

Late Quaternary Small Mammals and Paleotemperatures in Bulgaria and Italy

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Abstract: The aim of the study was to analyze the capacity of fossil remains of small mammals in the cave sediments for quantitative climate reconstructions. We have developed a number of small mammal-climate inference models using modern owl pellet samples from 144 sites. Canonical correspondence analysis was used to reveal the factors (climate parameters, agent of accumulation) that best reflect the main patterns of variation in the modern small mammal assemblages. Annual Mean Temperature, Maximal Temperature of Warmest Month, and Minimal Temperature of Coldest Month capture a large and statistically significant fraction of the overall variance in the recent small mammal data. Four inference models were tested. The results of cross-validation showed that Modern Analog Technique and Weighted Averaging Partial Least Squares (WAPLS) were the best in terms of performance statistics. Using these models it was possible to produce quantitative records of past temperatures based on small mammal stratigraphic cave sequences from Bulgaria (Cave 16 and Cave 15) and Italy (Castelcivita, Mura, and Continenza). For each locality both methods revealed similar trends in climate change, but differ somewhat in terms of specific values of the reconstructed temperatures. The differences between them were larger in non-analog situations. In this sense, WAPLS was considered more reliable in the reconstruction of climate features during Late Pleistocene. Reconstructions made on the basis of this method have important implications for understanding paleoenvironmental changes during Late Quaternary. The reconstructions support the previous qualitative interpretations and reconstructions based on other proxies.

Keywords: modern small mammal data; pellets; numerical analysis; paleoclimatic reconstruction; transfer functions; fossil small mammals

Introduction

A detailed understanding of the climate development throughout the past depends on suitable proxy data and their translation into quantitative climate information. Small mammals are especially promising in this respect. Several factors make them a good indicator group for the ecological conditions. Their remains and especially their teeth are well preserved in Quaternary cave sediments. Their occurrence here is a result of the feeding activity of raptors using the caves as shelters where they bring

their prey. It is widely accepted that in caves with large entrances birds of prey and especially owls are the main agent for accumulation of small mammal bones (ANDREWS 1990). These birds produce large numbers of pellets containing bones of their victims, which can be identified to species in most cases and recovered from sediments in quantities sufficiently large to permit estimation of relative abundance. Because of their small size and imperfect thermoregulation the small mammals are habitat-dependent,

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and the temperature in their immediate environment limits their distribution. Small mammal communities are typically species rich, containing plenty of ecological information. The large numbers of taxa provide important internal checks in datasets, thus increasing confidence of the environmental inferences. The environmental sensitivity and the rapid establishment (in geological sense) make small mammals sensitive indicators of paleoenvironmental change. Variations in the composition of local small mammals assemblages over time have been used in order to estimate climatic parameters (POPOV 1994, 2000, DI CANZIO 2005). For Late Quaternary, such studies are based primarily on the recent habitat requirements of the species, because all species present during this time interval are considered identical to modern species (POPOV 2000). Recently, more precise methods have been developed and successfully applied to infer past environmental conditions from the remains of various organisms (BIRKS 1995, 1998, 2004, DIXIT *et al.*, 1991, GUIOT 1990, OVERPECK *et al.* 1985). These methods require a training (calibration) set consisting of a large set of modern samples of comparable taphonomical type and corresponding climatic data. These data are used to ‘calibrate’ fossil assemblages and, on the basis of the relative abundances of the individual taxa present, infer the past climatic variables of an assemblage. Having in mind the taphonomy of small mammals in cave sediments, modern small mammal samples, based on owl pellets, cross-referenced with current distributions of climatic variables can provide the data required to infer temporal variations in climate from fossil small mammal data. There are several numerical approaches in this respect. Two of them are widely used during the last decades – modern analogues approach (called also modern analogue technique, MAT) and transfer function approach. MAT represents a procedure, where a modern-fossil analogue is recognized, and then a past environment is inferred by using the modern environment from the modern assemblage as an analogue. Among the limitations in this method are the occurrence of multiple modern analogues that differ widely in climate affinity or a situation where no modern analogues are recognized. The transfer function approach attempts to overcome these problems by using procedures for deriving and estimating modern species-climate transfer functions assuming linear or non-linear species response to an environmental factor. According to us these approaches have not been employed for small mammal data.

The objectives of the study were to assess the applicability of the quantitative approach to paleo-

climate reconstruction based on small mammal data, originating from pellets of birds of prey. In particular, based on analysis of present-day data set to determine which climatic variables have the most influence on the composition and structure of the small mammal spectra, to determine whether these variables are suitable for reconstruction from a statistical point of view, to compare the performance of several methods for reconstruction, to choose the best of them to be applied to the fossil small mammal data available, to evaluate the reliability of the quantitative reconstructions by comparing the results with these obtained based on another type of evidence.

The fossil small mammal material originated from several cave localities on Apennine and Balkan Peninsulas. Two sediment sequences (Castelcivita Cave, Italy and Cave 16, Bulgaria) contain Campanian Ignimbrite (CI) tephra and a rich record of small mammals (POPOV 2000, DI CANZIO 2005, GIACCIO *et al.* 2008). The previous reconstructions based on small mammals from these localities relied on applying multivariate analyses (ordinations). The obtained results were interpreted within the light of the traditional ecological groups and expressed in rather qualitative terms. In both localities cooling and drying was recorded near the CI tephra layer (for details see POPOV 2000, DI CANZIO 2005). Three other cave sequences spanning the temporal windows between ca. 13.0 and 8.0 cal Kyr B.P (Mura, Continenza in Italy and Cave 15 in Bulgaria) offer the possibility to evaluate the reliability of the reconstructions, having in mind that the Holocene temperatures must be higher than those around Heinrich 4 event (HE4) cold interval.

Material and Methods

Recent small mammal data

We compiled a training set of small mammal assemblages from pellets of birds of prey from literature sources. The spatial coverage of the data base is shown on Figure 1. The sites and respective literature sources, arranged by country and agent of accumulation are presented in Appendix 1.

The identification of the majority of small mammal taxa was generally consistent within the literature sources, but distinctions within some (sub) genera were not uniformly made, especially in publications dating before 1980. So, we did not include all taxa from the original sources, but rather combined some taxa into higher categories (combined original determinations in parentheses): *Talpa (europaea, le-*

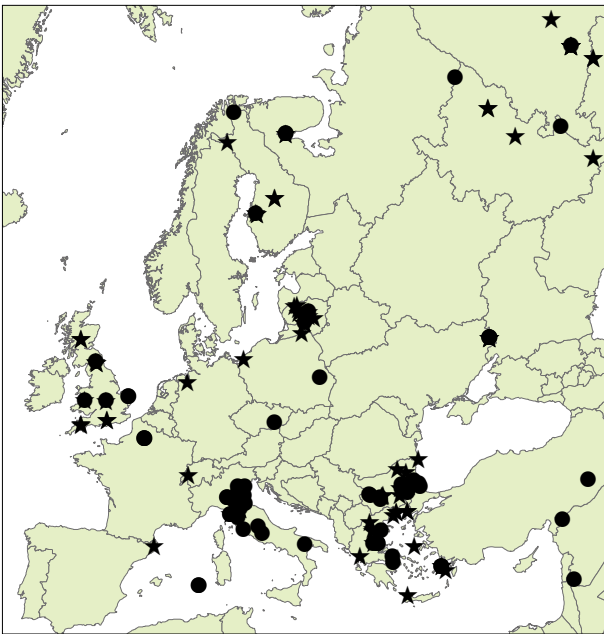


Fig. 1. Location of recent pellet small mammal assemblages. Circles – subsample 1 (SS1), asterisks – subsample 2 (SS2) used for verification of models (for details see text)

vantis), *Sorex* (*alpinus*, *araneus*, *caecutiens*, *isodon*, *minutus*, *minutissimus*, sp.), *Neomys* (*anomalous*, *fodiens*, sp.), *Crocidura* (*leucodon*, *suaveolens*, *rus-sula*, sp.), *Nannospalax* (*ehrenbergi*, *leucodon*, sp.), *Sylvaemus* (*flavicollis*, *microps*, *uralensis*, *sylvaticus*, sp., *tauricus*), *Mesocricetus* (*newtoni*, *auratus*), *Microtus* s. str. (*arvalis*, *agrestis*, *arvalis-agrestis*, sp.), *Terricola* (*subterraneus*, *thomasi*, *savi*, *duodecimcostatus*, *mariae*, sp.), *Clethrionomys* (*glareolus*, *rufocanus*, *rutilus*, sp.).

Synanthropic taxa (*Rattus* spp., *Mus* spp.) were excluded from the analysis. In addition, some large-sized species (*Lepus* spp., *Erinaceus* spp. and *Spermophilus* spp.), typical for the food of large owls were excluded from analysis to reduce the influence of predator size on the results. As a result of these procedures in 6 samples the number of species has proved to be small and their sums were under 5%. These samples were excluded from subsequent analyses.

Climate data

The initial climatic dataset consisted of 19 bioclimatic variables, with a spatial resolution of 30 arcseconds, available in WorldClim data base (HIJMAN et al. 2005, <http://www.worldclim.org/current.htm>). Shape files of geographical coordinates of sites were used to extract bioclimatic data, associated with each point using the free software package DIVA-GIS (ver-

sion 5.2) (HIJMAN et al., 2001), downloaded from the DIVA-GIS website (<http://www.diva-gis.org>). Among these variables the following were selected for analysis – Annual Mean Temperature (AMT), Maximal Temperature of Warmest Month (MTWM), Minimal Temperature of Coldest Month (MTCM), Annual Precipitation (AP), Precipitation of Wettest Month (PWM), Precipitation of Driest Month (PDM). These data were entered into a database file, containing the small mammal data. Longitude and latitude from the source data are stored as decimal degrees. Site coordinates are sometimes only approximate, but are sufficient to perform large scale analyses, especially having in mind that the owl pellets source radius can be at least several tens of kilometres for breeding season.

Numerical analyses

The modern data set consisted of 144 samples, 32 small mammal taxa, and 14 explanatory variables (6 climatic parameters and 8 bird species). In order to determine the total heterogeneity of the modern data set an unconstrained ordination was performed using detrended correspondence analysis (DCA). Canonical correspondence analysis (CCA) was employed to reveal the most important determinants of structure of modern pellet small mammal assemblages and to investigate which of these determinants affected most strongly the pellet small mammal assemblages. Prior to analyses, the data were transformed using the natural logarithm [$\ln(x + 1)$] to stabilize their variances and rare taxa were downweighted. These analyses were performed with the software package CANOCO version 4.5 (TER BRAAK and ŠMILAUER 2002).

We undertook paleoclimatic reconstructions using modern analogue technique (MAT) and four transfer-function techniques (OVERPECK et al. 1985, BIRKS 1995) – Partial Least Squares regression (PLS), Weighted Averaging (WA), Weighted Averaging Partial Least Squares (WAPLS), and Maximum Likelihood (ML).

Modern Analogue Technique (MAT) compares the fossil assemblage with modern assemblages using a dissimilarity index and selects, for each fossil assemblage, between three to ten of the closest modern assemblages (or best modern analogues). The climate parameters of these selected best analogues are then averaged to provide the climatic estimates of the fossil assemblage. We selected the square-chord distance dissimilarity coefficient, a robust ‘signal-to-noise’ metric (OVERPECK et al. 1985, GUIOT 1990). The number of analogues to use in the reconstructions was determined from the model

with lowest root mean square error of prediction (RMSEP). The number of analogues varied among data sets.

Transfer function methods used in the study can be separated in two groups – unimodal-based (WA, WAPLS, ML) and linear-based methods (PLS). Linear methods perform better for short gradients (< 1.5 standard deviation (SD) units) and unimodal methods are more suitable for long gradients (> 3 SD units), whereas both methods may be appropriate for intermediate gradient lengths (TER BRAAK and PRENTICE 1988). As DCA showed the gradients of the variables under study (see below) to be not very long (3.112-2.594 SD units), we used both unimodal – and linear- based transfer-function techniques.

WA estimates a taxon optimum by taking an average of the values for an environmental variable at each site where the taxon occurs and weighting this average by the taxon abundance at each of those sites (BIRKS 1995). Modifications of WA were tested with tolerance down-weighting (WA-Tol) and with both inverse and classical deshrinking.

WAPLS is a unimodal equivalent of PLS (TER BRAAK and JUGGINS 1993, TER BRAAK et al. 1993, TER BRAAK 1995, BIRKS 1995). It is an improvement over WA in that it takes account the residual correlations in the biological data (TER BRAAK and JUGGINS 1993, BIRKS 1995). According to TER BRAAK et al. (1993, p.556) it ‘...is recommended as a simple and robust alternative’ for species rich, noisy data over long (>2 SD units) environmental gradients. The optimal number of components for the resulting prediction model was determined according to the higher bootstrap determination coefficient (r^2) and the lower root mean square error of prediction (RMSEP) between observed and predicted values, using leave-one-out cross-validation. The number of components required to produce optimal performance varied among data sets.

ML fits a parabolic response curve to the data for each species and uses this to estimate species optima. On the basis of the estimated taxon–environment relationship, inferences are calculated by using the same likelihood formulation as employed for fitting the original regression equations.

In all analyses except MAT, species that occur in only a small number of samples (less than tree occurrences) were excluded, taking into account that significant errors in species optima and tolerance or regression coefficients may be introduced by considering taxa with low occurrences: *Nannospalax*, *Sicista subtilis*, *Dryomys nitedula*, *Eliomys quercinus*, *Cricetus cricetus*, *Mesocricetus*, *Meriones tristrami*, *Microtus gregalis*, *Myopus schisticolor*, *Chionomys*

nivalis. As a result 20 taxa were included in development of the transfer functions. In all analyses except ML the taxa values were $\log_{10}(x+1)$ transformed. In PLS, WA, and WAPLS the minimal adequate model was identified as having a combination of a high coefficient of determination (r^2_{jack}) between observed and predicted values, a low mean and maximum bias, and a low root mean squared error of prediction (RMSEP_{jack}), all assessed by leave-one-out (jackknifing) cross-validation. In WAPLS, only components giving a reduction in RMSEP_{jack} of 5% or more were retained. All models were implemented using the program C2 version 1.3 (JUGGINS 2003).

Fossil data set

The fossil data set, used in this study consists of Late Quaternary stratigraphic sequences into 5 caves – 3 in Italy and 2 in Bulgaria (Fig. 2). In all the analyses, the taxonomy in fossil data set was harmonised with the training-set material. *Ochotona pusilla*, *Allactaga major*, and *Eolagurus luteus*, occurring in the fossil samples, do not occur in the training set and have been excluded from the reconstruction.

Mura Cave. The material used in this study comes from the 2.4 m-thick upper part of the deposits, related to the Late Pleistocene-Holocene period and consists of a total of 4729 vertebrate remains most of the which (3216) attributed to small mammals (BON and BOSCATO 1996). 12 stratigraphic small mammal assemblages are separated in this sequence (Fig. 3).

Continenza Cave. The locality reveals a 4.5 m-thick Late Glacial – early Holocene stratigraphic

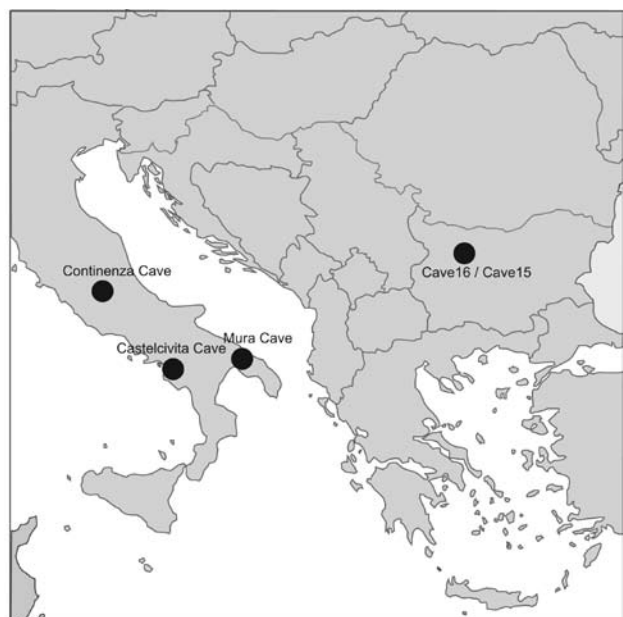


Fig. 2. Location of fossil small mammal localities

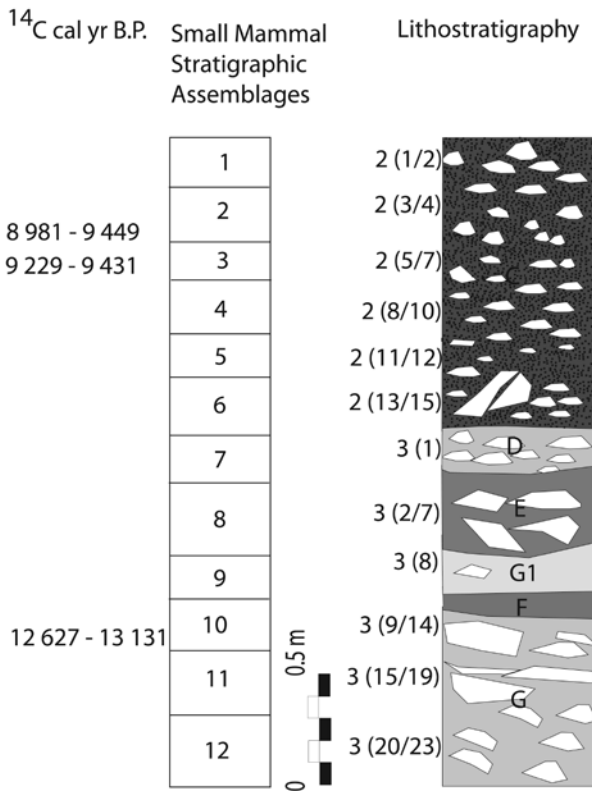


Fig. 3. Mura stratigraphy

interval spanning the temporal window between ca. 13.0 and 8.0 cal Kyr B.P. 1674 micromammal remains representing 34 taxa (DI CANZIO 2005) are distributed among 18 stratigraphic assemblages (Fig. 4).

Castelcivita Cave. Excavations evidenced a stratigraphic sequence of about 3m. The deepest cultural levels are referable to the Mousterian, followed by Uluzzini and Protoaurignacian strata (MASINI AND ABBAZZI 1997). Stratigraphic changes in the structure of 19 small mammal assemblages (Fig. 5) have been interpreted from a paleoecological point of view through Principal Component Analysis (DI CANZIO 2005). The sediments containing bones of small mammals lie beneath a layer of volcanic ash, identified as CI tephra (ca. 40 Kyr BP, calendar age). This layer is considered as an important temporal/stratigraphic marker for the Early Upper Paleolithic in southern Italy and eastern Europe (GIACCIO et al. 2008).

In the Italian localities the small mammal bones are derived in the large part by pellets of owls. This is demonstrated by the good state of preservation of the bone material. Most of the small mammal remains are represented by cranial bones and more or less well preserved whole mandibles and mandibles and long bones.

Cave16 and Cave 15, North Bulgaria (Fig. 6). Both caves are close to each other (about 50 meters

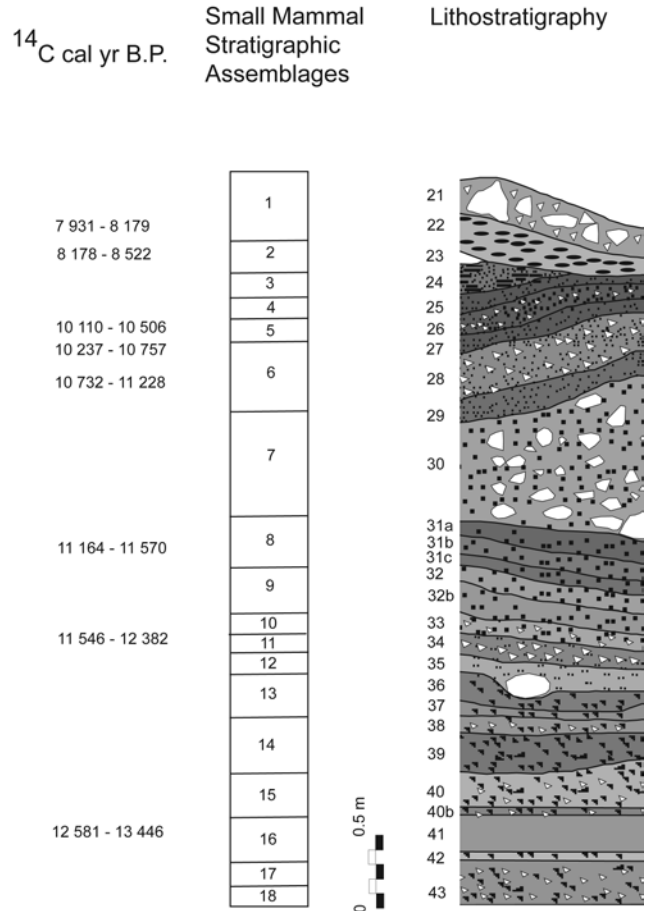


Fig. 4. Continenza stratigraphy

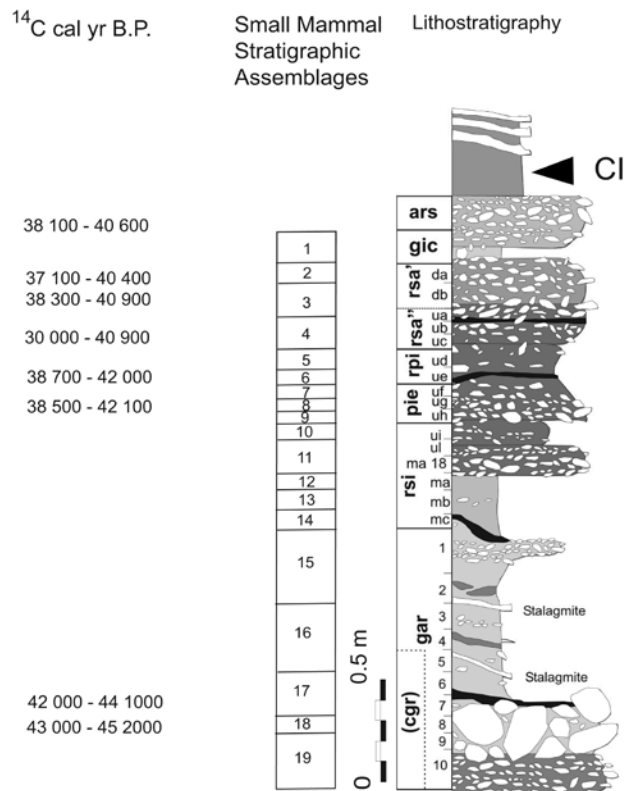


Fig. 5. Castelcivita stratigraphy. CI – tephra deposit.

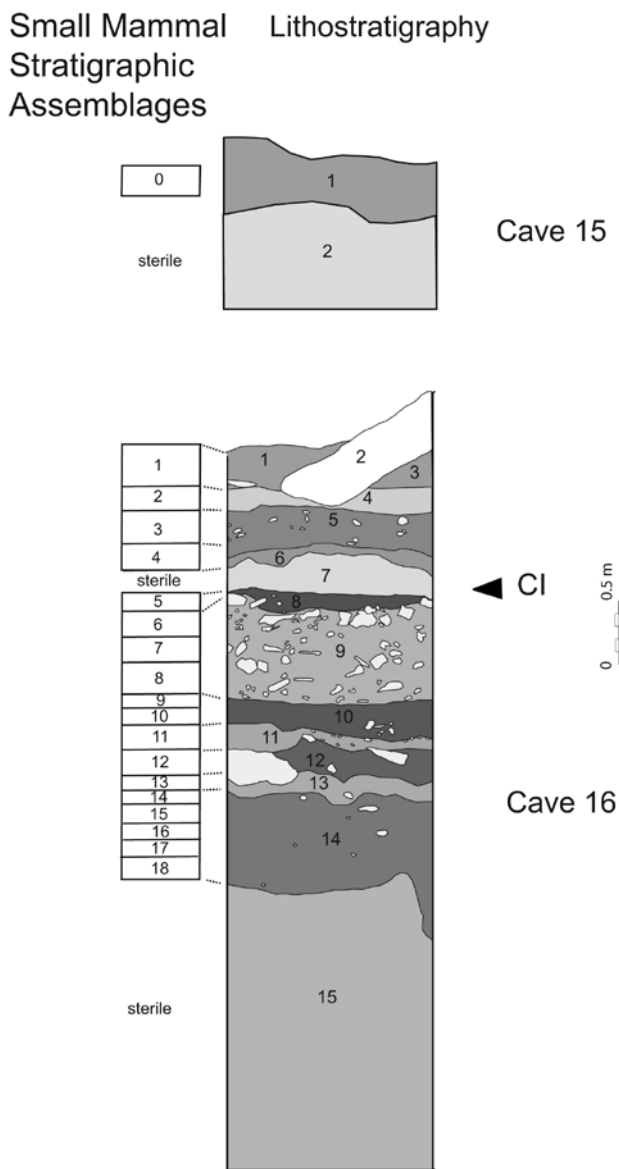


Fig. 6. Cave 16 and Cave 15 stratigraphy. CI – tephra deposit

distance). Cave 16 represents a large rock niche. Sediment thickness is about 4 m. The concentration of bones of small mammals in the sediments is very high. Among the well preserved bones whole anatomical elements, such as mandibles, limb bones, dominate, but also, albeit less frequently, fragments of the facial skull occur. Bones hardly bear traces of the chemical erosion. These characteristics of the bone material confirm that owls were the primary agents of small-mammal deposition. A well developed layer of volcanic ash lies within the upper part of the sequence. It is relatively thick, dense and compact, denoted as layer 7 in the original description of the lithology of the sequence (FERRIER 1994). According to the recent chemical analyses it was found that it refers to the CI tephra, i. e. identical to that in Castelcivita cave

in Italy (GIACCIO *et al.* 2008). Seventeen stratigraphic small mammal assemblages were defined in the sequence of Cave 16 (Fig. 6).

The small mammal assemblage in Cave 15 comes from the sediments, which are obviously of anthropogenic origin, located in a small room, whose entrance opens off the larger main chamber of this relatively short cave. The bone bearing deposit is about 50 cm thick. Along with the bones of small mammals, numerous fragments of Neolithic pottery were also found (GATSOV *et al.* 1990). On this basis, these sediments were referred to the middle Holocene. Changes in ecological appearance of the fossil small mammal assemblages as well as assumptions made on this basis for the paleoenvironmental changes correspond well with the age range of these localities (for details see POPOV 2000). Based on our preliminary analyses (POPOV 2000) of the sequences from Cave 16 and Cave 15, 18 stratigraphic small mammal assemblages were identified (Fig. 6). It can be assumed that the strata underlying tephra layer (layers 8 – 14, small mammal assemblages 5 – 18) correspond, at least partially, to the sequence of Castelcivita Cave thus offering a possibility for further examination of the reality of the reconstructions.

In total 68 stratigraphic fossil small mammal assemblages, containing 28 taxa (Fig. 7) were used in subsequent quantitative reconstructions.

Results

Analysis of recent data set – development of small mammal-inferred climatic models

Selection of explanatory variables. In order to identify the main factors that determine the spatial variability of the structure of the recent data set two types of ordination analysis were employed. First, to determine the total heterogeneity of the modern data set an unconstrained ordination using detrended correspondence analysis (DCA; HILL and GAUCH 1980) was performed. The length of the first axis (detrending by segments, non-linear rescaling) was 18.153 SD units, indicating that the data are too heterogeneous and many taxa deviate from the assumed model of linear response. So, we have chosen to use canonical correspondence analysis (CCA), an unimodal-based constrained ordination method to reveal the most important determinants of structure of modern pellet small mammal assemblages. In this analysis, the agent of accumulation, being a categorical variable with more than two categories (eight bird species), was coded as 8 dummy variables with variable' values

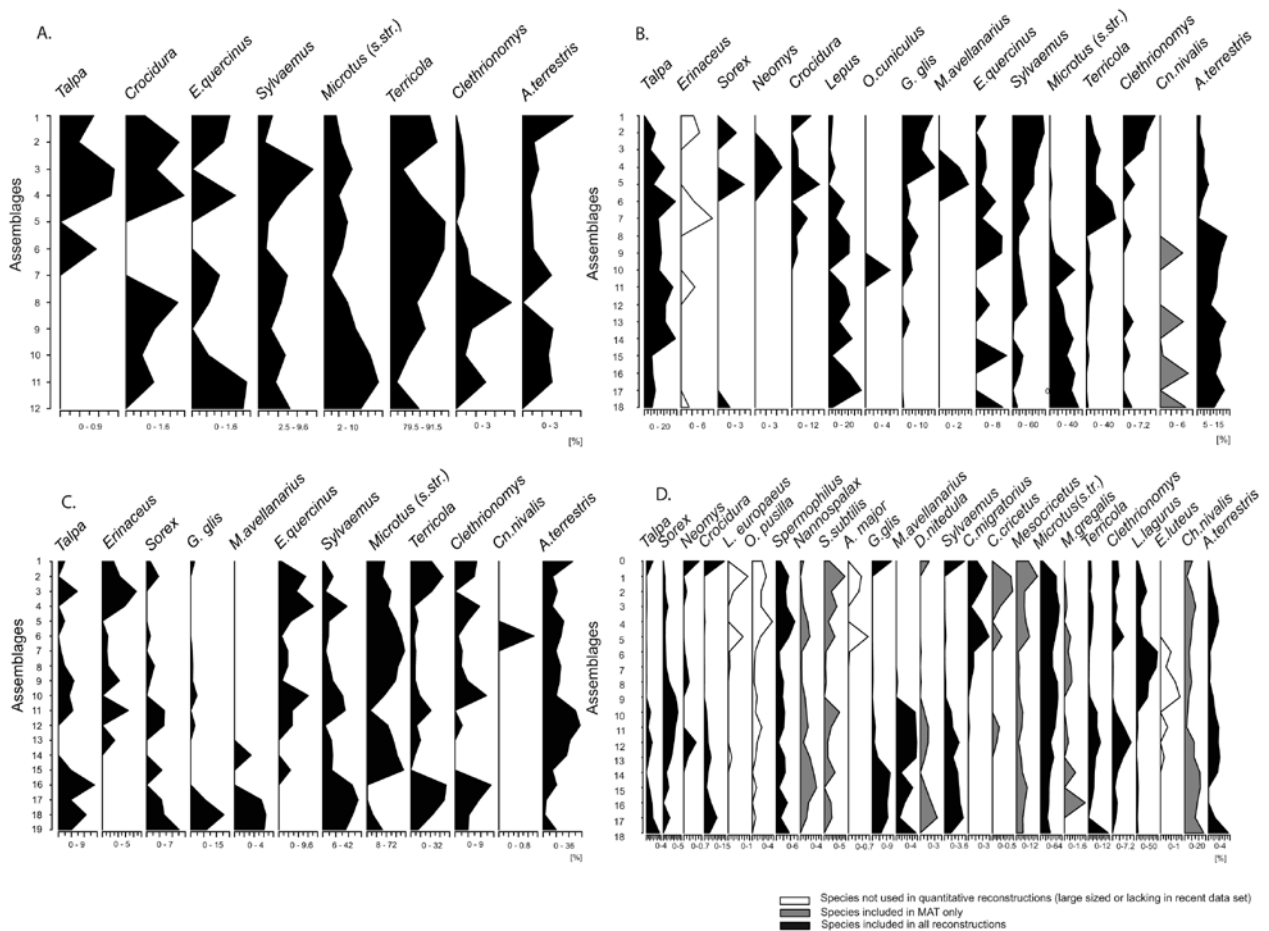


Fig. 7. Simplified small mammal stratigraphic diagrams. A. Mura; B. Continenza; C. Castelcivita; D. Cave 16 and Cave 15

equal either one or zero. Forward selection was used to remove redundant variables, leaving only those that explained significant amounts of variation in the species data (identified using unrestricted Monte Carlo permutation tests; TER BRAAK and ŠMILAUER 2002). Intra-set correlation coefficients between ordination axes and environmental variables were used, rather than canonical coefficients, to infer the importance of each parameter in predicting the species composition. Correlation coefficients have the advantage of not being affected if environmental variables are mutually correlated, as is frequently the case in empirical data (TER BRAAK 1995). The results of the permutation tests, correlation coefficients, and the ratios of the first constrained eigenvalue (λ_1) to the second unconstrained eigenvalue (λ_2) were used as criteria to identify the most appropriate environmental variables for quantitative reconstruction purposes (TER BRAAK 1988, BIRKS et al. 1990). Particular attention was paid to the latter criterion, as it serves as a good indicator of how effectively the variable is represented by axis 1 in the constrained analysis. As a general rule, quantitative inference models can be

successfully developed for environmental variables that have high λ_1/λ_2 ratios (TER BRAAK 1988).

In these analyses data for bird species with less than four sites were excluded (*Asio flammeus*, *Falco tinunculus*, *Glaucidium passerinum*, *Nyctea scandiaca*). Additionally, the dataset was analyzed several times using CCA for automatically detecting anomalous observations or extreme values through the CANOCO software. The possible causes for these extreme values were then examined. These extreme values are generally caused by over-representation of some rare taxa in species poor samples. Four samples were detected as outliers and were removed. The final CCA was performed on the reduced data set. Three climate variables (AMT, MTWM and MTCM) showed the highest degree of correlation with CCA axis 1 (Table 1). The remaining four variables show low (*Strix aluco*, SA) or no correlation with this axis. Only one variable (*Asio otus*, AO) shows a moderate correlation with the second axis. The first CCA axis (eigenvalue of 0.412) accounted for the greatest proportion of variation (15.3%). So, AMT, MTWM, and MTCM emerged as significant

drivers of small mammal distribution and abundance as presented by the modern data set. The second axis, representing the effect of a predator species (eigenvalue 0.147) was responsible for only 5.5% of the total variation of species data. On the basis of these results it can be assumed that the impact of the agent of accumulation is much less compared with climatic factors. Therefore, in further analyses the role of the three climatic factors (AMT, MTWM, and MTCM) is only considered.

To investigate which of the above three climatic variables affected most strongly the pellet small mammal assemblages, we ran separate CCAs in two variants. In the first variant, each CCA was constrained to one of three variables (AMT, MTWM, MTCM). In the second variant the other variables were entered as covariables (Table 2).

Of the three variables, AMT had the highest influence with a λ_1/λ_2 ratio of 0.835, capturing 13.9% of the variation in the data. MTWM and MTCM had lower λ_1/λ_2 ratios, capturing a lower amount the variation. These results indicated that AMT was most strongly correlated with PSMA composition, followed by MTWM and MTCM. However, the λ_1/λ_2 ratios were greatly altered after removing the effects of each of the other variables (Table 2), showing that small mammal assemblages have no unique relationship to any of these variables.

Inference models should only realistically be developed for variables that have first and second eigenvalue ratios (λ_1/λ_2) > 0.50 (DIXIT et al., 1991). Although the eigenvalue ratios for the variables are above this threshold value, it should be considered that these variables are not completely independent from one another. However, given that each of them explained a significant percentage of the variability of the data it may be assumed that relatively reliable inferences still can be obtained.

Range of variability of selected climatic variables for the entire modern data set are presented in Table 3. In this table the present-day values of the climatic variables for the area of each fossil locality are also given. These data would be useful to compare with reconstructions and to assess the extent of differences between recent and past temperatures. Since the values are derived from the electronic database referred to above, they differ somewhat from those that could be obtained from the nearest weather stations. However, these values are useful because they are based on data used to develop the models.

Selection of species-environment models. After the most influential environmental variables were determined, the next step of our study was to define

the most appropriate model for the reconstructions. To assess the relative performance of the models the modern data set was split into two equal subsets (SS1 and SS2) and two variants of analyses (A and B) were performed to validate one another. In the first one (A) SS1 was used to train the climate inference models and SS2 was used to test the prediction model. In the second variant (B) the setting of the analysis was the opposite. Samples for the subsets were chosen by selecting every second sample along the sample order, obtained by the sorting of random numbers, assigned to each sample. Before the analyses the two subsets were compared in terms of climatic parameters analyzed (Table 4). They are comparable to one another with regard to minimum, maximum, mean, and standard deviation of the variables and show no differences compared to the total data set, therefore providing appropriate replicates for the cross-validations.

The performance of each model was evaluated on the basis of the training data subset (SS1 or SS2) by statistical leave-one-out crossvalidation (TER BRAAK and JUGGINS 1993, BIRKS 1995) in terms of r^2 , RMSEP, average and maximum bias (Table 5).

Having in mind that the root mean square error of prediction (RMSEP) assesses the random differences between observed and predicted values, the maximum bias (MaxB) assesses the maximum error in any section of the environmental gradient and the coefficient of determination (r^2) is indicative of the strength of the relationship between observed and predicted values, the model with the best predictive power must be the one that has the lowest RMSEP, highest r^2 , and lowest MaxB. According to these criteria based on performance statistics (leave-

Table 1. Intrasets correlations of environmental variables with the first two axes of CCA of modern data set

Variable	Axis 1	Axis 2	F (all P < 0.05)*
AMT	0.8911	0.0005	22.17
MTWM	0.8481	0.0746	3.98
MTCM	0.7010	-0.0811	5.69
AP	-0.1290	-0.2407	4.03
PWM	0.0842	-0.0004	2.91
<i>Asio otus</i>	0.1920	-0.5454	6.63
<i>Strix aluco</i>	-0.4198	-0.0026	5.19

* The statistical significance of the effect of each variable was estimated by a Monte Carlo permutation test as each variable was added to the model. Abbreviations: AMT – Annual Mean Temperature, MTWM – Maximal Temperature of Warmest Month, MTCM – Mean Temperature of Coldest Month; AP – Annual Precipitation, PWM – Precipitation of Wettest Month.

Table 2. Summary of canonical correspondence analysis (CCA) for the training set in relation to AMT, MTWM and MTCM with and without covariables. For abbreviations see Table 1

Variable	Covariable	Eigenvalue 1 (λ_1)*	λ_1/λ_2 *	Species variance (%) explained by axis 1*
AMT		0.375	0.835	13.9
	MTWM	0.118	0.262	5.0
	MTCM	0.204	0.454	8.4
MTWM		0.346	0.770	12.9
	AMT	0.089	0.198	3.8
	MTCM	0.210	0.467	8.6
MTCM		0.258	0.574	9.6
	AMT	0.087	0.193	3.8
	MTWM	0.123	0.274	5.2

* The data are from CCA constrained to one variable at a time

Table 3. Recent Annual Mean Temperature (AMT), Maximal Temperature of Warmest Month (MTWM), and Minimal Temperature of Coldest Month (MTCM), associated with recent and fossil small mammal samples (geographic coordinates in decimal degrees)

Localities	Longitude, E	Latitude, N	AMT	MTWM	MTCM	Amplitude (MTWM-MTCM)
Modern data set, 143 sites	-4.15- 59.18	33 – 69.9	-0.8 – 18.9	15.8 – 38.0	-31.9 – 8.6	-
Cave 16/Cave 15	24.07	43.17	11.4	27.9	-4.8	32.7
Mura	17.3867	40.925	16.4	29.4	5.1	24.3
Castelcivita	15.2111	40.5075	16	28.4	6.4	22.0
Continenza	13.0917	42.2917	11.8	26.0	-0.1	26.1

one-out) the best models are as follows (Table 5): for AMT – WAPLS-c2 (SS1 and SS2), for MTWM – WAPLS-c2 (SS1) and WAPLS-c3 (SS2), for MTCM – MAT (SS1), WAPLS-c2 (SS2). On the other hand, MAT performs best with the independent test (sub) sets, showing lowest RMSEP and highest r^2 in nearly all cases (Table 5). According to the above criteria, among the models these based on Partial Least Squares regression (PLS) were the worst. Although these models performed relatively well on the basis of statistical jackknife cross validation, these results were not corroborated by the cross-validation, based on independent test samples. The above analyses indicate that the PLS models provided highly biased temperature estimates (great values of RMSEP-test). These results confirm the existing opinion (e.g. BIRKS 1995) that the performance of a model cannot be accurately assessed on the basis of the highest r^2 jack, and the lowest RMSEPjack, only (see Table 5), because leaving only one out changes the data too little and this would exaggerate the goodness of prediction.

Based on these data, it can be concluded that MAT and WAPLS are the best among the calibration methods under comparison in this article. Therefore,

further reconstructions of the climate indices are based on these methods. The whole training data set (144 owl pellet collecting sites, 32 taxa) is used for their development. The performance statistics of both models are shown on Table 6.

For both models the r^2 values are highest for AMT, and the lowest – for MTCM. On this basis it can be concluded that a greater degree of confidence with the AMT reconstructions, followed by this of MTWM and in the last place – this of MTCM.

Applying the models and evaluating the inferences

The WAPLS and MAT inference models based on the entire modern data set were applied to the small mammal stratigraphies (Fig. 7). Quantitative reconstructions of the three selected climatic parameters are shown in Figs. 8-11.

Mura Cave. In this sequence both models show virtually identical values for reconstructed climatic parameters (Fig. 8).

Continenza Cave. Both methods give comparable trends (Fig. 9). The differences concern the exact values of the reconstructed temperatures. The MAT-inferred temperature reconstructions suggest

Table 4. Descriptive statistics of the total training data set and the two subsets (SS1 and SS2) used for assessment of performance and validation of models

Variable	Total training set		SS1		SS2	
	M	SD	M	SD	M	SD
AMT	10.25	4.80	11.00	4.82	10.24	5.07
MTWM	26.07	4.73	27.00	4.76	25.92	4.70
MTCM	-3.54	6.65	-3.00	6.89	-3.45	6.98

For abbreviations see Table 1; M – Mean, SD – Standard Deviation

Table 5. Performance of the models, based on the reduced training subsets (SS1, variant A; SS2, variant B)

Variant	Variable and gradient length [°C]	Prediction model	Performance (jackknifed)				Test	
			r ²	AB	MB	RMSEP	r ²	RMSEP
A	AMT 19.7	PLS-c5	0.82	0.009	2.20	1.94	0.77	4.33
		WA_cla	0.83	-0.003	1.99	2.05	0.82	2.35
		WAPLS-c2	0.85	-0.038	2.39	1.80	0.83	2.37
		ML	0.79	0.466	2.59	2.16	0.83	2.23
		MAT	0.87	-0.245	3.21	2.08	0.84	2.73
	MTWM 22.2	PLS-c2	0.75	0.028	8.22	2.40	0.76	3.99
		WA_cla	0.83	0.031	2.30	2.06	0.72	2.89
		WAPLS-c2	0.84	-0.026	3.67	1.90	0.76	2.65
		ML	0.72	-0.165	3.78	2.75	0.73	2.91
		MAT	0.83	0.088	5.00	2.25	0.85	2.07
	MTCM 40.5	PLS-c5	0.71	0.037	5.98	3.48	0.67	7.58
		WA_cla	0.61	-0.031	5.37	4.98	0.70	4.43
		WAPLS-c2	0.65	0.021	6.49	3.85	0.70	4.09
		ML	0.58	1.120	3.64	4.53	0.66	5.33
		MAT	0.83	-0.5041	4.54	3.51	0.73	4.74
B	AMT 19.7	PLS-c4	0.76	0.042	4.02	2.42	0.81	5.74
		WATOL_cla	0.83	0.046	2.54	2.12	0.84	2.31
		WAPLS-c2	0.82	0.014	3.16	2.09	0.87	1.93
		ML	0.70	-0.034	3.52	2.90	0.78	2.05
		MAT	0.79	0.273	3.38	2.64	0.91	1.74
	MTWM 22.2	PLS-c5	0.76	0.017	2.53	2.26	0.71	5.19
		WATOL_cla	0.76	-0.003	3.01	2.26	0.85	2.40
		WAPLS-c3	0.81	-0.018	1.66	2.05	0.75	2.62
		ML	0.75	0.083	3.15	2.47	0.82	2.90
		MAT	0.79	0.559	4.23	2.56	0.85	2.39
	MTCM 40.5	PLS-c4	0.67	0.058	5.21	3.89	0.71	8.33
		WA_cla	0.67	-0.003	4.20	4.58	0.61	5.14
		WAPLS-c2	0.69	0.036	5.56	3.76	0.72	3.89
		ML	0.65	0.031	2.63	4.29	0.61	4.86
		MAT	0.67	-0.024	6.28	4.45	0.88	2.55

Notes and abbreviations: The performances are evaluated by cross-validated r² and root mean squared error of prediction (RMSEP), both for the calibration subset (jackknife) and for test reconstructions; average bias (AB) and maximum bias (MB) statistics are based on the differences between inferred and observed values in cross-validation (jackknife) for the calibration subset; PLS – Partial Least Squares regression, WA – Weighted Averaging, WAPLS – Weighted Averaging Partial Least Squares, ML – Maximum Likelihood, MAT – Modern Analogue Technique.

Table 6. WAPLS-c2 and MAT- leave-one-out (LOO) and bootstrap-derived error estimates based on the whole training data set. For abbreviations see Tables 1 and 5. k-closest analogues

Climatic parameter	Model	Estimate	k	RMSEP [°C]	r ²	MB [°C]
AMT	WAPLS-c2	LOO	-	2.05	0.82	2.57
	MAT	LOO	7	1.81	0.86	-2.79
	MAT	Bootstrap	8	2.04	0.92	-2.97
MTWM	WAPLS-c2	LOO	-	2.38	0.75	4.16
	MAT	LOO	5	1.88	0.84	4.60
	MAT	Bootstrap	8	2.08	0.91	5.58
MTCM	WAPLS-c2	LOO	-	3.49	0.72	4.39
	MAT	LOO	5	3.12	0.78	-5.48
	MAT	Bootstrap	6	3.55	0.87	-5.07

generally warmer climate than the WAPLS-inferred reconstructions.

Castelcivita Cave (Fig. 10). MAT and WAPLS reconstructions show similar trends but here, in contrast to Cave 16 (see below), MAT tends to produce higher values especially at the bottom of the sequence.

Cave 16 and Cave 15. The climatic parameters, reconstructed from MAT and WAPLS models show consistent trends between these two techniques (Fig. 11). They are also consistent with the previous qualitative palaeoenvironmental interpretation. It should be noted however, that the values obtained on the basis of MAT showed greater variability. Although in most cases the MAT-inferred values fall within the sample-specific prediction errors defined by WAPLS it should be noted that the differences are greatest at the top of the sequence of Cave 16. In this area MAT predicts consistently lower temperatures, particularly in terms of AMT and MTCM.

Discussion

Factors affecting small mammals and their indication potential

CCA of the 32 small mammal taxa in 144 owl pellet samples shows a strong and statistically significant relationship between modern small mammal assemblages, deriving from owl pellets and three temperature parameters. However, rather surprisingly, precipitation parameters were not important drivers. This is most likely due to several reasons. First, the level of rainfall has a very large variability, depending on both the general geographical regularities, and the local features, associated mostly with relief. The seasonal structure of rainfall is more variable than temperature indicators. Second, the humidity of the

climate to a large extent depends on the temperature. Thus, high summer temperatures often determine the existence of a dry climate. Furthermore, rainfall affects small mammals through other, intermediate factors (e.g., soil permeability and soil water-holding capacity, plants, vegetation structure, etc.). It follows that as humidity, also the nature of vegetation and the appearance of small mammal assemblages are mainly determined by temperatures. The present analysis showed that the link between climate moisture and precipitation is not direct, and any reconstruction of moisture and precipitation using small mammal evidence appears unreliable.

Analysis of the modern data set also shows that at the continental scale the agent of accumulation is of secondary importance. This is particularly important for paleoecological interpretations because regardless of carefully conducted taphonomic studies it is not always possible to precisely identify the agent of accumulation. In many cases, given the long period of accumulation of the remains in a particular layer, it is likely that they are the product of the activity of various owl species. Furthermore, the results of this study confirm the view expressed by us earlier (POPOV 2000) that actually the whole complex of predators and their victims is a function of climate and respective ecological conditions.

MAT or WAPLS?

The reconstructions, presented above based on MAT and WAPLS showed that despite the similarity in trends, the two methods demonstrated some differences in terms of exact reconstructed values. This raises the question which of them gives a more reliable reconstruction. An important starting point for the analysis in this respect is the widely accepted fact that MAT tends to provide unreliable palaeoenvironmental reconstructions if no good

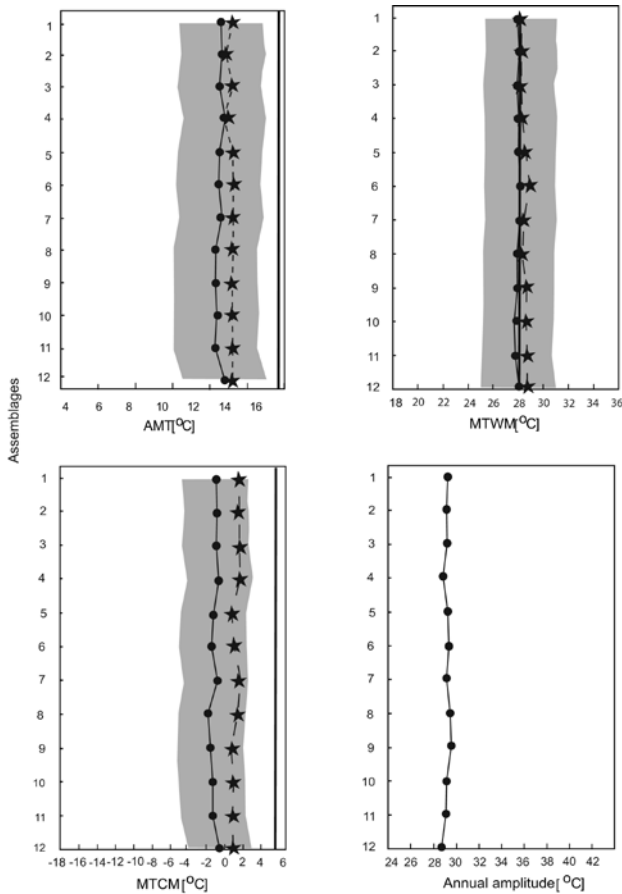


Fig. 8. Small mammal-inferred quantitative climate reconstructions at Mura Cave using Weighted Averaging Partial Least Squares (WAPLS; circles) and Modern Analogue Technique (MAT; asterisks). Shaded – sample-specific prediction errors defined by WAPLS. Thick vertical line – recent temeraure. AMT – Annual Mean Temperature, MTWM – Maximal Temperature of Warmest Month, MTCM – Minimal Temperature of Coldest Month.

modern analogues exist for the fossil assemblages. Conversely, transfer function methods and WAPLS in particular, perform well in ‘no analogue’ situations (BIRKS 2004), because it uses a multivariate indicator-species approach to reconstruct past environments on the basis of specific taxon–environment relationships. Experiments with simulated data of reconstruction performance under ‘no analogue’ situations (TER BRAAK 1995, BIRKS 1998) show that WAPLS performs remarkably well as long as there are reliable estimates of the regression coefficients in the inference model for some of the taxa of high numerical importance (high effective numbers of occurrences or N2 values; HILL 1973) in the fossil data.

A useful measure of non-analogue situation is the minimum dissimilarity (minDC) between a fossil sample and the training set samples. According to BIRKS et al. (1990) samples with coefficients below

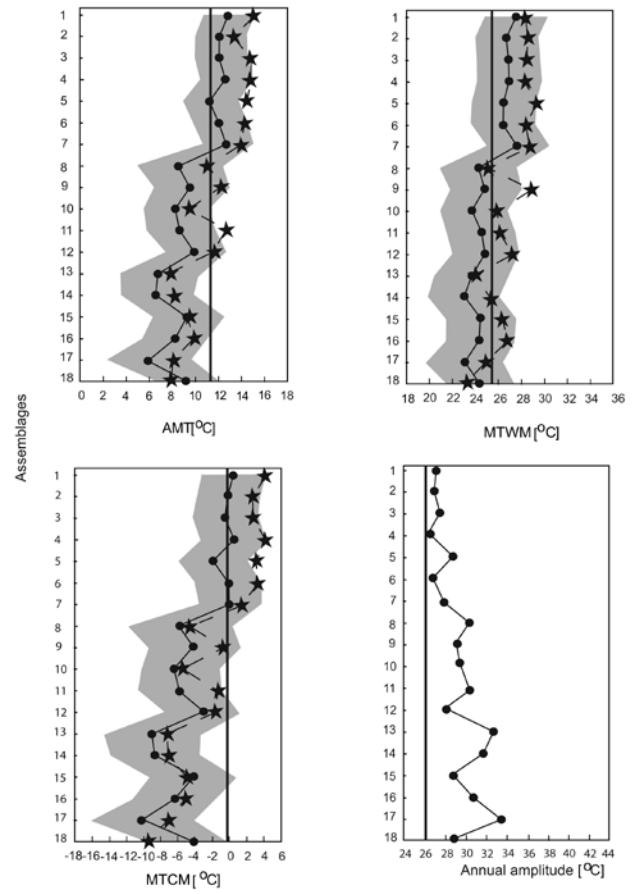


Fig. 9. Small mammal-inferred quantitative climate reconstructions at Continenza Cave using WAPLS and MAT. For abbreviations and symbols see Fig. 8

the 10th percentile were considered to have good analogues in the training set whilst the estimates associated with ‘no close analogue’ (dissimilarity coefficient \geq 10th percentile) samples should be treated with caution. Percentiles of the dissimilarities (square chord distance) for the training set are as follows: 5% – 0.1341, 10% – 0.2260, 20% – 0.3737. In order to determine whether the differences between estimates, based on both models depend of the degree of dissimilarity, graphs, representing the differences against the above percentiles are constructed of for each climatic parameter (Fig. 12). Obviously, the range of differences between estimates, obtained by the two methods dramatically increases in levels of minimal dissimilarity over the 10th percentile (minDC = 0.23). It is clear that the more non-analogue situation is, the greater the difference between the reconstructions obtained

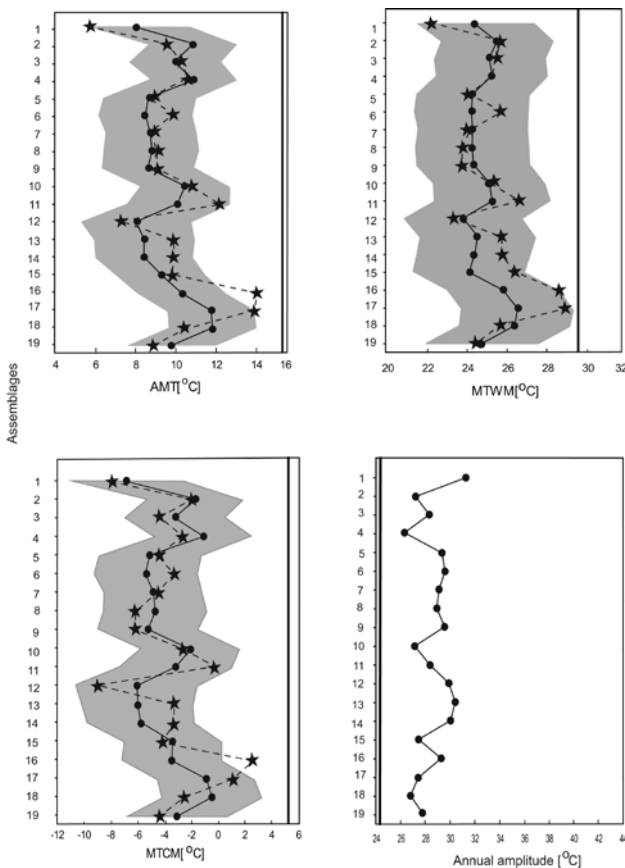


Fig. 10 Small mammal-inferred quantitative climate reconstructions at Castelcivita Cave using WAPLS and MAT. For abbreviations and symbols see Fig. 8

from these methods. Thus, assemblages above this threshold were considered to have no analogs in the calibration set. Given that WAPLS performs well in ‘no analogue’ situations it can be assumed that the reconstructions based of MAT for samples above 10th percentile are uncertain.

The minimal dissimilarity values for fossil assemblages are shown in Fig. 13. Nearly all fossil assemblages from Cave 16, Cave 15, Castelcivita Cave, and Continenza Cave (49 assemblages or 72% of fossil data set) have a minimal dissimilarity greater than 10th percentile, i. e. they have no close analogues in the modern training data set. This non-analogue situation means that the temperatures, inferred by MAT may be unreliable.

The sequence of Mura Cave gives further support to these inferences. All assemblages in this sequence show very low values of minimal dissimilarity, under the 5th percentile. As it might be expected, the values reconstructed on the basis of MAT are very similar to those obtained by WAPLS. These data indirectly support the argument that it is most likely the observed large range of differences

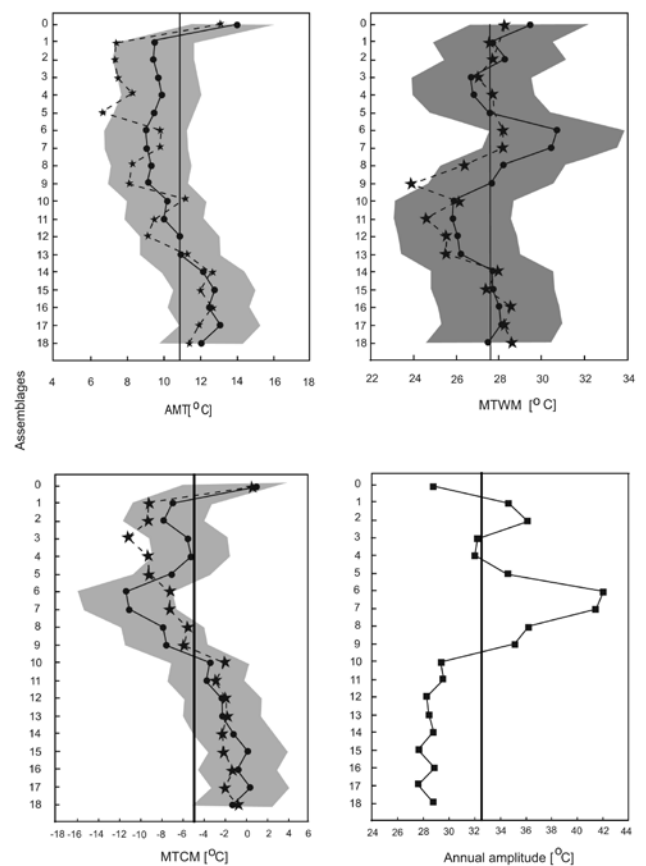


Fig. 11. Small mammal-inferred quantitative climate reconstructions at at Cave16-Cave 15 using WAPLS and MAT. For abbreviations and symbols see Fig. 8

between the two methods due to a bed performance of MAT in non-analogue situations. In this context WAPLS is considered the most reliable calibration method.

Statistically, our analysis also indicates that WAPLS is a reliable method, as assessed by two main lines of evidence. First, CCA demonstrated that small mammal–temperature relationships in the studied area are significant. Second, performance statistics (r^2 and RMSEP for models) show that these models significantly predict observed AMT, MTWM, and MTCM.

r^2 is a common measure of goodness of fit in the transfer function approach. The values of r^2 for our transfer functions (0.77-0.88 for AMT, 0.68-0.78 for MTCM, 0.61-0.70 for MTCM) are quite high, and comparable to those of temperature transfer functions developed for other groups of organisms (e.g. SHEN et al. 2006).

The RMSEP is commonly considered as a measure of the predictive ability of the training set (BIRKS 1995). The values of RMSEP for AMT are 9.6-12.94%, for MTWM – 10.04-12.56%, and for

MTCM – 10.17-11.82% as percentage of the respective gradient lengths. By comparison with the other published models for pollen or aquatic organisms based on similar methods (e.g. SHEN *et al.* 2006), they can be considered low. This shows a superior performance of our derived transfer functions in prediction power.

Comments on reconstructions based on WAPLS

Mura Cave. Reconstructions of climate parameters indicate a stable climate along the entire sequence. Mean annual temperatures are about 3°C lower than today, due mainly to significantly lower winter temperatures that were 6 – 7 °C lower than today.

Continenza Cave. According to the reconstructions, despite of the clear fluctuations a well expressed tendency to warming of climate can be observed, which corresponds with the age of small mammal assemblages representing the transition from Younger Drias to Holocene. The Holocene period shows average temperature reconstructions which are comparable to the observed temperatures in this area (Table 3, Fig. 9).

Castelcivita Cave. Based on the reconstructions it can be found that the earliest warm period in the sequence is connected to the layers gar: 6 / 7 and 8. Thus, the reconstruction combined the interpretation of the two principal component axes in our previous study (DI CANZIO 2005). Palaeoenvironmental interpretations of these axes were very similar. These reconstructions confirm this, namely that differences in temperature conditions are those that determine changes in fossil small mammal assemblages. The next warm climatic episode is associated with layers *rsi: ma 18* and *ui*. This fully corresponds to the previous analysis made on the basis of PCA (DI CANZIO 2005). Warming recorded in the upper part of the sequence is associated with layers *rsa''* and *rsa'*. It corresponds with the warming (separated by a poorly pronounced cool period), registered on the basis of PCA (DI CANZIO 2005). It can be said that the reconstruction of temperature change is in agreement, as with the initial fossil data and with the interpretations made previously, using other more subjective methods.

As a whole the small mammal sequence from Castelcivita Cave registers much cooler climate than the modern one (Table 3). Average annual temperatures have been 6-8 °C lower than current ones. Summer and especially winter temperatures were also lower than the current ones. The seasonal amplitude in this part of Italy has also been greater than today.

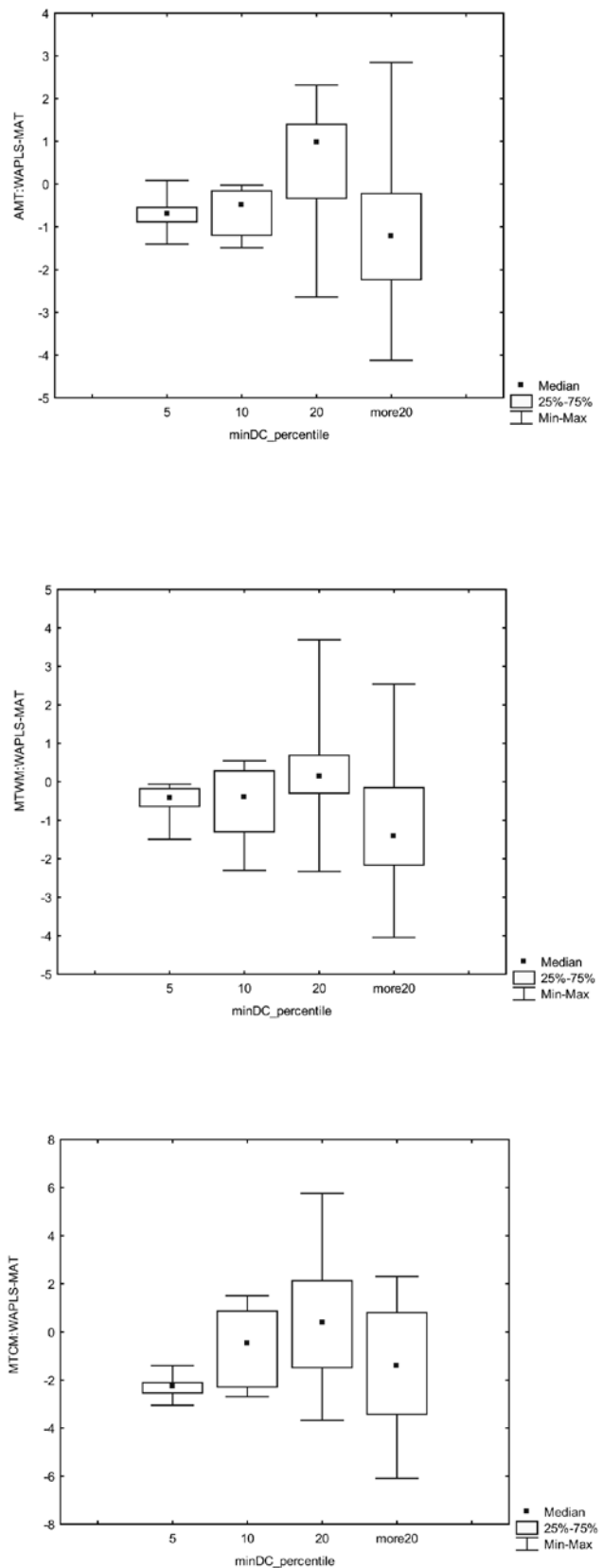


Fig. 12. Differences between reconstructions based on MAT and WAPLS depending on fossil minimal dissimilarity percentile (minDC_percentile) of every ensemble. For abbreviations see Fig. 8

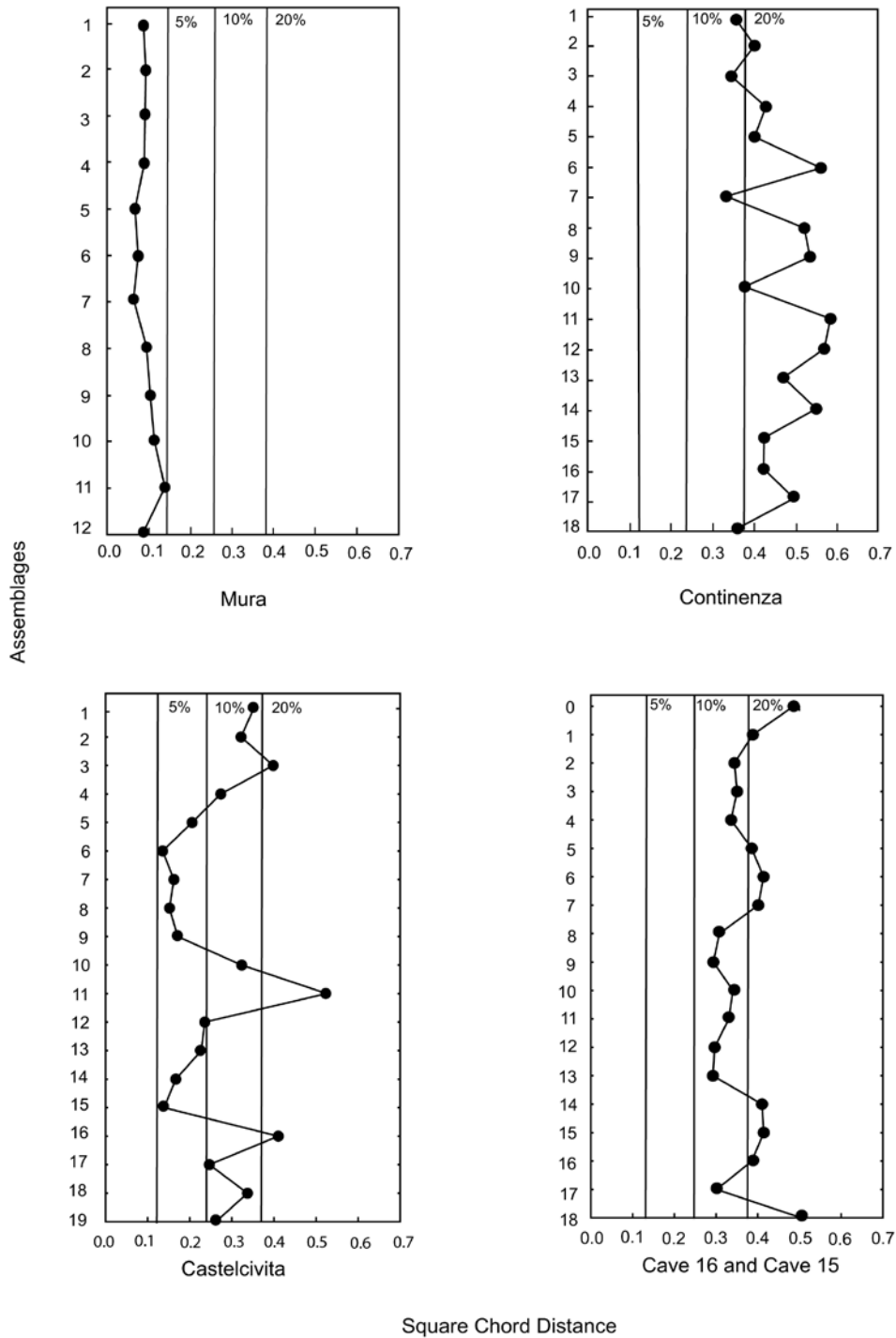


Fig. 13. Time series plots of the minimum dissimilarity (square chord distance) between each fossil assemblage and the PSMA training set. The vertical lines are drawn at various percentiles of the distribution of the pair-wise dissimilarities for the training set assemblages

Cave 16 and Cave 15. Throughout the period covered by the sequence, the AMTs were similar to the contemporary ones. They are within the limits set by the sample specific standard error of the reconstruction. However, it should be noted that at the bottom of the sequences there are intervals with temperatures slightly higher than today, and

at the top of the sequences, especially for layer 9, the temperatures were lower than current ones. The Holocene temperatures during the deposition of bone bearing sediment in Cave 15 were somewhat higher than present-day temperatures.

Maximum annual temperature (MTWM) was also similar to the modern one. It should be noted

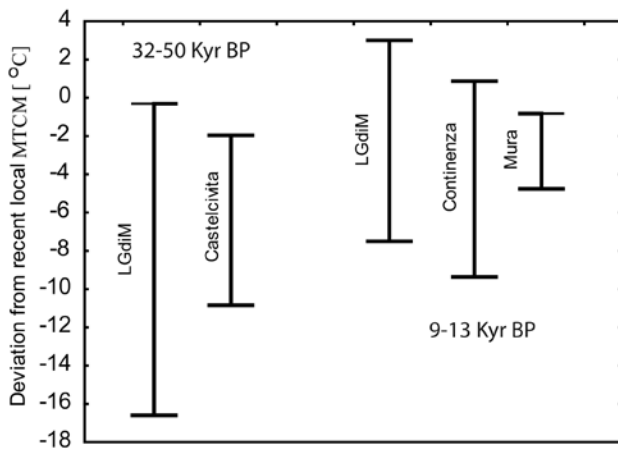


Fig. 14. Comparison of reconstructions based on pollen record from Lago di Monticchio (LGdiM), (data from <ftp://ftp.ncdc.noaa.gov/pub/data/paleo/paleolimnology/europe/italy>) and reconstructed temperatures based on small mammals from Castelcivita, Mura and Contineza Caves. The data are presented as deviations from the recent temperatures in the respective areas, derived from WorldClim database. MTCM – Minimal Temperature of Coldest Month

however, that it was about 2 °C lower in the layers 12, 11, 10, and by 2-3 °C higher at the top of layer 9.

The reconstructed changes in winter temperatures (MTCM) are better pronounced. They were 3-5 °C higher than today during the deposition of the lower layers. Then a gradual cooling occurred, especially well expressed in the upper part of layer 9, reaching 5-8 °C. Winter temperatures, reconstructed on the basis of the Holocene small mammal assemblage from Cave 15 were higher than today.

The seasonal amplitude changes were also great. Initially, the amplitude was less than the modern one in the area, and significantly higher during the deposition of the upper parts of layer 9.

The reconstructed climate indices are also in agreement with paleontological and lithological data. For example, climate recorded at the bottom of the sequence, although similar to the present-day one, had a different structure, which explains the combination of ecological groups of species that today do not occur together. Small amplitude and low summer temperatures in the layers 13-10 makes this climate similar to today's mountain climate in Bulgaria. It is different however in terms of the relatively soft winters. Significantly greater seasonal amplitude, recorded in layer 9, due to decreased winter temperatures and increased summer temperatures, is very well established in the ecological appearance of small mammal assemblages, and the lithology of this layer (dominance of angular rubble and large limestone blocks, see Fig. 6).

The differences between the Pleistocene and modern temperatures are better pronounced in the Castelcivita Cave sequence than in Cave 16 in Bulgaria, whose sequence at least partially corresponds with the Italian cave. On the other hand, winter temperatures have not reached such low levels as in Bulgaria. In this respect, the comparison of climate reconstructions made on the basis of small mammal assemblages located directly under CI tephra layers of both caves would be particularly informative. For the Italian cave this is the assemblage from layer *gic*, and for Cave 16 this is layer 8 (Figs. 5 and 6). For both localities the small mammal-inferred temperature parameters are lower than today, while the amplitudes are higher. The inferred quantitative values for both areas are similar. This speaks of the existence of a well pronounced climate cooling and continentalization. In comparative terms (relative to present day) the differences are more strongly expressed in the Italian locality. This indicates that geographical differences in climate during this period were different from today. The modern climates of both areas are well distinguished. In Italy it is warmer and with low amplitude.

The temperature reconstructions based on WAPLS are generally in a good correspondence with our understanding and interpretation of the palaeoenvironmental development in the areas under study described above.

Reliability of reconstructions

There are several means of evaluating how reliable the paleoclimatic reconstructions are. The most powerful evaluation procedures are 1) to validate the reconstruction against known historical records or 2) other independent paleoenvironmental records (BIRKS 1995).

The first approach can be applied in respect of the Holocene assemblages (Cave 15, Mura, Contineza). It should be expected that the reconstructed temperatures will be similar to the recent ones, especially compared with the reconstructions for the Late Pleistocene ones. Indeed, for most of the Holocene assemblages, the contemporary temperatures fall within the error range of the model (Figs. 11-13). The estimates of the temperature parameters for the Holocene assemblages are in agreement with the recent ones in the respective areas (see Table 3). For Mura, the uppermost assemblage, belonging to the earliest part of the Holocene (younger than 9.499 Kyr, Mesolithic) the reconstructed temperatures are slightly lower compared to recent ones, as it can be expected having in mind the general temperature trend during this

time interval. With Continenza Cave, the uppermost small mammal assemblages (s.21/22) are younger than 8 Kyr (Neolithic) the estimated versus modern temperatures (in parentheses) are as follows: AMT – 11.4 (11.8), MTWM – 27.9 (26), MTCM – -4.7(-0.5). It seems to indicate that derived transfer functions can provide reliable paleoclimatic estimates.

Comparison with independent paleoenvironmental records is difficult for Bulgaria because no quantitative climate reconstruction has been published. For Italy, there are some proxy records of MTCM (pollen), derived from lake sediments of Lago Grande di Monticchio (LGdiM), (40° 56' N, 15° 35' E, 656 m above sea level, Core D 1990 + core J 1994), covering the past 101530 yr. (HUNTLEY *et al.*, 1999, ALLEN *et al.* 2000a, b, ALLEN *et al.* 2002). In order to take into account the local climatic variation the comparisons between quantifications inferred from both types of proxies are presented as differences in relation to the recent ones in the respective area. Detailed correlation of small mammals sequences with the respective parts of pollen stratigraphy is difficult to establish given the highly sporadic karstic record and as a result many of the LGdiM records may not have direct equivalents in the small mammal record. For this reason comparisons are made within two time-spans based on calibrated ¹⁴C dates for the fossil sequences (Figs. 3-5) and the lamination-based calendar years for the pollen sequence of the LGdiM. Having in mind that the LGdiM chronology appears to be less accurate around 33 000 calendar yr BP (ALLEN *et al.* 2000b) as an additional stratigraphic benchmark for the comparisons of the results from Castelcivita Cave, the CI tephra layer (MT-8 in LGdiM stratigraphy) was used. As a result the coldest month mean temperature reconstructions for pollen zones 6-11 from LGdiM sequence were chosen for comparison with the reconstructions of MTCM based on Castelcivita small mammal sequence. Only ranges were considered having in mind the different resolutions of both types of palaeoenvironmental proxies which in turn may affect the comparability of means. It can be seen from the data presented on Fig. 14 that there is a fairly good correspondence between the reconstructions of MTCM based on pollen and small mammals. These comparisons indicate the overall reliability of the reconstructed temperatures based on small mammals.

Conclusions

This paper presents the first quantitative temperature reconstruction using small mammal stratigraphic assemblages preserved in Late Quaternary cave

sediments. It clearly demonstrates the importance of small mammals as a means of reconstructing past temperatures, quantitatively by means of modern calibration data-sets and transfer functions. The analysis of the modern calibration data of small mammal assemblages from owl pellets across the large temperature and precipitation gradients of Europe reveals that among the different prediction variables tested here, the Annual Mean Temperature, Maximal Temperature of Warmest Month, and Minimal Temperature of Coldest Month are the most important determinants of the spatial (geographical) variability of the structure of small mammal assemblages from owl pellets. The impact of precipitation parameters (Annual Precipitation, Precipitation of Wettest Month, Precipitation of Driest Month) and the agent of accumulation is much less compared with temperatures.

Among five tested species-environment models Modern Analogue Technique (MAT) and Weighted Averaging Partial Least Squares (WAPLS) were identified as being superior to Partial Least Squares regression, Weighted Averaging, and Maximum Likelihood. When applied to fossil data set WAPLS and MAT revealed similar patterns of Late Quaternary temperature changes. However, additional analyses indicated that MAT based inferences for non-modern-analogue fossil samples appear to be less reliable than those based on WAPLS. Reconstructed temperatures agree well with the previous qualitative interpretations, known climate trends and reconstructions based on other proxies.

The reconstructed temperatures shows significant climate differences between Balkan and Appennine Peninsulas during the the cold period associated with the CI tephra layer (before ca. 40 ka BP). In Bulgaria (Cave 16) due to its geographical location changes of amplitude, respectively, of climate continentality are much better pronounced in comparison with Apennine Peninsula. It can be supposed that changes in summer temperatures and climate continentality have a strong indirect effect on small mammals as they affect the appearance of vegetation, and from there affect the nature of the habitats. Relatively low summer temperatures, respectively lower amplitudes, cause less arid climate and wide spread forest. Conversely, high summer temperatures in conditions of continental climate, leading to droughts in the vegetation season cause prevalence of grass vegetation and open habitats. That is why, on the basis of indirect climatic reconstructions it is difficult to distinguish the influence of temperature from the impact of climate humidity on small mammal assemblages. In this sense, the pro-

posed approach for paleoclimatic reconstructions is promising, since it is a much more objective, quantitative and ensures comparability of results obtained from different geographic areas, often very different in terms of their species composition.

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Appendix 1. Training data set of small mammal assemblages from pellets of birds of prey from literature sources

Bulgaria, 32 sites: *Asio otus* (Simeonov, 1964), *Bubo bubo* (Mitev and Boev, 2006; Simeonov et al., 1998), *Strix aluco* (Simeonov, 1963), *Tyto alba* (Miltchev et al., 2004; Simeonov et al., 1981), Czech Republic, 1 site: *Asio flammeus* (Bencová et al., 2006), Finland, 8 sites: *Aegolius funereus* (Jaderholm, 1987; Korpimäki, 1988), *Asio otus* (Korpimäki, 1992), *Falco tinunculus* (Korpimäki, 1986), *Nyctea scandiaca* (Hakala et al., 2006), *Strix uralensis* (Jaderholm, 1987), France, 3 sites: *Asio flammeus*, *Asio otus*, *Tyto alba* (Chaline et al., 1974), Great Britain, 16 sites: *Strix aluco* (Petty, 1999), *Tyto alba* (Love et al., 2000), Germany, 1 site, *Tyto alba* (Temme, 2006), Greece, 26 sites: *Asio otus*, *Athene noctua*, *Bubo bubo* (Alivizatos et al., 2005), *Tyto alba* (Niethammer, 1989; Alivizatos et al., 2005, Bontzorlos et al., 2005), Italy, 21 sites: *Asio otus* (Capizzi et al., 1998; Guidoni et al., 1999; Riga, Capizzi, 1999; Cecere and Vicini, 2000), *Strix aluco* (Capizzi et al., 1998; Guidoni et al., 1999), *Tyto alba* (Contoli et al., 1977; Capizzi et al., 1998), Lithuania, 14 sites: *Asio otus* (Balčiauskienė, 2006; Balčiauskienė et al., 2006), *Strix aluco* (Balčiauskienė et al., 2005; Balčiauskienė and Narusevicius, 2006; Balčiauskienė, 2006; Balčiauskienė et al., 2006), Poland, 3 sites: *Asio otus* (Skierczynski, 2003), *Athene noctua* (Grzywaczewski et al. 2006), *Strix aluco* (Zmihorski and Osojca, 2006), Romania, 1 site, *Asio otus* (Schnapp, 1968), Russian Federation, 20 sites: *Aegolius funereus* (Boiko and Shutova, 2005), *Asio otus* (Gibet, 1972), *Glaucidium passerinum* (Boiko and Shutova, 2005), *Strix nebulosa* (Karyakin, 1998), Spain, 3 sites: *Asio otus* (Amat and Soriguer, 1981; Saavedra, 1987), *Tyto alba* (Amat and Soriguer, 1981), Switzerland, 1 site, *Tyto alba* (Roulin, 2004), Syria, 2 sites: *Tyto alba* (Shehab, 2005; Shehab and Al Charabi, 2006), Turkey, 1 site: *Asio otus* (Seckin and Coskun, 2006), Ukraine, 8 sites: *Asio otus*, *Athene noctua* (Kondatrenko and Tovpynec, 2001).

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