8	1.5	370.0	9.2	Prohaska, 1976

N	Locality	T (°C)	Tp (0.1 °C)	Tmax (°C)	Tmin (°C)	Mta (°C)	It (0.1 °C)	Itc (0.1 °C)	W (months)	VAP (months)	FVAP (months)	Io	P (mm)	D (months)	References
38	Zinder	28.3	3396.0	33.0	22.5	10.5	733.0	733.0	0.0	12.0	3.1	1.6	530.5	8.9	Griffiths, 1972a
39	Voi	24.9	2988.0	27.0	22.5	4.5	699.0	654.0	0.0	12.0	4.6	1.8	538.0	7.4	Griffiths, 1972b
40	Jaipur	25.0	3000.0	33.2	15.1	18.1	552.0	552.5	0.0	12.0	3.4	2.2	648.1	8.6	Rao, 1981b
41	Roque Saenz Peña	21.3	2556.0	27.3	15.2	12.1	517.0	517.0	0.0	12.0	9.6	3.9	990.0	2.4	Prohaska, 1976
42	Ziguinchor	26.8	3216.0	28.5	24.0	4.5	748.0	703.0	0.0	12.0	5.3	5.1	1626.0	6.7	Griffiths, 1972a
43	Moundou	27.0	3240.0	30.5	24.5	6.0	760.0	730.0	0.0	12.0	6.2	3.8	1232.0	5.8	Griffiths, 1972a
44	Mtwara	25.9	3108.0	27.0	24.0	3.0	739.0	679.0	0.0	12.0	6.6	3.7	1159.0	5.5	Griffiths, 1972b
45	Patna	26.2	3144.0	32.4	17.3	15.1	608.0	608.0	0.0	12.0	4.8	3.5	1109.8	7.2	Rao, 1981b
46	Tumaco	25.9	3108.0	26.4	25.3	1.1	765.0	686.0	0.0	12.0	12.0	10.1	3128.0	0.0	Snow, 1976
47	Paramaribo	27.3	3276.0	28.5	26.4	2.1	801.0	732.0	0.0	12.0	12.0	6.7	2208.2	0.0	Snow, 1976
48	Kribi	25.8	3096.0	27.0	24.5	2.5	748.0	683.0	0.0	12.0	12.0	9.8	3028.0	0.0	Bultot & Griffiths, 1972
49	Yangambi	24.7	2964.0	25.5	24.0	1.5	727.0	652.0	0.0	12.0	12.0	6.2	1828.0	0.0	Bultot & Griffiths, 1972
50	Medan	27.1	3252.0	28.1	26.3	1.8	797.0	725.0	0.0	12.0	12.0	6.7	2174.0	0.0	Sukanto, 1969

Appendix 2. Values for each studied climatic variable in the localities used for the validation of the quantitative bioclimatic model. N is the number assigned to each locality in Hernández Fernández & Peláez-Campomanes (2003). For the abbreviations see Table 1. For more information on the localities see Hernández Fernández & Peláez-Campomanes (2003)

N	Locality	T (°C)	Tp (0.1 °C)	Tmax (°C)	Tmin (°C)	Mta (°C)	It (0.1 °C)	Itc (0.1 °C)	W (months)	VAP (months)	FVAP (months)	Io	P (mm)	D (months)	References
51	Ust Kamchatsk	-0.9	435.0	12.2	-12.8	25.0	-265.0	-210.0	6.0	3.5	3.5	6.4	670.0	0.0	Lydolph, 1977
52	Saskatoon	2.0	836.0	19.3	-17.6	36.9	-332.0	-59.0	5.0	5.0	5.0	3.2	352.0	0.0	Hare & Hay, 1974
53	Riga	5.6	818.0	17.1	-5.0	22.1	-44.0	-18.0	4.0	5.3	5.3	5.4	566.0	0.0	Lydolph, 1977
54	Budapest	11.2	1352.0	22.2	-1.1	23.3	90.0	128.0	1.0	7.7	7.6	4.3	630.0	0.1	Okolowicz, 1977
55	Dairen	10.3	1343.0	24.5	-5.2	29.7	-1.0	128.0	3.0	7.1	7.1	4.1	575.4	0.0	Watts, 1969
56	Portland	12.6	1512.0	20.3	4.6	15.7	218.0	218.0	0.0	9.1	6.6	7.1	1075.0	2.5	Court, 1974
57	Charleston	18.3	2196.0	26.7	10.0	16.7	383.0	383.0	0.0	12.0	12.0	5.7	1250.0	0.0	Court, 1974
58	Niza	14.8	1776.0	22.7	7.5	15.2	298.0	298.0	0.0	12.0	9.5	4.9	862.0	2.5	Arléry, 1970
59	Kweilin	19.4	2328.0	28.4	9.2	19.2	378.0	384.2	0.0	12.0	12.0	8.4	1966.1	0.0	Watts, 1969
60	Smara	21.7	2604.0	27.7	14.8	12.9	513.0	513.0	0.0	12.0	0.0	0.1	35.8	12.0	Font Tullo, 1955
61	Puerto Ayacucho	27.2	3264.0	29.5	25.2	4.3	776.0	729.0	0.0	12.0	8.9	6.9	2249.0	3.1	Snow, 1976
62	Tabou	26.0	3120.0	27.5	24.0	3.5	740.0	685.0	0.0	12.0	11.7	7.6	2383.0	0.3	Bultot & Griffiths, 1972
63	Kuala Lumpur	26.2	3144.0	26.8	25.8	1.0	778.0	698.0	0.0	12.0	12.0	7.7	2409.0	0.0	Rao, 1981a

Supplementary Material S1. Significance levels for each coefficient in the multiple linear regressions for each studied climatic factor (see Table 1) as a function of the bioclimatic components from the whole fauna (see Table 3). b, significance for the intercept; aII-IX, significance for the slopes of the different bioclimatic components.

Climatic factor	b	aII	aII/III	aIII	aIV	aV	aVI	aVII	aVIII	aIX
T	0.000	0.087	0.182	0.635	0.543	0.027	0.118	0.000	0.000	0.000
Tp	0.000	0.055	0.123	0.685	0.441	0.031	0.005	0.000	0.000	0.000
Tmax	0.000	0.151	0.784	0.595	0.396	0.666	0.308	0.949	0.490	0.000
Tmin	0.000	0.362	0.060	0.949	0.123	0.005	0.264	0.000	0.000	0.000
Mta	0.751	0.678	0.234	0.658	0.081	0.072	0.954	0.000	0.000	0.134
It	0.000	0.227	0.063	0.932	0.165	0.005	0.185	0.000	0.000	0.000
Itc	0.000	0.065	0.038	0.804	0.274	0.012	0.004	0.000	0.000	0.000
W	0.827	0.613	0.568	0.819	0.265	0.659	0.054	0.000	0.000	0.000
VAP	0.000	0.724	0.808	0.871	0.135	0.050	0.001	0.000	0.000	0.000
FVAP	0.000	0.188	0.000	0.000	0.000	0.011	0.076	0.000	0.000	0.000
Io	0.096	0.440	0.801	0.374	0.111	0.997	0.187	0.163	0.112	0.045
P	0.000	0.183	0.003	0.001	0.000	0.481	0.651	0.000	0.000	0.002
D	0.043	0.249	0.000	0.000	0.000	0.211	0.471	0.001	0.432	0.362

Supplementary Material S2. Significance levels for each coefficient in the multiple linear regressions for each studied climatic factor (see Table 1) as a function of the bioclimatic components from the rodent fauna (see Table 4). b, significance for the intercept; aII-IX, significance for the slopes of the different bioclimatic components.

Climatic factor	b	aII	aII/III	aIII	aIV	aV	aVI	aVII	aVIII	aIX
T	0.000	0.676	0.561	0.657	0.087	0.017	0.016	0.000	0.000	0.000
Tp	0.000	0.647	0.486	0.480	0.046	0.010	0.000	0.000	0.000	0.000
Tmax	0.000	0.362	0.741	0.777	0.572	0.609	0.114	0.387	0.046	0.000
Tmin	0.000	0.683	0.168	0.281	0.005	0.003	0.066	0.000	0.000	0.000
Mta	0.753	0.318	0.181	0.287	0.008	0.041	0.766	0.000	0.000	0.020
It	0.000	0.840	0.216	0.335	0.008	0.003	0.036	0.000	0.000	0.000
Itc	0.000	0.860	0.245	0.255	0.011	0.003	0.000	0.000	0.000	0.000
W	0.984	0.901	0.774	0.664	0.709	0.629	0.025	0.000	0.000	0.000
VAP	0.000	0.636	0.891	0.856	0.354	0.035	0.000	0.000	0.000	0.000
FVAP	0.000	0.023	0.000	0.000	0.000	0.004	0.138	0.000	0.000	0.000
Io	0.030	0.383	0.489	0.263	0.076	0.954	0.071	0.124	0.062	0.015
P	0.000	0.007	0.000	0.000	0.000	0.290	0.467	0.000	0.000	0.000
D	0.213	0.041	0.000	0.000	0.000	0.124	0.179	0.000	0.703	0.342

Supplementary Material S3. Significance levels for each coefficient in the multiple linear regressions for each studied climatic factor (see Table 1) as a function of the bioclimatic components from the macromammal fauna (see Table 5). b, significance for the intercept; aII-IX, significance for the slopes of the different bioclimatic components.

Climatic factor	b	aII	aII/III	aIII	aIV	aV	aVI	aVII	aVIII	aIX
T	0.000	0.047	0.026	0.062	0.871	0.057	0.640	0.000	0.000	0.000
Tp	0.000	0.018	0.009	0.032	0.444	0.074	0.075	0.000	0.004	0.000
Tmax	0.000	0.074	0.131	0.087	0.549	0.834	0.246	0.909	0.962	0.000
Tmin	0.000	0.303	0.054	0.490	0.722	0.019	0.723	0.000	0.000	0.000
Mta	0.755	0.663	0.590	0.508	0.475	0.071	0.268	0.000	0.000	0.404
It	0.000	0.179	0.035	0.295	0.747	0.019	0.879	0.000	0.000	0.000
Itc	0.000	0.037	0.006	0.102	0.625	0.047	0.155	0.000	0.000	0.000
W	0.798	0.948	0.800	0.897	0.051	0.146	0.001	0.000	0.000	0.000
VAP	0.000	0.894	0.699	0.766	0.319	0.581	0.372	0.000	0.005	0.000
FVAP	0.000	0.538	0.000	0.000	0.047	0.207	0.750	0.000	0.033	0.000
Io	0.110	0.759	0.840	0.442	0.140	0.361	0.012	0.073	0.013	0.003
P	0.000	0.585	0.003	0.005	0.007	0.209	0.125	0.000	0.001	0.067
D	0.456	0.576	0.000	0.000	0.011	0.369	0.373	0.112	0.786	0.829

Supplementary Material S4. Significance levels for each coefficient in the multiple linear regressions for each studied climatic factor (see Table 1) as a function of the bioclimatic components from the whole fauna without Chiroptera (see Table 6). b, significance for the intercept; aII-IX, significance for the slopes of the different bioclimatic components.

Climatic factor	b	aII	aII/III	aIII	aIV	aV	aVI	aVII	aVIII	aIX
T	0.000	0.138	0.122	0.346	0.283	0.025	0.093	0.000	0.000	0.000
Tp	0.000	0.097	0.077	0.361	0.173	0.026	0.002	0.000	0.000	0.000
Tmax	0.000	0.132	0.539	0.294	0.587	0.607	0.227	0.773	0.428	0.000
Tmin	0.000	0.598	0.071	0.934	0.070	0.007	0.260	0.000	0.000	0.000
Mta	0.754	0.477	0.336	0.479	0.074	0.078	0.983	0.000	0.000	0.103
It	0.000	0.407	0.065	0.743	0.085	0.006	0.177	0.000	0.000	0.000
Itc	0.000	0.150	0.035	0.584	0.111	0.012	0.002	0.000	0.000	0.000
W	0.857	0.734	0.677	0.926	0.304	0.576	0.019	0.000	0.000	0.000
VAP	0.000	0.587	0.888	0.998	0.165	0.055	0.001	0.000	0.000	0.000
FVAP	0.000	0.118	0.000	0.000	0.000	0.004	0.200	0.000	0.000	0.000
Io	0.068	0.458	0.651	0.371	0.099	0.998	0.107	0.135	0.091	0.025
P	0.000	0.085	0.001	0.001	0.000	0.477	0.850	0.000	0.000	0.001
D	0.160	0.218	0.000	0.000	0.000	0.116	0.186	0.001	0.621	0.769