



The bioclimatic model: a method of palaeoclimatic qualitative inference based on mammal associations

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ABSTRACT

Aim The bioclimatic model is a new method for palaeoclimatic reconstruction built on the assumption of a significant correlation between climate and mammal community composition. The goal of this approach is to infer past climatic conditions using mammal fossil associations as source data.

Location The study used mammal faunas from all over the world to develop the bioclimatic model. As an example of the potential of the model, we have applied it to Quaternary faunas from Eurasia.

Methods The proposed model was constructed by applying multivariate discriminant analysis to modern mammal faunas and climates from throughout the world. The model was validated with a different set of modern faunas than those used in the discriminant analysis, including some from transitional zones between different climates (ecotones). To test the reliability of the method in the Pleistocene, the results have been compared to those obtained with data from other disciplines, such as palaeobotany.

Results The results obtained in the validation of the model show that more than 90% of the localities have been classified correctly. Comparisons of results in the late Pleistocene-Holocene of Barová between a palaeobotanical study and the bioclimatic analysis show the latter to be highly accurate. The results for early Pleistocene faunas show somewhat drier and more open climatic conditions for Europe than the present day, with larger areas of steppe environments.

Main Conclusions The bioclimatic model could be used to infer climatic conditions from mammal faunas. The results presented in this work provide a preliminary example of the potential that bioclimatic analysis has as a tool for palaeoclimatic inference. Finally, this method offers the opportunity to standardize data coming from vertebrate palaeontology for use in the construction and evaluation of climatic models.

Key words Bioclimatology, discriminant analysis, Europe, Mammalia, mammalian communities, palaeoclimatology, palaeoecological method, Pleistocene, Rodentia.

INTRODUCTION

During the last 30 years numerous studies have been carried out in order to reconstruct past climates and to build models to help us understand how, when, and why the global climate changes happened. These studies have focused on aspects

such as marine and atmospheric circulation, tectonics and palaeovegetation (CLIMAP, 1976; COHMAP, 1988; PRISM, 1995; Prentice & Webb III, 1998; Kohfeld & Harrison, 2000), and little attention has been paid to the important source of data available from disciplines like vertebrate palaeontology, particularly from mammal palaeontology.

There are abundant works on palaeoecological and palaeoclimatic reconstruction based on mammals (van de Weerd & Daams, 1978; Andrews *et al.*, 1979; Legendre, 1986; de Bonis *et al.*, 1992; van der Meulen & Daams, 1992; van Dam, 1998; Hernández Fernández *et al.*, 2003). The approaches of

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Climate		Zonobiome (mainly vegetation type)	
I	Equatorial	I	Evergreen tropical rain forest
II	Tropical with summer rains	II	Tropical deciduous woodland
II/III	Transition tropical semiarid	II/III	Savanna
III	Subtropical arid	III	Subtropical desert
IV	Winter rain and summer drought	IV	Sclerophyllous woodland-shrubland
V	Warm-temperate	V	Temperate evergreen forest
VI	Typical temperate	VI	Nemoral broadleaf-deciduous forest
VII	Arid-temperate	VII	Steppe to cold desert
VIII	Cold-temperate (boreal)	VIII	Boreal coniferous forest (Taiga)
IX	Arctic	IX	Tundra

Table 1 Climatic typology used in this paper (modified from Walter, 1970) and its relationships with world vegetation types. Walter (1970) considers II/III as a zonoecotone between tropical forests and deserts but we apply it as a zonobiome because it is traditionally used in palaeoecology due to its unique faunal community

those authors, nevertheless, offered interpretations at a quite restricted scale. They are important to the understanding of ecological or climatic evolution through time at a local scale but are difficult to extrapolate to a wider scale and thus to compare with data from other areas. Therefore, it is important to develop new methods that can be used to make climatic reconstruction and environmental interpretations at a much broader geographical scale. Hernández Fernández (2001a) developed just such a methodology, bioclimatic analysis, to make palaeoclimatic interpretations based on mammal associations. He showed the high correlation attainable between mammal associations and specific climatic and vegetation typologies (Walter, 1970; see Table 1), and thus the power of the analysis of mammal associations as a proxy for climatic reconstruction. In the same paper he also analysed the climatic discrimination among several sets of mammal groups, such as entire mammal faunas, rodent faunas, macromammal faunas and whole faunas without bats. The reason for doing these analyses is because in the fossil record it is quite common to have fossil associations composed only of large mammals or small mammals due to taphonomic or sampling biases.

The aim of the present paper is to present models for each of the mammal groups indicated above and validate them with modern faunas not used to build the model. Additionally, the model will be applied to several fossil mammal faunas, comparing the interpretations obtained using mammal assemblages with interpretations based on data from different sources, such as palynological studies.

MATERIALS AND METHODS

Hernández Fernández (2001a) described the analytical methodology in detail. In the following paragraphs we will present only a summary of the approach.

Faunal data for 50 localities from all over the world (with the exception of Australia) and from all climates (following

the climatic typology of Walter, 1970; Table 1) form the database of this study (Appendix 1 in Hernández Fernández, 2001a). Five localities containing both faunal and climatic information were selected from each climate zone in order to have comparable data for all biomes. Each locality was selected in such a way that it represents the average climatic conditions within its climate zone and that the localities from a single climate zone were as widely scattered as possible all over the world. The faunal list of each locality has been obtained from the literature (see References in Hernández Fernández, 2001a).

For every locality a species by climate matrix is made. The value assigned to each of the species in each climate 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 in it, being n the number of climates in which the species is present. See Hernández Fernández (2001a) for a more detailed description on the determination of the climate zones inhabited by a species. The Bioclimatic Component (BC) is the representation in a specific locality of each of the 10 existing climates. Each of the 10 BC values for every locality is calculated according to the formula:

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

where i is climate zone i and S is the number of species in the locality. The 10 BC values of a locality constitute its bioclimatic spectrum. The latter are the data 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, distributed all over the world (Hernández Fernández, 2001a), are available as supplementary material (Appendix 1) in the journal's web site and in the web page of one of the authors (M.H.F.) at the National Museum of Natural Sciences of Madrid web site (<http://www.mncn.csic.es/>).

Table 2 New modern localities studied in this work. N, locality numbers are consecutive to those in Hernández Fernández (2001a)

N	Climate zone	Locality	Country	Latitude	Longitude	Altitude	References
51	VIII/IX	Ust Kamchatsk	Russia	56°14'-N	162°28'-E	6 m	Corbet (1978)
52	VI/VIII	Saskatoon	Canada	52°08'-N	106°38'-W	157 m	Hall (1981)
53	VI/VIII	Riga	Latvia	56°58'-N	24°04'-E	3 m	Corbet (1978)
54	VI/VII	Budapest	Hungary	47°31'-N	19°02'-E	120 m	Corbet (1978)
55	VI	Dairen	China	38°54'-N	121°38'-E	96 m	Corbet (1978)
56	IV/VI	Portland	USA	45°32'-N	122°40'-W	9 m	Hall (1981)
57	V	Charleston	USA	32°54'-N	80°02'-W	100 m	Hall (1981)
58	IV/VI	Niza	France	43°40'-N	7°12'-E	5 m	Corbet (1978)
59	II/V	Kweilin	China	25°15'-N	110°10'-E	167 m	Corbet (1978); Corbet & Hill (1992)
60	III	Smara	Sahara W	26°44'-N	11°26'-W	140 m	Corbet (1978)
61	II	Puerto Ayacucho	Venezuela	5°41'-N	67°38'-W	99 m	Eisenberg (1989)
62	I/II	Tabou	Ivory Coast	4°55'-N	7°22'-E	4 m	Kingdon (1971–82); Dorst & Dandelot (1973); Nowak (1991)
63	I	Kuala Lumpur	Malaysia	3°07'-N	101°42'-E	34 m	Corbet & Hill (1992)

The proposed models have been built using discriminant analysis. In this analysis, we used the different BC_i that form the bioclimatic spectrum as variables. Therefore, each locality is an operational faunistic unit characterized by 10 variables. Then, based on the obtained bioclimatic spectra, we calculate a series of discriminant functions (Appendix 2, and at <http://www.mncn.csic.es/>) and calculate to which climate zone a locality has the highest probability of association. All calculations were done using SPSS version 11.01.

The validation of the model was done using 13 new recent faunas (Table 2), distinct from the 50 used to calculate the discriminant functions. Some of these localities, distributed throughout the world, are located in the proximity of ecotones between two or more climate zones. Since the main application of the model will be the inference of past climatic conditions and its evolution through time, we have decided to include these ecotone faunas to check the power of the model and its reliability for faunas with transitional climatic characterization. Bioclimatic spectra of whole faunas, rodent faunas, macromammal faunas and whole faunas without bats of the 13 new localities are shown in Appendix 3 and at <http://www.mncn.csic.es/>.

As set out above, the purpose of this model is to allow a climatic classification of fossil faunas and thus, to provide a tool to relate past faunal variation through time and space. As an example of the results that could be obtained and its reliability, when compared with other sources of data and interpretations, rodent faunas from two late Pleistocene–Holocene superposed levels from the Barová Cave (Czech Republic), where faunal and palynological data are available (Svoboda *et al.*, 2000), have been studied. The lower selected level is

layer 12. The upper selected level, composed of layers 10b, 10c and 9, has a minimum sample size of rodent fossils adequate to obtain accurate palaeoclimatic inferences (Daams *et al.*, 1999). These three layers show a qualitatively homogeneous faunal composition and the results would not be affected by their combination.

In addition, 12 early Pleistocene fossil mammal assemblages from Eurasia (of an approximate age of 1.8 ma; Table 3, Fig. 1) were analysed by the method developed in this study. Since most of these assemblages have reported exclusively small mammals, we will use the model developed for rodent faunas. There are no data available on how much time is represented by each faunal assemblage. The length of the concentration period varies from hours in some catastrophic fossil sites (Behrensmeyer & Schindel, 1983) to a century in macromammals fossil sites with eschatological origin (Behrensmeyer, 1982). According to Behrensmeyer (1982), time resolution for attritional assemblages could be 10²–10³ years, and possibly more, in small mammal fossil sites, because of condensation and reelaboration (or reworking) processes (*sensu* Fernández-Lopez, 2000). Nevertheless, Agustí & Martín Suárez (1986) and Álvarez Sierra *et al.* (1990) consider that micromammal fossils are unlikely to be reelaborated (or reworked) because of their fragility. Furthermore, any shift in the biome due to climatic variation has to be reflected in sedimentary changes. Since the sampling methodology considers as a fossil fauna only the specimens coming from a single stratum, we consider that the climatic conditions were probably similar, despite the time involved in the formation of some of our fossil localities. Therefore, application of the bioclimatic analysis would not suffer from the

Table 3 Literature sources of the Eurasian early Pleistocene sites used in this work. N, numbers in Fig. 1. Cl., current climate zone (see Table 1). S, number of rodent species. E, sedimentary environment (K, karstic; A, alluvial)

N	Fossil site	Country	Cl.	S	E	References
1	Quibas	Spain	IV	5	K	Montoya <i>et al.</i> (1999)
2	Bagur 2	Spain	IV	9	K	López Martínez <i>et al.</i> (1976); Martín Suárez & Mein (1991); Laplana (1999)
3	Mas Rambault 1	France	IV	8	K	Chaline & Michaux (1966); Chaline (1972); Chaline & Michaux (1974); Martín Suárez & Mein (1991); Aguilar <i>et al.</i> (1993)
4	Les Valerots	France	VI	16	K	Chaline (1972); Chaline & Michaux (1974); Bartolomei <i>et al.</i> (1975); Nadachowski (1991); Nadachowski & Garapich (1998)
5	Neuleiningen 5	Germany	VI	6	K	Maul (1996)
6	Monte Peglia A	Italy	IV/VI	8	K	van der Meulen (1973); Nadachowski & Garapich (1998)
7	Chlum 6	Czech Republic	VI	19	K	Bartolomei <i>et al.</i> (1975); von Koenigswald & Heinrich (1999)
8	Villany 5	Hungary	VI	16	K	Kretzoi (1956); van der Meulen (1974); Jánossy (1986); Montuire (1995)
9	Kamyk	Poland	VI	20	K	Kowalski (1975); Nadachowski (1990a); Nadachowski (1990b); Daoud (1993); Garapich & Nadachowski (1996); Nadachowski (1998)
10	Betfia 9a	Rumania	VI	14	K	Terzea (1995); Terzea (1996); Hír & Venczel (1998)
11	Tiligul	Ukraine	VII	21	A	Rekovets & Nadachowski (1995)
12	Dodogol 1	Russia	VII	5	A	Alexeeva (1998)

time-averaged sample present in some small mammal fossil assemblages.

Application of the bioclimatic analysis to ancient mammal faunas deals with a very common problem in palaeoecology: the occurrence of nonanalogous faunas, or so-called disharmonic faunas (Lundelius *et al.*, 1987). Mammal species must migrate if they are to survive climate change. Palaeoecologists have demolished the notion that ecological communities can be considered as ancient, coevolved entities, since climate change evokes differential responses in the constituent taxa. Thus, the taxonomic composition of biomes during one climatic phase can be very different from that during another phase (FAUNMAP, 1996). Climatic oscillations on the Milankovitch time scale enables repeated mixing of faunas during some phases, and disjunctions during others. These data require a dynamic perspective on mammal biogeography and raise the problem of the incidence of nonanalogous faunas. Bioclimatic analysis assigns climate zones (biomes) to

the localities on the basis of the taxonomic composition of communities or fossil associations, but the bioclimatic spectrum is an emergent property of the locality based on functional bioclimatic characteristics of its constituent taxa. Thus, two mammal assemblages need not have any taxa in common in order to be assigned to the same climate zone, making the bioclimatic analysis fairly independent from modern analogues in terms of mammal communities.

Potential limitations in this methodology include the possible existence of unknown biomes in the past or that modern biomes have different characteristics than in the past. This problem is stronger when the age of taxa or localities increases, although we think that Plio-Pleistocene biomes have been substantially similar to modern ones (CLIMAP, 1976; PRISM, 1995). Nevertheless, we are developing a complementary model for quantitative inference that will be useful in addressing this problem (M. Hernández Fernández & P. Peláez-Campomanes, in prep.).

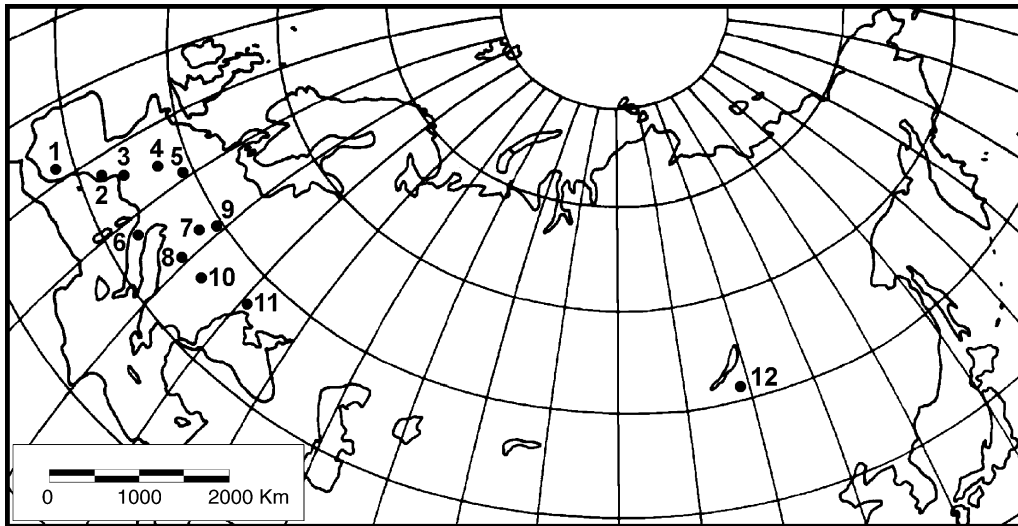


Fig. 1 Location of the 12 early Pleistocene fossil sites used in this work. Numbers as in Table 3.

RESULTS AND DISCUSSION

The bioclimatic model

The discriminant functions used for the model are shown in Appendix 2. The percentages of localities classified correctly are 98% for whole faunas, 94% for rodent faunas, 90% for macromammal faunas and 96% for whole faunas without bats (Hernández Fernández, 2001a).

The bioclimatic spectra of the 13 localities used for validation (Appendix 3) show, in general, more even distribution of the different bioclimatic components (BC, *sensu* Hernández Fernández, 2001a) than the 50 localities used to build the model. Our interpretation of this observation is that the differences of distribution of the bioclimatic spectra are due to the relative position of the localities in the climatic zone. The 50 localities used in the model come from areas in the middle of climatic dominions, thus *a priori* with a higher proportion of taxa characteristic of the corresponding climatic zone, while several of the validation localities come from ecotone areas between two climate zones and thus include a higher degree of mixed taxa.

The result obtained in the validation of the model shows that more than 90% of the 13 localities have been classified correctly. The differences between the groups of mammals show that, as for the 50 original localities used to construct the model (Hernández Fernández, 2001a), the reliability of the rodent faunas, whole faunas and whole faunas without bats is very high, with the macromammal fauna the least accurate (Table 4). Despite the small differences in the classifications obtained for each of the four groups of mammal faunas, it is important to note the high degree of accuracy

expressed by all. This is important since, as was discussed above, the associations of fossil mammals are frequently composed exclusively of only one of these groups due to sampling or taphonomic bias. This method could therefore be used to infer climatic conditions from micromammals, macromammals, or entire faunas.

It is possible to obtain additional information and interpretations by carefully studying the characteristics of the localities where the model fails. Puerto Ayacucho belongs to the tropical with summer rains climate zone (II) but it has been classified as transitional tropical semiarid climate zone (II/III) by the bioclimatic analysis of the whole fauna, macromammals and the whole fauna without bats. This is probably due to the fact that the landscape physiognomy of Los Llanos (Venezuela) corresponds to a savanna due to edaphic conditions (Walter, 1970). The rodent fauna, on the other hand, classifies this locality correctly. The higher discriminant capacity of the latter group could be due to a stronger relationship with vegetation physiognomy in the macromammals while rodents do not have this stronger dependence and thus reflect a closer relationship with climatic conditions. This observation is supported by the results of Hernández Fernández (2001a). In that work, Voi (Kenya) was assigned to a macroclimate of tropical forest by the rodent fauna, while the macromammals classified it as savanna. The climate of that locality is not typical of savanna, which perhaps explains the incorrect assignment from the rodent fauna. Another possible cause of the different identified climate by the two mammal groups could be that the landscape perception scale is different in rodents and in macromammals. The former can find a greater variety of appropriate microhabitats while the

Table 4 Discriminant analysis results for 13 new localities (P_1 , probability of the highest probability climate zone; P_2 , probability of the second highest probability climate zone; =, the second highest probability climate zone is the same as the highest probability climate zone)

Climate zone	Locality	Whole faunas				Rodent faunas			
		highest probability climate zone	P_1	2nd highest probability climate zone	P_2	highest probability climate zone	P_1	2nd highest probability climate zone	P_2
VIII/IX	Ust Kamchatsk	VIII	1.000	=		IX	0.996	VIII	0.004
VI/VIII	Saskatoon	VI	0.792	VIII	0.208	VIII	0.985	VI	0.015
VI/VIII	Riga	VI	1.000	VIII	< 0.001	VI	0.999	VIII	0.001
VI/VII	Budapest	VI	1.000	VII	< 0.001	VI	1.000	VIII	< 0.001
VI	Dairen	VI	1.000	VIII	< 0.001	VI	1.000	VIII	< 0.001
IV/VI	Portland	VI	1.000	VII	< 0.001	VI	1.000	VIII	< 0.001
V	Charleston	V	1.000	=		V	1.000	=	
IV/VI	Niza	IV	0.956	VI	0.044	VI	0.999	IV	< 0.001
II/V	Kweilin	V	1.000	II	< 0.001	V	1.000	II	< 0.001
III	Smara	III	1.000	=		III	1.000	=	
II	Puerto Ayacucho	II/III	0.974	II	0.026	II	0.997	II/III	0.003
I/II	Tabou	I	1.000	=		I	1.000	=	
I	Kuala Lumpur	I	1.000	=		I	1.000	=	

Climate zone	Locality	Macromammal faunas				Whole faunas without bats			
		highest probability climate zone	P_1	2nd highest probability climate zone	P_2	highest probability climate zone	P_1	2nd highest probability climate zone	P_2
VIII/IX	Ust Kamchatsk	VIII	1.000	VI	< 0.001	VIII	1.000	VI	< 0.001
VI/VIII	Saskatoon	VI	0.890	VIII	0.110	VIII	0.745	VI	0.255
VI/VIII	Riga	VI	0.963	VIII	0.037	VI	0.999	VIII	< 0.001
VI/VII	Budapest	VI	0.998	IV	0.002	VI	1.000	VIII	< 0.001
VI	Dairen	VI	0.955	V	0.045	VI	1.000	VIII	< 0.001
IV/VI	Portland	VI	0.999	VIII	0.001	VI	1.000	VIII	< 0.001
V	Charleston	VI	0.561	V	0.424	V	1.000	=	
IV/VI	Niza	VI	0.988	IV	0.012	VI	0.795	IV	0.205
II/V	Kweilin	V	1.000	VI	< 0.001	V	1.000	=	
III	Smara	III	0.999	=	< 0.001	III	1.000	=	
II	Puerto Ayacucho	II/III	0.980	II	0.020	II/III	0.945	II	0.055
I/II	Tabou	I	1.000	=		I	1.000	=	
I	Kuala Lumpur	I	1.000	=		I	1.000	=	

macromammals have a more restricted range of habitats because of their larger body size. Perhaps for this reason the rodents are more greatly influenced by climate than large mammals, while the macromammals may be more influenced by landscape scale characteristics, that is to say, by the major habitats in an area.

A similar explanation can be determined for the classification of Charleston in the temperate climate zone (VI) using macromammals, although it actually belongs in the warm temperate climate zone (V). This incorrect classification could be due to the similarity of, and the gradual change between, the large mammal faunas from climate zones V and VI of

eastern North America. There is a relatively low number of large mammal species exclusive to the temperate evergreen forest of the south-eastern North America climatic dominion. Most of its large mammal species also inhabit the nemoral broadleaf-deciduous forest of the eastern North America climatic dominion. This similarity is more pronounced in localities near the ecotone V/VI. Therefore, relatively low values of BC V are attained in localities close to the north edge of the south-eastern North America climatic dominion.

Hence, the results shown in Table 4 indicate that it is possible to detect situations where the fauna comes from an ecotone, the boundary area between two climate zones. Another

Table 5 Bioclimatic spectra of the Eurasian rodent fossil sites used in this work. Numbers for fossil sites as in Fig. 1

Fossil site	I	II	II/III	III	IV	V	VI	VII	VIII	IX
<i>Late Pleistocene-Holocene</i>										
Barová 9–10c–10b	0.000	0.000	0.000	0.000	9.259	0.000	53.704	9.259	24.074	3.704
Barová 12	0.000	1.389	1.389	1.389	6.944	0.000	21.759	7.870	36.574	22.685
<i>Early Pleistocene</i>										
1 Quibas	2.857	22.857	2.857	2.857	29.524	2.857	6.667	19.524	10.000	0.000
2 Bagur 2	0.000	11.111	0.000	2.222	25.370	0.000	14.259	30.926	16.111	0.000
3 Mas Rambault 1	0.000	12.500	0.000	2.500	34.792	0.000	22.292	16.042	11.875	0.000
4 Les Valerots	0.000	0.000	0.000	6.667	15.000	6.250	25.417	26.458	13.958	6.250
5 Neuleiningen 5	0.000	0.000	0.000	14.444	14.444	0.000	8.889	25.556	22.778	13.889
6 Monte Peglia A	0.000	0.000	0.000	10.833	23.333	12.500	15.000	23.333	15.000	0.000
7 Chlum 6	0.000	0.000	0.000	5.614	12.807	0.000	34.737	20.702	21.579	4.561
8 Villany 5	0.893	0.893	0.000	13.750	25.060	0.893	14.643	29.226	12.560	2.083
9 Kamyk	0.000	0.625	0.625	12.625	18.458	0.000	19.292	31.792	13.458	3.125
10 Betfia 9a	1.020	1.020	0.000	7.619	8.639	1.020	22.925	40.782	14.592	2.381
11 Tiligul	1.276	1.276	0.595	13.294	22.863	2.228	13.339	35.561	9.569	0.000
12 Dodogol 1	0.000	0.000	0.000	10.667	10.667	0.000	10.667	47.333	20.667	0.000

example is that of Saskatoon, located in the ecotone between climate zones VI (temperate climate zone) and VIII (boreal climate zone). It can be observed that the highest probable climate is different depending on the group used to classify it. Using the whole fauna and the macromammals the most probable climate is VI, while using rodents and whole fauna without bats, climate VIII is identified. Furthermore, the highest probability climate (P_1 in Table 4) is usually lower than 0.90, while in situations where the locality is located in the more central parts of the dominion, the probability of the most probable climate is always close to 1.00. For those cases where the ecotone is not detected, the reason could be due to: (1) young boundaries (the boundaries were established recently) (2) the relative geographical extent of both climate zones, one of them being much larger than the other and thus the main source of taxa, or (3) one of the climates showing a higher proportion of characteristic taxa for that climate. The latter case indicates that there are climate zones in which faunas have more cosmopolitan taxa with a low proportion of typical taxa for that climate zone, while in others the proportions of these characteristic taxa may be quite high (Appendix 1) (M. Hernández Fernández & E.S. Vrba, in prep.).

Bioclimatic classification of fossil associations

Barová Cave (late Pleistocene–Holocene)

The bioclimatic spectra of both fossil rodent associations are shown in Table 5. The results obtained from the model show a change from a boreal climate in Barová 12 (the highest probability climate zone is VIII, $P_1 = 1.000$; the second highest

probability climate zone is VI, $P_2 < 0.001$) to a temperate climate in Barová 9–10c–10b (the highest probability climate zone is VI, $P_1 = 1.000$; the second highest probability climate zone is VIII, $P_2 < 0.001$). These results agree with the palynological analysis presented by Svobodová (1992), showing a change from a landscape dominated by tree genera representative of boreal coniferous forests (*Pinus*, *Picea*, *Juniperus* and *Salix*) in the lower level (layer 12) to a nemoral broadleaf-deciduous forest dominated by *Corylus* and *Betula* in the upper level (layers 9–10c–10b).

Eurasian early Pleistocene

The bioclimatic characterization of the extinct species from the early Pleistocene Eurasian sites has been carried out by studying the dental morphology of the species and comparing it with the morphology of modern taxa, assigning the extinct species to the morphologically closest living species or group of species (Hernández Fernández, 2001b; Hernández Fernández & Peláez-Campomanes, 2003). For those extinct taxa included in a phylogenetic clade in which the extant representatives all have a similar climatic distribution, we assume they had the same distribution as the extant species.

Problems derived from actualism force us to be cautious. Correlation between dental morphology and climatic ranges could be different for fossil taxa, and climatic ranges of extinct taxa could be unlike those of extant taxa. Thus we have adopted a conservative approach to the study of climatic ranges of fossil taxa. Extinct genera have been analysed as a whole for comparison with extant genera (Hernández Fernández & Peláez-Campomanes, 2003). Relatively little uncertainty is introduced when all of the species in a taxon present

Table 6 Qualitative bioclimatic analysis results for rodent faunas from the Eurasian basal early Pleistocene (P_1 , probability of the highest probability climate zone; P_2 , probability of the second highest probability climate zone)

Fossil site	Qualitative bioclimatic analysis			
	Highest probability climate zone	P_1	2nd highest probability climate zone	P_2
1 Quibas	IV	1.000	VI	< 0.001
2 Bagur 2	VII	0.561	VI	0.432
3 Mas Rambault 1	IV	1.000	VI	< 0.001
4 Les Valerots	VI	0.999	VII	< 0.001
5 Neuleiningen 5	VIII	0.486	VII	0.339
6 Monte Peglia A	VI	0.902	VII	0.097
7 Chlum 6	VI	0.999	VIII	0.001
8 Villany 5	VII	0.840	IV	0.120
9 Kamyk	VII	0.538	VI	0.462
10 Betsia 9a	VII	0.570	VI	0.430
11 Tiligul	VII	0.999	VI	0.001
12 Dodogol 1	VII	1.000	VI	< 0.001

similar bioclimatic characterization, and indeed this is often the case. However, it is sometimes necessary to assign taxa to numerous different BC. Such taxa have reduced discriminatory power, but they still can provide useful information for a global analysis to help distinguish, for example, between forests and open lands.

It can be admitted that some climatic range assignments may be over- or under-estimated. However, the intention is not to define species as key climatic indicators, thus they must not be used directly as evidence for the climate of localities that contain those taxa. This bioclimatic characterization is an important methodological step for the bioclimatic analysis. Nevertheless, the latter is robust against a limited number of errors in the assignments. The influence of small errors associated with the incorrect assignment of species is weak because the whole fauna (or the rodent fauna) is used for the climatic inference for a locality.

The obtained bioclimatic spectra of the studied fossil rodent associations are shown in the Table 5. The results of the qualitative bioclimatic analysis shown in Table 6 indicate that there is a set of localities where the model assigns them a climate with a high probability, above 90%, such as Quibas, Mas Rambault 1, Les Valerots, Monte Peglia A, Chlum 6, Tiligul and Dodogol 1, while for others the probabilities for the two more probable climates are similar, such as in Bagur 2, Neuleiningen 5, Kamyk and Betsia 9. This difference among localities could be due, as pointed out in the validation of the model, to the position of each locality within the climatic zones. Localities where the probability is high would be situated

far away from the climate zone boundaries, while those with low probabilities could be situated close to the boundary between climatic zones.

Initially examining localities classified with a high probability, we can infer that during the early Pleistocene the Mediterranean climate (IV) was established along the Mediterranean coast at least at its western part. East Europe and Central Asia at that time showed a typical steppe climate (VII) as indicated by the results obtained for Tiligul (Ukraine) and Dodogol 1 (Russia). Finally, a third group of localities indicate the presence of a broadleaf-deciduous forest biome (VI). The localities of climate zone VI are Les Valerots (France), Monte Peglia A (Italy) and Chlum 6 (Czech Republic). So far, the results obtained are similar to what we observe in present day climatic distribution (Allué Andrade, 1990). The differences arise when we study the localities classified with low probabilities. All those localities but Neuleiningen 5 (Germany) have steppe (VII) as the most probable climate, although the probability of the broadleaf-deciduous forest biome (VI) is only slightly lower. This could be interpreted as indicative of more open and drier conditions in central Europe than nowadays, with the steppe penetrating more deeply into central Europe from the East. With the few localities studied here it is not possible to establish if the steppe zoniobiome formed a continuous band reaching Spain (Bagur 2), or if there were just small patches scattered through a more extended zoniobiome VI. The presence nearby of areas of climatic zone VI could be the reason for the high probability of this climate as the second probable climatic zone. Neuleiningen 5 has a very specific climatic classification. The most probable climate zone is boreal (VIII), with climatic zone VII as the next most probable. One interpretation could be that the boreal climate zone, at that time, occupied a small patch related to mountain ranges, as can be observed in the present day. However, the high proportion of BC VII on the bioclimatic spectrum of this locality could indicate that the steppe zoniobiome was also present in western Germany during the Early Pleistocene, indicating boundary conditions between steppe and taiga (VII/VIII).

CONCLUSIONS

The results presented in this work provide a preliminary example of the potential that bioclimatic analysis has as a tool for palaeoclimatic inference. The application of the model to fossil mammal associations from large areas and with similar ages offers the possibility to construct palaeoclimatic maps when combined with palaeogeographical reconstructions. It also offers the potential to study climatic evolution at different scales in time and space. Finally, the method offers the opportunity to standardize data coming from vertebrate palaeontology for use in the construction and evaluation of palaeoclimatic models.

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SUPPLEMENTARY MATERIAL

The following material is available from <http://www.blackwellpublishing.com/products/journals/suppmat/GEB/GEB057/GEB057sm.htm>

Appendix 1.1 Whole mammal faunal bioclimatic spectra of the localities.

Appendix 1.2 Rodentia faunal bioclimatic spectra of the localities.

Appendix 1.3 Large mammal faunal bioclimatic spectra of the localities.

Appendix 1.4 Whole mammal without Chiroptera faunal bioclimatic spectra of the localities.

Appendix 2.1 Coefficients for discriminant functions calculated from whole mammal faunal bioclimatic components and centroids, for each discriminant function, for every locality's biome group.

Appendix 2.2 Coefficients for discriminant functions calculated from rodent faunal bioclimatic components and centroids, for each discriminant function, for every locality's biome group.

Appendix 2.3 Coefficients for discriminant functions calculated from large mammal faunal bioclimatic components and centroids, for each discriminant function, for every locality's biome group.

Appendix 2.4 Coefficients for discriminant functions calculated from whole mammal without Chiroptera faunal bioclimatic components and centroids, for each discriminant function, for every locality's biome group.

Appendix 3.1 Whole mammal faunal bioclimatic spectra of the 13 new localities used for the validation of the bioclimatic model.

Appendix 3.2 Rodentia faunal bioclimatic spectra of the 13 new localities used for the validation of the bioclimatic model.

Appendix 3.3 Large mammal faunal bioclimatic spectra of the 13 new localities used for the validation of the bioclimatic model.

Appendix 3.4 Whole mammal without Chiroptera faunal bioclimatic spectra of the 13 new localities used for the validation of the bioclimatic model.

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BIOSKETCHES

Manuel Hernández Fernández has a broad interest in the area of evolutionary biology, encompassing 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 the structure of Cenozoic mammal communities integrating evolutionary and community ecology theories in studies with a multispecies perspective. His studies also provide extensive data sets for subsequent analyses of the evolution of mammalian lineages.

Data associated to

HERNÁNDEZ FERNÁNDEZ, M. & PELÁEZ-CAMPOMANES, P. (2003) The bioclimatic model: a method to palaeoclimatic qualitative inference based on mammal associations. *Global Ecology and Biogeography*, 12 (6), 507-517.

Appendix 1.1

Whole mammal faunal bioclimatic spectra of the localities. Each column represents a bioclimatic component (see Table 1), and BC_i values (BC_i = $\sum CR_i / 100/S$) are shown for each locality.

Locality	I	II	II/III	III	IV	V	VI	VII	VIII	IX
Barrow	0.000	1.209	1.209	1.890	3.794	2.162	10.540	7.366	31.969	39.860
Port Harrison	0.000	0.794	0.794	1.814	4.671	3.243	15.385	13.005	22.528	37.766
Malye-Karmaerly	0.000	1.587	1.587	3.628	3.628	3.628	3.628	3.628	25.057	53.628
Mys Chelyuskin	0.000	1.235	1.235	1.235	1.235	1.235	4.938	1.235	32.716	54.938
Mys Schmidta	0.000	0.694	0.694	0.694	1.944	0.694	7.674	3.507	42.049	42.049
Fairbanks	0.000	0.705	2.584	2.055	4.416	3.463	22.101	9.601	45.712	9.363
Fort Smith	0.605	1.209	4.293	3.840	5.523	4.849	22.808	12.887	37.944	6.041
Kajaani	0.726	1.043	0.635	1.043	8.166	2.737	25.546	9.594	41.737	8.773
Serov	0.518	0.745	0.454	0.745	7.873	2.465	26.241	10.764	43.928	6.267
Erbogachen	0.876	1.259	0.766	0.766	4.822	2.121	12.293	7.121	55.397	14.579
Rapid City	1.139	3.505	8.216	8.641	9.934	6.575	19.718	31.769	8.907	1.596
Puerto Santa Cruz	2.105	4.142	14.050	7.661	9.883	11.272	15.849	34.420	0.617	0.000
Fort Schevchenko	1.675	2.215	1.506	5.052	16.491	2.342	8.619	58.973	2.160	0.966
Urumchi	0.926	1.296	1.296	2.963	9.574	1.963	8.741	65.963	5.407	1.870
Paotou	0.236	0.777	1.202	2.925	7.322	2.038	8.386	72.570	3.578	0.966
Prince Rupert	0.309	1.080	4.837	3.911	6.411	4.698	28.726	15.763	29.559	4.707
Cleveland	1.858	4.685	5.093	4.665	5.982	11.677	33.470	14.304	16.121	2.146
Evangelistas	1.458	4.887	11.554	8.284	11.169	12.900	30.876	17.964	0.908	0.000
Vlissingen	0.968	1.587	1.239	1.587	20.066	3.643	41.814	10.368	15.710	3.018
Tsingtao	5.474	6.821	3.862	1.539	8.314	16.193	37.658	14.952	4.418	0.770
New Orleans	5.451	9.355	6.650	5.194	5.021	37.883	17.542	8.641	3.938	0.325
Puerto Montt	1.723	5.245	7.291	4.942	17.367	42.518	13.308	6.533	1.073	0.000
Corrientes	17.391	32.869	18.115	1.612	1.694	25.219	1.284	1.612	0.205	0.000
Foochow	16.255	22.343	5.595	1.038	3.873	33.804	12.685	2.340	1.916	0.152
Kagoshima	5.659	6.770	2.663	1.687	4.627	36.085	34.085	3.020	4.270	1.130
Fresno	2.016	5.462	11.794	12.429	29.435	4.620	13.306	13.632	6.423	0.882
Santiago de Chile	2.298	4.690	12.432	12.217	37.701	13.131	10.251	6.518	0.762	0.000
Sanlucar de Barrameda	2.310	4.430	3.372	4.113	39.896	6.303	24.266	9.690	4.610	1.009
Aleppo	2.026	5.589	6.517	8.739	41.271	5.354	15.299	11.684	2.763	0.757
Esfahan	0.577	3.276	4.601	10.608	44.282	3.979	11.668	16.912	3.065	1.032
Phoenix	2.772	9.240	21.504	27.371	10.326	4.266	7.427	13.490	3.452	0.152
Arica	5.177	5.177	15.025	40.783	18.056	8.207	2.146	4.419	1.010	0.000
Assuan	2.676	13.027	16.360	37.127	17.451	5.831	3.146	2.584	1.400	0.397
Mascate	2.450	11.919	13.368	34.279	22.685	5.293	2.830	4.486	1.587	1.104
Lüderitz Bay	5.537	13.146	21.003	37.146	14.527	8.027	0.408	0.204	0.000	0.000
Las Piedras	30.769	32.491	28.788	1.170	0.768	4.541	0.521	0.775	0.175	0.000
Catamarca	7.615	18.742	44.514	5.594	3.773	11.581	2.088	5.655	0.437	0.000
Zinder	6.485	27.304	37.145	12.637	7.510	8.510	0.272	0.136	0.000	0.000
Voi	8.378	36.424	29.066	10.615	6.434	8.832	0.167	0.084	0.000	0.000
Jaipur	14.233	29.296	33.831	10.802	5.130	3.904	1.723	1.082	0.000	0.000
Roque Saenz Peña	15.817	33.237	24.583	2.660	1.891	18.686	1.250	1.635	0.240	0.000
Ziguinchor	16.192	39.272	21.434	8.928	5.980	7.839	0.236	0.118	0.000	0.000
Moundou	11.124	39.671	24.726	8.432	6.379	9.313	0.236	0.118	0.000	0.000
Mtwara	11.150	46.505	19.326	7.148	5.198	10.394	0.187	0.093	0.000	0.000
Patna	17.398	38.922	28.207	6.551	3.660	3.303	1.469	0.490	0.000	0.000
Tumaco	44.932	28.115	19.003	1.137	0.746	4.926	0.363	0.609	0.170	0.000
Paramaribo	46.245	29.179	18.401	0.686	0.361	4.488	0.227	0.347	0.067	0.000
Kribi	69.971	17.420	5.558	2.360	1.799	2.819	0.073	0.000	0.000	0.000
Yangambi	65.496	19.607	5.950	2.774	2.274	3.820	0.079	0.000	0.000	0.000
Medan	69.883	20.111	5.002	0.612	0.522	2.588	0.990	0.196	0.098	0.000

Appendix 1.2

Rodentia faunal bioclimatic spectra of the localities. Each column represents a bioclimatic component (see Table 1), and BC_i values ($BC_i = \sum CRI_i / 100/S$) are shown for each locality.

Locality	I	II	II/III	III	IV	V	VI	VII	VIII	IX
Barrow	0,000	0,000	0,000	0,000	0,000	0,000	6,667	0,000	46,667	46,667
Port Harrison	0,000	0,000	0,000	0,000	0,000	0,000	22,222	22,222	22,222	33,333
Malye-Karmaerly	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	25,000	75,000
Mys Chelyuskin	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	25,000	75,000
Mys Schmidta	0,000	0,000	0,000	0,000	0,000	0,000	6,667	0,000	46,667	46,667
Fairbanks	0,000	0,000	1,333	1,333	1,333	3,000	24,333	8,778	51,000	8,889
Fort Smith	0,000	0,000	2,619	2,619	2,619	3,214	23,690	16,548	48,690	0,000
Kajaani	1,010	1,010	1,010	1,010	8,586	3,283	29,798	3,283	47,980	3,030
Serov	0,654	0,654	0,654	0,654	5,556	2,124	27,124	7,026	53,595	1,961
Erbogachen	1,389	1,389	1,389	1,389	8,681	1,389	19,097	4,514	56,597	4,167
Rapid City	0,000	0,909	6,136	5,227	3,712	4,470	22,955	44,924	11,667	0,000
Santa Cruz	0,000	0,000	13,542	7,292	7,292	4,167	16,667	51,042	0,000	0,000
Fort Schevchenko	0,505	0,505	0,505	2,020	10,354	0,505	4,293	80,808	0,505	0,000
Urumchi	1,010	1,010	1,010	1,010	5,556	1,010	1,010	87,374	1,010	0,000
Paotou	0,529	0,529	0,529	0,529	0,529	0,529	0,529	95,767	0,529	0,000
Prince Rupert	0,000	0,000	2,821	2,821	4,744	3,462	30,000	18,462	37,692	0,000
Cleveland	0,000	3,137	3,333	2,157	2,157	13,627	42,255	13,824	19,510	0,000
Evangelistas	0,000	1,818	11,667	5,303	8,333	7,879	44,242	20,758	0,000	0,000
Vlissingen	2,116	2,116	2,116	2,116	13,228	4,200	45,172	3,009	23,148	2,778
Tsingtao	1,389	5,556	1,389	1,389	4,514	8,681	46,181	26,389	4,514	0,000
New Orleans	1,538	6,667	4,103	4,103	1,538	52,436	20,128	6,026	3,462	0,000
Puerto Montt	0,000	2,500	5,625	4,167	15,625	55,625	13,958	2,500	0,000	0,000
Corrientes	7,738	42,500	15,119	0,000	0,000	31,786	1,429	1,429	0,000	0,000
Foochow	11,788	28,455	2,965	2,965	2,965	37,278	10,808	0,654	2,124	0,000
Kagoshima	4,894	2,116	2,116	2,116	4,200	40,311	36,144	0,926	7,176	0,000
Fresno	0,000	4,444	8,222	8,222	47,333	1,333	14,000	11,778	4,667	0,000
Santiago de Chile	0,000	0,000	6,944	7,639	61,111	10,417	11,806	2,083	0,000	0,000
Sanlucar de Barrameda	2,822	2,822	2,822	2,822	48,192	5,600	25,970	1,235	7,716	0,000
Aleppo	1,270	2,270	2,270	7,270	55,603	2,520	17,103	8,639	3,056	0,000
Esfahan	0,585	1,637	4,708	16,111	50,760	0,585	8,918	14,795	1,901	0,000
Phoenix	0,000	4,808	21,859	41,731	4,231	1,731	6,603	15,897	3,141	0,000
Arica	0,000	0,000	25,000	36,111	19,444	11,111	0,000	8,333	0,000	0,000
Asswan	3,243	6,814	13,957	37,766	25,266	3,600	3,600	3,175	2,579	0,000
Mascate	5,079	5,079	11,746	31,746	31,746	5,079	5,079	2,222	2,222	0,000
Lüderitz Bay	1,754	8,246	17,018	56,491	12,632	3,860	0,000	0,000	0,000	0,000
Las Piedras	26,667	26,667	46,667	0,000	0,000	0,000	0,000	0,000	0,000	0,000
Catamarca	1,471	16,373	62,451	4,902	0,000	7,549	1,176	6,078	0,000	0,000
Zinder	3,684	29,123	54,561	6,316	5,439	0,877	0,000	0,000	0,000	0,000
Voi	10,889	44,074	24,074	8,630	5,556	6,778	0,000	0,000	0,000	0,000
Jaipur	4,841	25,619	36,175	20,619	7,841	0,952	0,952	3,000	0,000	0,000
Roque Saenz Peña	2,500	49,500	24,500	0,000	0,000	19,500	2,000	2,000	0,000	0,000
Ziguinchor	21,923	48,846	22,564	2,051	2,051	2,564	0,000	0,000	0,000	0,000
Moundou	18,986	43,261	23,696	2,319	4,855	6,884	0,000	0,000	0,000	0,000
Mtwarra	16,222	52,833	12,833	3,556	5,056	9,500	0,000	0,000	0,000	0,000
Patna	6,052	40,357	32,024	12,579	4,940	1,190	1,190	1,667	0,000	0,000
Tumaco	74,306	15,972	7,639	0,000	0,000	2,083	0,000	0,000	0,000	0,000
Paramaribo	68,860	21,491	8,333	0,000	0,000	1,316	0,000	0,000	0,000	0,000
Kribi	80,833	13,526	1,667	1,026	1,026	1,923	0,000	0,000	0,000	0,000
Yangambi	68,295	19,922	3,643	1,628	2,093	4,419	0,000	0,000	0,000	0,000
Medan	84,620	11,647	0,386	0,386	0,386	2,188	0,386	0,000	0,000	0,000

Appendix 1.3

Large mammal faunal bioclimatic spectra of the localities. Each column represents a bioclimatic component (see Table 1), and BC_i values ($BC_i = \sum CRI_i / 100/S$) are shown for each locality.

Locality	I	II	II/III	III	IV	V	VI	VII	VIII	IX
Barrow	0,000	1,954	1,954	3,053	6,129	3,492	12,540	9,976	27,924	32,979
Port Harrison	0,000	1,111	1,111	2,540	6,540	4,540	14,873	11,540	24,873	32,873
Malye-Karmaerly	0,000	2,222	2,222	5,079	5,079	5,079	5,079	5,079	25,079	45,079
Mys Chelyuskin	0,000	2,222	2,222	2,222	2,222	2,222	8,889	2,222	28,889	48,889
Mys Schmidta	0,000	1,587	1,587	1,587	4,444	1,587	12,778	8,016	34,206	34,206
Fairbanks	0,000	1,693	2,646	3,598	9,265	5,312	18,153	12,598	34,820	11,915
Fort Smith	1,209	2,419	4,573	5,253	8,621	6,875	19,221	12,872	28,065	10,892
Kajaani	1,099	1,954	0,855	1,954	8,053	4,591	20,232	13,822	35,617	11,825
Serov	0,840	1,494	0,654	1,494	9,099	4,981	24,785	16,942	33,609	6,102
Erbogachen	1,190	2,116	0,926	0,926	5,866	4,200	16,978	14,200	41,978	11,620
Rapid City	2,016	3,603	8,079	10,784	14,946	8,013	15,517	21,517	11,375	4,149
Santa Cruz	1,389	5,972	14,722	6,597	11,597	17,847	17,431	23,056	1,389	0,000
Fort Schevchenko	2,286	3,979	3,979	8,423	17,042	4,931	11,265	39,042	6,026	3,026
Urumchi	1,111	1,852	1,852	2,963	12,852	3,185	13,407	52,296	6,741	3,741
Paotou	0,000	1,411	1,411	4,056	12,297	3,316	12,297	55,816	6,874	2,522
Prince Rupert	0,794	1,587	3,798	3,798	8,441	5,465	25,108	12,012	28,679	10,317
Cleveland	2,859	4,013	7,206	7,855	11,448	9,024	19,295	14,370	19,214	4,715
Evangelistas	1,010	6,162	12,071	10,707	11,465	16,010	23,434	18,131	1,010	0,000
Vlissingen	1,020	2,834	1,814	2,834	20,402	5,283	29,331	15,045	16,406	5,028
Tsingtao	9,968	10,709	6,423	2,646	8,661	21,328	22,995	8,265	7,312	1,693
New Orleans	8,082	9,034	11,098	8,161	9,876	17,495	15,828	12,495	6,979	0,952
Puerto Montt	1,389	7,014	9,514	4,514	23,056	27,222	15,347	10,556	1,389	0,000
Corrientes	19,298	33,947	18,158	0,000	2,368	21,667	1,754	2,807	0,000	0,000
Foochow	15,817	16,188	6,823	0,847	3,021	38,243	13,521	2,823	2,347	0,370
Kagoshima	5,844	6,854	1,010	2,309	5,426	28,608	30,426	7,698	7,698	4,127
Fresno	2,558	5,378	10,516	12,320	17,496	8,548	14,551	16,180	9,946	2,506
Santiago de Chile	1,111	7,278	16,278	9,778	21,278	17,611	11,778	13,778	1,111	0,000
Sanlucar de Barrameda	2,041	7,426	6,406	6,406	28,566	6,304	17,851	14,280	7,477	3,243
Aleppo	3,697	7,838	6,998	8,959	31,130	7,208	10,640	14,701	6,158	2,670
Esfahan	1,099	4,591	4,591	8,254	40,818	7,228	9,792	12,540	7,595	3,492
Phoenix	6,457	12,428	16,865	15,123	13,488	7,547	8,564	13,001	6,021	0,505
Arica	11,111	11,111	11,111	11,111	11,111	11,111	11,111	11,111	11,111	0,000
Asswan	3,810	9,841	9,841	44,762	11,429	9,206	4,762	3,175	1,587	1,587
Mascate	1,786	8,800	8,800	33,502	21,002	7,460	4,960	7,341	3,175	3,175
Lüderitz Bay	2,585	12,075	27,948	26,995	17,472	10,884	1,361	0,680	0,000	0,000
Las Piedras	30,233	33,358	20,858	1,587	0,694	9,400	1,587	1,587	0,694	0,000
Catamarca	6,725	18,216	43,216	2,515	5,146	11,462	3,567	8,567	0,585	0,000
Zinder	4,984	25,271	30,952	15,081	9,286	13,452	0,649	0,325	0,000	0,000
Voi	4,004	31,317	31,190	12,478	8,286	12,074	0,433	0,216	0,000	0,000
Jaipur	14,753	31,777	29,853	6,291	5,559	7,482	3,187	1,099	0,000	0,000
Roque Saenz Peña	19,048	33,651	25,714	0,952	0,952	16,825	0,952	1,905	0,000	0,000
Ziguinchor	15,275	35,325	19,460	8,530	8,338	12,248	0,549	0,275	0,000	0,000
Moundou	7,242	35,387	23,755	9,137	8,929	14,658	0,595	0,298	0,000	0,000
Mtwara	6,511	44,171	18,165	8,366	7,188	14,860	0,493	0,246	0,000	0,000
Patna	11,913	42,092	27,806	4,141	4,651	6,437	2,449	0,510	0,000	0,000
Tumaco	51,249	27,175	12,360	0,941	0,412	5,570	0,941	0,941	0,412	0,000
Paramaribo	53,519	24,572	12,291	0,668	0,292	7,028	0,668	0,668	0,292	0,000
Kribi	75,313	12,568	3,581	1,326	2,208	4,725	0,280	0,000	0,000	0,000
Yangambi	70,319	14,719	4,552	1,752	2,652	5,719	0,286	0,000	0,000	0,000
Medan	64,620	22,312	4,890	0,000	0,870	4,364	2,120	0,549	0,275	0,000

Appendix 1.4

Whole mammal without Chiroptera faunal bioclimatic spectra of the localities. Each column represents a bioclimatic component (see Table 1), and BC_i values ($BC_i = \sum CRI_i / 100/S$) are shown for each locality.

Locality	I	II	II/III	III	IV	V	VI	VII	VIII	IX
Barrow	0,000	1,209	1,209	1,890	3,794	2,162	10,540	7,366	31,969	39,860
Port Harrison	0,000	0,794	0,794	1,814	4,671	3,243	15,385	13,005	22,528	37,766
Malye-Karmaerly	0,000	1,587	1,587	3,628	3,628	3,628	3,628	3,628	25,057	53,628
Mys Chelyuskin	0,000	1,235	1,235	1,235	1,235	1,235	4,938	1,235	32,716	54,938
Mys Schmidta	0,000	0,694	0,694	0,694	1,944	0,694	7,674	3,507	42,049	42,049
Fairbanks	0,000	0,705	2,584	2,055	4,416	3,463	22,101	9,601	45,712	9,363
Fort Smith	0,619	1,239	4,050	3,585	5,310	4,619	23,016	12,853	38,521	6,189
Kajaani	0,794	1,141	0,694	1,141	6,848	2,994	24,816	8,410	43,566	9,596
Serov	0,564	0,811	0,494	0,811	7,092	2,684	25,240	10,240	45,240	6,824
Erbogachen	0,876	1,259	0,766	0,766	4,822	2,121	12,293	7,121	55,397	14,579
Rapid City	0,933	2,872	7,537	8,048	9,358	6,364	19,221	33,727	10,019	1,921
Santa Cruz	0,694	2,986	14,132	6,944	9,444	11,007	17,049	37,049	0,694	0,000
Fort Schevchenko	1,875	2,479	1,686	5,654	13,891	2,026	7,462	61,430	2,417	1,081
Urumchi	0,958	1,341	1,341	3,065	9,904	2,031	9,042	64,789	5,594	1,935
Paotou	0,253	0,830	0,830	2,670	6,798	1,609	7,177	75,738	3,065	1,032
Prince Rupert	0,358	0,717	3,973	2,898	5,801	3,920	29,027	13,973	33,866	5,466
Cleveland	1,758	4,233	4,704	4,190	5,771	10,671	33,423	14,090	18,587	2,575
Evangelistas	0,505	3,990	11,869	8,005	9,899	11,944	33,838	19,444	0,505	0,000
Vlissingen	1,203	1,972	1,539	1,972	17,102	3,769	41,092	9,093	18,509	3,749
Tsingtao	5,949	7,596	3,980	1,881	7,384	14,421	36,952	15,497	5,400	0,941
New Orleans	4,889	8,594	7,053	5,169	4,945	36,689	17,718	10,120	4,402	0,420
Puerto Montt	0,617	4,228	6,728	3,858	17,191	47,932	13,025	5,802	0,617	0,000
Corrientes	15,043	36,795	17,137	0,513	1,154	26,111	1,368	1,880	0,000	0,000
Foochow	14,582	22,167	5,546	1,458	2,712	38,097	11,334	1,842	2,048	0,214
Kagoshima	5,212	4,471	2,328	1,693	3,669	36,614	35,614	3,193	5,693	1,513
Fresno	1,246	4,329	9,568	10,447	33,139	4,677	13,756	13,695	7,922	1,221
Santiago de Chile	0,483	3,164	12,150	9,686	42,585	13,092	11,280	7,077	0,483	0,000
Sanlucar de Barrameda	2,910	5,423	3,836	3,836	43,899	4,622	21,122	7,034	5,804	1,513
Aleppo	2,101	4,730	4,390	8,358	43,125	4,594	15,229	12,445	3,947	1,081
Esfahan	0,726	2,594	4,261	12,764	46,526	3,002	9,907	15,070	3,853	1,297
Phoenix	2,786	7,812	20,380	29,759	8,956	4,138	7,060	14,693	4,199	0,218
Arica	2,222	2,222	23,889	30,556	20,556	8,889	2,222	7,222	2,222	0,000
Asswan	3,187	8,159	12,159	42,063	19,063	6,130	3,730	2,921	2,016	0,571
Mascate	2,480	7,237	9,320	36,255	23,755	6,567	4,067	6,448	2,282	1,587
Lüderitz Bay	2,867	10,422	21,880	41,255	15,561	7,123	0,595	0,298	0,000	0,000
Las Piedras	28,489	31,405	27,239	1,058	0,463	7,100	1,892	1,892	0,463	0,000
Catamarca	4,430	17,379	52,208	3,875	2,507	10,242	2,251	6,823	0,285	0,000
Zinder	4,635	26,137	41,248	11,492	7,092	8,825	0,381	0,190	0,000	0,000
Voi	6,957	36,386	30,271	10,136	6,588	9,316	0,230	0,115	0,000	0,000
Jaipur	10,642	27,764	35,554	12,091	5,699	4,539	2,112	1,599	0,000	0,000
Roque Saenz Peña	13,824	37,647	25,392	1,176	0,588	18,431	1,176	1,765	0,000	0,000
Ziguinchor	16,539	40,459	21,312	6,610	5,796	8,773	0,340	0,170	0,000	0,000
Moundou	10,533	39,607	24,503	6,878	6,753	11,190	0,357	0,179	0,000	0,000
Mtwara	10,226	47,386	18,302	6,169	5,686	11,802	0,286	0,143	0,000	0,000
Patna	10,465	41,179	29,274	7,149	4,512	4,632	1,973	0,816	0,000	0,000
Tumaco	59,362	23,648	10,722	0,518	0,227	4,260	0,518	0,518	0,227	0,000
Paramaribo	57,972	25,619	10,177	0,373	0,163	4,785	0,373	0,373	0,163	0,000
Kribi	77,617	13,683	3,232	1,196	1,360	2,795	0,117	0,000	0,000	0,000
Yangambi	69,979	17,698	4,467	1,602	1,953	4,175	0,125	0,000	0,000	0,000
Medan	72,307	18,543	3,246	0,154	0,640	3,310	1,339	0,307	0,154	0,000

Appendix 2.1

Coefficients for discriminant functions calculated from whole mammal faunal bioclimatic components and centroids, for each discriminant function, for every localities biome group (climates with higher correlation with the BC corresponding for a function are pointed in bold).

<i>Coefficients</i>	Func 1	Func 2	Func 3	Func 4	Func 5	Func 6	Func 7	Func 8	Func 9
BC I	0,367	-0,009	0,078	0,056	0,182	0,033	-0,059	0,046	0,028
BC II	0,335	-0,059	0,192	-0,063	0,047	0,080	0,083	0,049	-0,153
BC II/III	0,350	0,054	0,093	0,095	0,102	0,063	0,129	0,030	0,167
BC III	0,313	0,285	0,110	-0,219	0,168	0,079	-0,063	0,029	-0,039
BC IV	0,362	0,052	0,194	0,217	-0,022	0,120	-0,029	0,095	-0,005
BC V	0,343	-0,179	0,264	-0,112	0,022	0,065	-0,092	0,118	0,057
BC VI	0,251	0,047	0,202	-0,005	0,146	0,040	0,045	-0,122	-0,023
BC VII	0,290	0,051	0,206	-0,013	0,114	-0,058	0,038	0,088	-0,003
BC VIII	0,301	-0,006	0,264	0,009	0,201	0,165	0,027	0,150	0,012
Constante	-30,435	-1,898	-16,726	-0,303	-9,873	-6,037	-1,535	-4,790	-0,223
<i>Centroids</i>	Func 1	Func 2	Func 3	Func 4	Func 5	Func 6	Func 7	Func 8	Func 9
I	5,100	-3,327	-5,206	2,112	3,487	-1,063	-2,186	-0,049	-0,149
II	3,841	-2,641	-1,328	-1,323	-1,580	0,826	2,539	0,268	-1,675
II/III	3,861	-0,498	-2,595	0,307	-0,753	0,562	3,305	-0,128	1,569
III	2,507	8,594	-1,956	-4,009	0,115	1,312	-1,548	0,050	0,003
IV	1,983	3,043	1,697	5,550	-3,388	1,201	-1,366	0,222	-0,110
V	2,163	-6,638	3,247	-3,230	-2,266	0,057	-2,427	0,288	0,547
VI	-1,247	0,326	3,235	0,120	1,258	-0,389	0,376	-3,000	-0,170
VII	-0,500	2,690	2,683	-0,033	0,406	-5,359	0,849	1,042	-0,049
VIII	-3,550	-0,412	4,218	0,607	4,036	2,970	0,739	1,302	0,037
IX	-14,157	-1,137	-3,994	-0,102	-1,315	-0,118	-0,282	0,005	-0,004

Appendix 2.2

Coefficients for discriminant functions calculated from rodent faunal bioclimatic components and centroids, for each discriminant function, for every localities biome group (climates with higher correlation with the BC corresponding for a function are pointed in bold).

<i>Coefficients</i>	Func 1	Func 2	Func 3	Func 4	Func 5	Func 6	Func 7	Func 8	Func 9
BC I	0,270	-0,003	-0,085	0,082	0,019	0,000	0,091	0,041	-0,011
BC II	0,109	0,092	0,105	0,047	0,073	-0,017	0,080	0,031	0,092
BC II/III	0,150	0,112	0,035	0,004	0,091	0,016	0,096	0,051	-0,092
BC III	0,166	0,142	-0,028	0,017	-0,095	0,116	0,133	0,014	0,046
BC IV	0,064	0,214	-0,053	0,085	0,030	-0,088	0,046	0,074	0,000
BC V	0,230	0,025	0,145	0,137	-0,079	0,008	0,049	0,091	-0,032
BC VI	0,020	0,055	0,024	0,099	0,053	-0,014	0,124	-0,078	0,005
BC VII	0,051	0,071	-0,005	0,113	0,060	0,064	0,057	0,060	0,007
BC VIII	0,034	0,030	0,013	0,053	0,015	-0,004	0,158	0,128	0,004
Constante	-10,749	-7,541	-1,485	-6,660	-2,593	-0,543	-8,725	-4,180	0,-240
<i>Centroids</i>	Func 1	Func 2	Func 3	Func 4	Func 5	Func 6	Func 7	Func 8	Func 9
I	12,751	-5,459	-5,740	0,724	0,235	-0,708	0,078	-0,072	0,012
II	4,152	0,932	3,991	-1,693	2,367	-0,692	-0,346	0,012	1,768
II/III	4,057	2,250	2,282	-3,232	2,949	0,433	0,256	0,123	-1,564
III	2,572	5,471	-1,831	-2,174	-3,760	3,120	1,071	-0,296	0,324
IV	-3,001	7,331	-3,227	1,308	-0,177	-3,906	-1,362	0,279	-0,096
V	4,627	-1,715	6,381	2,983	-3,227	-0,573	-1,051	0,391	-0,465
VI	-4,790	-0,884	0,666	2,032	0,767	-0,284	1,775	-2,694	-0,104
VII	-4,619	0,343	-1,498	3,430	2,351	3,916	-1,806	0,700	0,071
VIII	-6,488	-2,432	-0,130	0,332	-0,038	-0,829	3,750	1,768	0,079
IX	-9,261	-5,836	-0,895	-3,710	-1,466	-0,476	-2,366	-0,211	-0,025

Appendix 2.3

Coefficients for discriminant functions calculated from large mammal faunal bioclimatic components and centroids, for each discriminant function, for every localities biome group (climates with higher correlation with the BC corresponding for a function are pointed in bold).

<i>Coefficients</i>	Func 1	Func 2	Func 3	Func 4	Func 5	Func 6	Func 7	Func 8	Func 9
BC I	0,342	0,094	0,162	0,147	0,030	0,027	-0,001	0,040	0,040
BC II	0,267	0,240	-0,047	0,164	-0,020	0,070	-0,037	0,080	-0,114
BC II/III	0,282	0,178	0,031	0,154	0,113	0,047	-0,042	-0,049	0,151
BC III	0,287	0,226	0,109	0,156	0,150	0,019	0,125	0,036	-0,041
BC IV	0,271	0,240	0,095	0,107	0,012	-0,102	-0,120	0,122	0,038
BC V	0,174	0,299	0,090	0,151	-0,114	0,019	0,122	0,160	0,116
BC VI	0,248	0,213	0,093	0,152	-0,016	0,006	-0,049	-0,190	-0,095
BC VII	0,219	0,256	0,116	0,049	0,042	0,146	0,012	0,085	0,027
BC VIII	0,207	0,291	0,128	0,351	0,075	0,072	0,005	0,169	0,079
Constante	-24,002	-21,138	-7,661	-14,825	-2,359	-3,328	0,412	-4,630	-1,959
<i>Centroids</i>	Func 1	Func 2	Func 3	Func 4	Func 5	Func 6	Func 7	Func 8	Func 9
I	6,995	-6,486	2,704	0,252	-0,497	0,217	-0,107	0,116	-0,066
II	2,825	0,363	-4,206	0,486	-0,636	0,613	-0,370	0,688	-0,973
II/III	3,080	-0,305	-3,208	0,272	1,032	0,577	-0,439	-0,840	1,097
III	2,046	1,284	0,179	-0,098	2,861	-1,177	1,814	0,121	-0,237
IV	0,467	2,054	0,813	-1,331	0,096	-2,255	-1,685	0,617	0,185
V	0,063	1,967	-0,115	-0,079	-3,417	-0,491	1,420	0,261	0,502
VI	-1,013	1,874	1,240	0,718	-0,707	-0,325	-0,337	-1,859	-0,668
VII	-0,819	2,565	1,836	-3,270	0,468	2,238	-0,076	0,203	-0,026
VIII	-3,530	1,831	1,904	3,912	0,633	0,924	-0,382	0,694	0,211
IX	-10,112	-5,146	-1,146	-0,862	0,167	-0,320	0,161	-0,001	-0,025

Appendix 2.4

Coefficients for discriminant functions calculated from whole mammal without Chiroptera faunal bioclimatic components and centroids, for each discriminant function, for every localities biome group (climates with higher correlation with the BC corresponding for a function are pointed in bold).

<i>Coefficients</i>	Func 1	Func 2	Func 3	Func 4	Func 5	Func 6	Func 7	Func 8	Func 9
BC I	0,408	0,026	0,021	0,044	0,173	0,081	0,001	0,049	0,022
BC II	0,257	0,221	0,191	0,015	0,032	0,094	0,056	0,044	-0,127
BC II/III	0,330	0,160	0,033	0,033	0,038	0,120	0,110	0,044	0,134
BC III	0,347	0,208	-0,093	-0,258	0,176	0,105	-0,039	0,023	-0,053
BC IV	0,320	0,251	-0,007	0,227	0,019	0,086	-0,058	0,090	0,003
BC V	0,276	0,169	0,287	-0,070	0,134	0,036	-0,125	0,114	0,045
BC VI	0,218	0,198	0,092	0,039	0,149	0,105	0,060	-0,113	-0,017
BC VII	0,252	0,211	0,072	0,001	0,166	-0,006	0,075	0,085	-0,004
BC VIII	0,274	0,216	0,115	0,012	0,192	0,210	0,015	0,154	0,006
Constante	-27,771	-17,312	-7,844	-1,399	-10,920	-8,709	-1,554	-4,984	-0,046
<i>Centroids</i>	Func 1	Func 2	Func 3	Func 4	Func 5	Func 6	Func 7	Func 8	Func 9
I	8,775	-8,960	-1,300	1,839	2,408	-0,219	-0,200	-0,027	-0,130
II	2,514	0,415	3,777	-0,573	-3,804	0,489	1,626	0,254	-1,649
II/III	3,409	-0,064	0,765	-0,750	-3,601	0,920	2,806	-0,022	1,579
III	3,850	2,640	-6,398	-6,166	-0,008	0,579	-1,733	-0,124	-0,185
IV	1,449	4,239	-3,653	6,389	-2,297	-0,291	-2,380	0,239	0,051
V	0,327	0,455	7,934	-1,810	0,380	-1,424	-3,602	0,239	0,493
VI	-2,111	2,270	1,231	0,951	2,327	0,723	,798	-2,914	-0,112
VII	-1,311	3,166	-0,981	-0,026	2,928	-4,398	2,621	0,882	-0,045
VIII	-3,766	1,669	1,053	0,728	3,690	4,218	0,571	1,503	0,007
IX	-13,137	-5,829	-2,429	-0,582	-2,024	-0,598	-0,507	-0,030	-0,009

Appendix 3.1

Whole mammal faunal bioclimatic spectra of the new 13 localities used for the validation of the bioclimatic model.

<i>Whole mammal</i>	I	II	II/III	III	IV	V	VI	VII	VIII	IX
Ust Kamchatsk	0,571	1,016	0,444	1,016	4,721	1,587	8,387	4,387	52,387	25,483
Saskatoon	1,298	1,963	5,113	4,779	6,604	6,107	24,311	18,755	27,496	3,574
Riga	1,124	1,356	1,058	1,058	12,970	3,112	39,883	9,897	24,878	4,661
Budapest	0,818	1,203	1,289	1,794	20,560	3,237	42,656	16,556	10,517	1,370
Dairen	5,451	5,809	2,929	1,639	7,883	14,442	32,291	13,336	13,144	3,077
Portland	1,492	2,966	6,119	6,940	16,004	5,704	34,021	12,428	12,022	2,306
Charleston	4,803	7,690	5,254	4,539	5,138	39,152	19,113	10,005	3,975	0,332
Niza	1,600	2,298	1,873	2,386	30,236	4,364	37,236	10,221	8,705	1,083
Kweilin	20,065	23,732	6,279	1,127	2,598	31,465	11,132	2,194	1,408	0,000
Smara	4,359	6,996	15,971	35,018	23,480	5,018	2,198	4,762	1,099	1,099
Puerto Ayacucho	31,994	33,612	26,749	1,112	0,566	4,886	0,426	0,573	0,082	0,000
Tabou	63,442	20,721	5,811	3,453	2,671	3,805	0,097	0,000	0,000	0,000
Kuala Lumpur	71,967	18,593	4,840	0,499	0,536	2,386	0,955	0,156	0,068	0,000

Appendix 3.2

Rodentia faunal bioclimatic spectra of the new 13 localities used for the validation of the bioclimatic model.

<i>Rodentia</i>	I	II	II/III	III	IV	V	VI	VII	VIII	IX
Ust Kamchatsk	0,000	0,000	0,000	0,000	4,167	0,000	8,333	0,000	52,083	35,417
Saskatoon	0,000	0,000	2,037	2,037	2,037	5,278	29,537	21,204	37,870	0,000
Riga	1,494	1,494	1,494	1,494	9,337	2,965	46,592	2,124	31,046	1,961
Budapest	1,270	1,270	1,270	1,270	13,770	2,520	52,937	11,806	13,889	0,000
Dairen	1,235	1,235	1,235	1,235	7,716	4,012	46,605	12,346	24,383	0,000
Portland	0,000	0,000	2,444	2,444	20,778	3,000	49,333	9,333	12,667	0,000
Charleston	1,667	4,444	1,667	1,667	1,667	54,722	22,500	7,222	4,444	0,000
Niza	1,494	1,494	1,494	1,494	31,396	2,965	43,161	0,654	15,850	0,000
Kweilin	17,758	21,925	3,175	3,175	3,175	28,175	19,841	1,389	1,389	0,000
Smara	2,857	2,857	12,381	45,714	31,429	0,000	0,000	4,762	0,000	0,000
Puerto Ayacucho	32,778	38,333	21,667	2,222	0,000	5,000	0,000	0,000	0,000	0,000
Tabou	77,167	17,167	2,583	0,917	0,917	1,250	0,000	0,000	0,000	0,000
Kuala Lumpur	84,839	10,480	0,651	0,651	0,651	1,506	0,651	0,285	0,285	0,000

Appendix 3.3

Large mammal faunal bioclimatic spectra of the new 13 localities used for the validation of the bioclimatic model.

<i>Large mammal</i>	I	II	II/III	III	IV	V	VI	VII	VIII	IX
Ust Kamchatsk	1,299	2,309	1,010	2,309	7,698	3,608	13,001	9,971	40,274	18,521
Saskatoon	2,016	3,032	6,841	7,413	11,575	6,775	18,479	15,146	21,575	7,149
Riga	1,905	2,646	1,693	1,693	16,820	4,931	25,153	15,153	25,312	4,693
Budapest	1,786	3,373	2,480	2,480	18,745	5,516	26,558	20,308	14,355	4,400
Dairen	7,381	7,998	4,427	2,205	7,866	19,625	27,218	13,091	7,668	2,522
Portland	2,735	4,460	8,238	8,860	12,514	8,787	19,398	15,309	14,972	4,727
Charleston	6,761	6,761	10,241	9,417	11,395	18,263	16,340	12,494	7,228	1,099
Niza	2,041	3,855	2,834	2,834	21,423	6,304	26,780	16,066	12,834	5,028
Kweilin	15,952	15,952	7,718	0,595	2,619	37,966	13,661	3,065	2,470	0,000
Smara	7,333	10,190	20,190	23,048	13,048	9,048	5,714	5,714	2,857	2,857
Puerto Ayacucho	30,578	30,578	23,170	1,411	0,617	10,207	1,411	1,411	0,617	0,000
Tabou	67,629	15,890	4,840	1,905	3,318	6,108	0,311	0,000	0,000	0,000
Kuala Lumpur	60,753	24,018	6,161	0,292	0,923	5,311	2,250	0,292	0,000	0,000

Appendix 3.4

Whole mammal without Chiroptera faunal bioclimatic spectra of the new 13 localities used for the validation of the bioclimatic model

<i>Without Chiroptera</i>	I	II	II/III	III	IV	V	VI	VII	VIII	IX
Ust Kamchatsk	0,571	1,016	0,444	1,016	4,721	1,587	8,387	4,387	52,387	25,483
Saskatoon	0,988	1,486	4,726	4,353	6,393	5,184	24,549	18,340	29,988	3,995
Riga	1,384	1,669	1,302	1,302	11,052	3,189	37,761	8,122	28,482	5,737
Budapest	1,173	1,725	1,415	1,415	16,927	3,014	43,920	15,167	13,278	1,965
Dairen	4,799	5,169	3,026	1,693	8,146	14,090	32,534	13,780	13,582	3,180
Portland	1,310	2,137	4,711	5,704	15,961	5,148	37,038	11,467	13,737	2,786
Charleston	4,153	6,601	5,410	4,451	5,254	38,461	19,346	11,274	4,603	0,446
Niza	2,129	2,749	1,587	1,587	28,057	3,382	38,422	7,383	12,987	1,717
Kweilin	16,426	18,807	6,018	1,134	2,522	36,760	13,902	2,420	2,011	0,000
Smara	4,359	6,996	15,971	35,018	23,480	5,018	2,198	4,762	1,099	1,099
Puerto Ayacucho	33,189	32,252	21,835	1,419	0,347	7,773	1,419	1,419	0,347	0,000
Tabou	70,895	17,979	4,003	1,555	1,972	3,447	0,149	0,000	0,000	0,000
Kuala Lumpur	71,252	18,621	3,796	0,418	0,744	3,358	1,428	0,267	0,117	0,000