



Atti del 6° Convegno Nazionale di Archeozoologia

Centro visitatori del Parco dell'Orecchiella

21-24 maggio 2009

San Romano in Garfagnana - Lucca

a cura di

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Body size variability in cave bears from the Southern Alps

Variazione della stazza corporea nell'orso delle caverne nelle Alpi meridionali

Summary - During the Last Glacial, the cave bear (*Ursus spelaeus* Rosenmüller, 1794) was widely spread in Europe from the Atlantic coast to the Ural Mountains. The vast numbers of its remains found in caves have enabled scholars to obtain a fairly complete picture of its geographical distribution, anatomy, evolution and pathology. In spite of this wealth of cave bear remains, however, many important aspects of its palaeobiology remain poorly understood. One such aspect regards the reason behind the diachronic variations in body size, which are usually linked to sexual dimorphism, polytypism, continual or clinal geographic variation and continual intraspecific variability. This paper is aimed at further clarifying the diachronic variations in cave bear body size by studying the material originating from the Southern Alps. The results of the study showed that oscillations in temperature and humidity might have been one of the main factors influencing the size variability of cave bears of each sex excavated at the studied sites, with individuals originating from colder (and possibly also damper) periods having been larger. Such a conclusion is in line with the biology of extant brown and black bears and is linked by the authors to the supposed prolongation of the energy-saving dormancy period in harsher climates.

Riassunto - Durante l'ultimo glaciale l'orso delle caverne (*Ursus spelaeus* Rosenmüller, 1794) fu distribuito in Europa dall'Atlantico agli Urali. Il grande numero di resti ritrovati ha permesso agli studiosi di ottenere una abbastanza buona conoscenza della sua distribuzione geografica, anatomia, evoluzione e patologie. Altri aspetti importanti della paleobiologia di questa specie, al contrario, rimangono non ben chiariti. Una delle problematiche che necessitano di approfondimenti è quella che tratta i fattori all'origine della variazione diacronica della stazza corporea. Essa viene solitamente legata al dimorfismo sessuale, politipismo, variazione clinale o geografica, nonché alla variabilità intraspecifica continua. L'obiettivo generale di questa comunicazione è di contribuire alla chiarificazione della problematica della variazione diacronica della stazza corporea nell'orso delle caverne studiando reperti provenienti dalle Alpi meridionali. I risultati indicano che le oscillazioni di temperatura e di umidità possano essere stati tra i fattori principali ad aver contribuito alla variazione della grandezza nell'orso delle caverne di entrambi i sessi, con gli individui vissuti in periodi caratterizzati da clima più ostile che in media mostrano una stazza maggiore. Questa conclusione sembra essere confermata dai risultati delle ricerche sull'orso bruno e sull'orso nero americano attuali che, ai deterioramenti climatici rispondono con il prolungamento del periodo di torpore invernale.

Key words: Würm, Southern Alps, cave bear, size variability, climate.

Parole chiave: Wurmiano, Alpi meridionali, orso delle caverne, variazione della stazza corporea, clima.

INTRODUCTION

During the Last Glacial, the cave bear (*Ursus spelaeus* Rosenmüller, 1794) was widely spread in Europe from the Atlantic coast to the Ural Mountains. The vast number of its remains found in caves have prompted palaeontologists to intensively study its geographical distribution, anatomy, evolution, pathology, genetics etc. in order to better understand the palaeobiology of the species. An interesting fact that emerged from these studies is the existence of evident diachronic variations in body size, which are usually linked to sexual dimorphism (e.g. Kurtén 1955; Baryshnikov *et al.* 2003; Grandal d'Anglade, López-González 2005; Toškan 2007), polytypism (e.g. Hofreiter *et al.* 2002; Orlando *et al.* 2002; Rabeder *et al.* 2004), continual or clinal geographic variation (e.g. Kurtén 1955; 1968;

Rabeder *et al.* 2000), adaptation to differential altitude of the habitat (e.g. Ehenberg 1929; Rabeder *et al.* 2008) and continual intraspecific variability (e.g. Kurtén 1955; Thenius 1958; Grandal d'Anglade 1993; Perego *et al.* 2001; Toškan 2007).

Recently, Toškan (2008) proposed an alternative interpretation of these variations, linking them to oscillations in temperature and humidity. According to his thesis, individuals from colder (and possibly also damper) periods grew larger relative to those that lived in a more temperate (and dry) climate. Such a response to extreme environmental conditions is thought to have been even more pronounced in pregnant females and females with yearlings, as they were liable for the energy costs of reproductive processes. Even though Toškan's conclusions seem to be in line with the biology of extant brown and black bears, their validity is yet to be

ascertained. All the more so since the cave bear remains he analysed all originated from a single site (i.e. Divje babe I, W Slovenia). In this paper we aim at verifying the above thesis by amplifying the original (i.e. Divje babe) data set with cave bear material from two northwestern-Italian cave sites: Caverna Generosa (Como province, Lombardy) and Grotta Sopra Fontana Marella (Varese province, Lombardy; Fig. 1).

SITES

Divje babe I

Divje babe I is a 45 m long and up to 15 m wide horizontal cave, lying 230 m above the bed of the Idrijca River near Cerklno in western Slovenia (450 m a.s.l.). The thickness of the Pleistocene clastic sediments – composed mostly of autochthonous dolomite blocks, rubble, sand and silt – exceeds 13 m. Excavation established 26 *ad hoc* delineated geological layers (time span: approx. 115–35/40 ky BP), which Turk (2003) subsequently pooled together into three new basic stratigraphic units, the so-called Facies A to C. More than 90 (Blackwell *et al.* 2007 and there cited sources) available ^{14}C (AMS) and ESR dates have shown that facies A and B formed in the Oxygen Isotopic Stage 3 (= OIS 3) and Facies C in OIS 5a–5d. OIS 4 is almost not represented in the cave, since a pause in sedimentation occurred at that time. The transition between facies A and B corresponds with layer 7 (i.e. approx. 50,000 years B.C.) and the transition between facies B and C with the layer 11/12 (i.e. approx. 74,000 B.C.), thereby corresponding to the radiometrically determined chronological border between OIS 5 and OIS 4 (Turk *et al.* 2001; Blackwell *et al.* 2007). The above chronology is further corroborated by sedimentological, palaeobotanical and palaeontological data (Turk 2007).

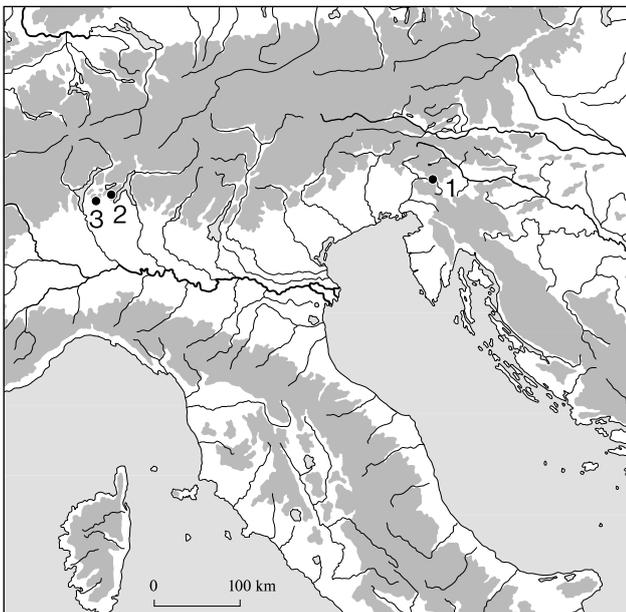


Fig. 1. Location of the studied sites. Legend: 1 – Divje babe I; 2 – Caverna Generosa; 3 – Grotta Sopra Fontana Marella.

Caverna Generosa

The Caverna Generosa cave opens at an altitude of 1450 m a.s.l. on the steep southern slope of the Monte Generoso Massif between the Lugano and the Como lakes in northern Italy. It forms a complex group of galleries and inner chambers: after the first narrow passage ('Cunicolo'), which is about 25 m long, there is a small hall called 'Saletta'. From there a narrow siphon leads further into the cave to a notably wider hall named 'Sala Terminale' (i.e. Terminal room), where the here studied cave bear remains were collected. The recovery of several flakes, including a few Levallois specimens, proves the incursions of Mousterian groups (Bona *et al.* 2007). Sedimentological and palaeontological data, as well as radiocarbon dates, place both the cave-bear and the human frequentations of the cave in the first part of the OIS 3.

The stratigraphic sequence of the 'Sala Terminale' is composed of 13 levels, of which only the youngest six have been investigated in detail. All the five available AMS ^{14}C dates from Caverna Generosa were obtained by analysing cave bear bones originating from this complex of levels, fixing their deposition in the time span between approximately 39 and 51 ky BP (Bona 2004, Fig. 2). According to the small mammal remains, the environment of the time changed progressively from scarcely arboreal (levels 5, 6, 8, 9 and III) to arboreal-brush with small open spaces (levels 0, 1, 2, 2b, A, B, I; Bona 2006; Bona *et al.* 2007, 308 f).

Grotta Sopra Fontana Marella

The Grotta Sopra Fontana Marella cave is located a few kilometres west of Caverna Generosa in Varese province. It opens on the north-eastern slope of the calcareous-dolomitic massif of Monte Campo dei Fiori at 1040 m a.s.l. (i.e. above the maximum extension of the glaciers). The deposit fills a vertical fissure with intense karstic phenomena. The thickness of the investigated sequence is about 2 m and includes 12 stratigraphic levels. In this paper we discuss the cave bear remains originating from three of the four upper levels, which were radiometrically dated to approximately 22 ky BP (FM1 and FM2) and 4 ky BP (FM4). The latter age disagrees both with stratigraphical evidence and the extinction dating of *U. spelaeus*, hence it has to be considered wrong. FM4 being indeed older than 22 ky BP (~26,000 cal BP) is further confirmed by the results of the aminoacid racemization analysis (Perego *et al.* 2001).

The climate during the deposition of FM4, as suggested both by small mammal remains (Bona 2006) and by palynological data (Perego 1993), was relatively mild and wet, thus allowing for a large spreading of forest trees (mainly *Betula* and *Pinus*) on the Campo dei Fiori slope. Levels FM1 and FM2, by contrast, were formed in a much

colder period, resulting in an environment characterized by wide open land and restricted wooded areas. Indicative of this is the dominance of *Microtus arvalis* together with the scarcity of *Glis glis*, *Myodes glareolus* and *Arvicola terrestris* as well as the floral arrangement typical of grassland and steppe (e.g. *Artemisia* sp., *Ephedra fragilis*, *Centaurea* sp., *Alchemilla* sp.).

MATERIAL AND METHODS

In the case of Divje babe I and Caverna Generosa, the diachronic variations in body size were followed by comparing the sizes of completely preserved fused metacarpals of different geological age. Since the cave bear shows a well-marked sexual dimorphism (cf. Kurtén 1955; Reisinger, Hohenegger 1998; Grandal d'Anglade 2000; Rabeder 2001), it was necessary for the metacarpals to be sexed (Tab. 1). This was done using the Principal Component Analysis (PCA) and the Discriminant Function Analysis (DFA).

The first part of the sexing procedure consisted in applying the PCA to the correlation matrix of standardized data for eight linear measurements of metacarpals 1 to 5 from facies A and C of Divje babe I. The standardization was aimed at substituting the absolute differences in values of individual dimensions between metacarpals with the relative deviation of individual specimens from the average value of the given dimension in the reference sample (in our case represented by the metacarpals from facies B of the same site, i.e. Divje babe I). By doing so we were allowed to pool together all the metacarpals 1 to 5 to form a uniform and thus much larger statistical sample (Toškan 2007, 397 f).

As is known the principal component analysis (PCA) is a mathematical procedure that uses an orthogonal transformation to convert a set of observations of possibly correlated variables into a set of values of uncorrelated variables called principal components. The number of principal components is less than or equal to the number of original variables. This transformation is defined in such a way that the first principal component (PC 1) has as high a variance as possible (that is, accounts for as much of the variability in the data as possible; StatSoft Inc. 2001). Consequently, in biometry PC 1 is as a rule seen as a proxy for body size, which we took advantage of to sex the cave bear metacarpals basing ourselves on the distribution of the first principal component scores (PC 1 scores).

Since the referential sample for standardizing the linear measurements was composed of metacarpals

Site	Males	Females	Total
Divje babe I	187	136	323
Caverna Generosa	72	119	191

Tab. 1. The number of analysed male and female metacarpals from Divje babe I and Caverna Generosa. The sexing procedure is explained in the text.

from facies B (see above), the latter could not have been sexed by applying the same approach. Instead, specimens originating from facies B of Divje babe I – as well as those from Caverna Generosa – were sexed by using the predictive classification of cases within the Discriminant Function Analysis (DFA; Toškan 2009, 36 f). DFA is a statistical analysis to predict a categorical dependent variable by one or more continuous or binary independent variables. It is statistically the opposite of ANOVA or MANOVA, which is used to predict one (ANOVA) or multiple (MANOVA) continuous dependent variables by one or more independent categorical variables. In simple terms, discriminant function analysis is classification - the act of distributing things into classes or categories of the same type (StatSoft Inc. 2001). In our case the model for the predictive classification of cases has been finalized (i.e. the discriminant functions have been derived) based on the metric data related to the already sexed metacarpals from Divje babe I - facies A and C.

The so obtained results were further tested for reliability by comparing them to those inferred from the bimodal distribution of geometric means (GM) calculated by using the same set of linear measurements (cf. Green *et al.* 2007, 190). Because of major inconsistencies between the results of the two sexing methods in the case of metacarpals 5, only metacarpals 1 to 4 were included in further analyses. As far as metacarpals 1 to 4 are concerned, the inhomogeneities between the two methods were very few and were eventually corrected. Finally, the total number of sexed metacarpals to be analysed in detail equalled 681 for Divje babe I and 191 for Caverna Generosa.

The overall size of the metacarpals from Divje babe I was calculated as the geometric mean of all eight linear measurements drawn from a particular metacarpal (Fig. 2): greatest length (gL), medio-lateral breadth of the proximal end (pB), antero-posterior breadth of the proximal end (pH), smallest medio-lateral breadth of the diaphysis (sDB), smallest dorso-palmar or dorso-plantar breadth of the diaphysis (sDH), greatest medio-lateral breadth of the distal end (gdB), medio-lateral breadth

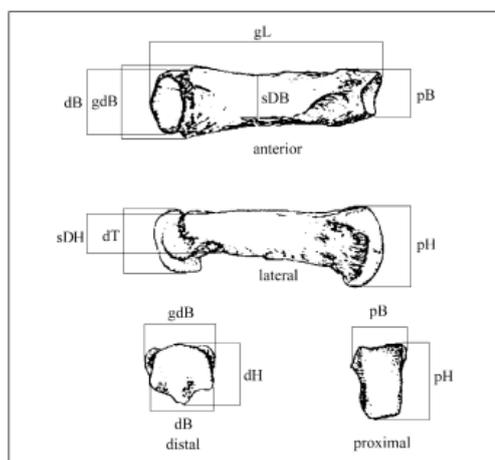


Fig. 2. Cave bear (*Ursus spelaeus*) metacarpal with indicated measurements.

of the distal epiphysis (dB) and antero-posterior breadth of the distal end (dH). In the case of Caverna Generosa the latter two (i.e. dB and dH) have not been measured and thus could not be used in the calculation of GM. Irrespective of this, the geometric mean is considered to have effectively combined multiple measurements into a single measure of size (cf. Jungers *et al.* 1995; Green 2007) in both of the mentioned cave-sites. In comparing the size of metacarpals of different geological ages the average value and standard deviations were used, as the metric data are normally distributed. Consequently, the statistical significance of differences was tested by the one-way analysis of variance. Statistical analysis was performed using STATISTICA for WINDOWS program package (StatSoft. Inc. 2001).

In the case of Grotta Sopra Fontana Marella, the conclusions presented in this paper are not based on our own data but on those published by Perego *et al.* (2001). In the absence of metacarpal measurements, the emphasis has been placed on (mostly nonlength) dimensions of extremities' long bones. In total, metric data concerning 15 humeri, 21 ulnae, 12 radii, 14 tibiae and 10 femuri of adult cave bears have been taken into consideration (Perego *et al.* 2001, Fig. 7). Due to the small sample sizes, reliable sexing of these bones was not feasible (cf. Perego *et al.* 2001, 459). Nevertheless, by comparing the size of the cave bear remains from this site to those originating from Divje babe I the sex ratio could have been assessed at least approximately.

RESULTS

Divje babe I

The distribution of geometric mean scores for metacarpals from facies C (dated to OIS 5a) and those from facies A and B (dated to OIS 3) is shown in figures 3 and 4. It is evident that the average size of specimens from facies C lags behind that of metacarpals from facies A and B, with the difference being above the level of statistical significance (F-test: $p < 0.05$). The only exception in this sense is represented by male metacarpals 3, with the p-value of the F-test equalling 0.065. However, even in this case, the specimens from facies A and B did surpass in average overall size those from facies C. Similar conclusions can be drawn from analyses of metric data collected on long bones (Jambrešić, Turk 2007) and teeth (Debeljak 2002).

Further comparisons of the size of metacarpals in which specimens from colder intervals of OIS 3 (i.e. of facies A and B) are compared to those from more temperate phases of the same period, are in progress. The first preliminary results seem to be in line with what has been described above, i.e. that specimens associated with a colder climate tend to be larger. It has to be said that the observed discrepancies are not as evident as in comparing bears from OIS 5 and OIS 3, however, nor are the differences in the climate. Again, as above, the differences are more evident in females. An exception to this rule seems to be represented by metacarpals 1, which show no trend (or even the opposite one). This might possibly be explained

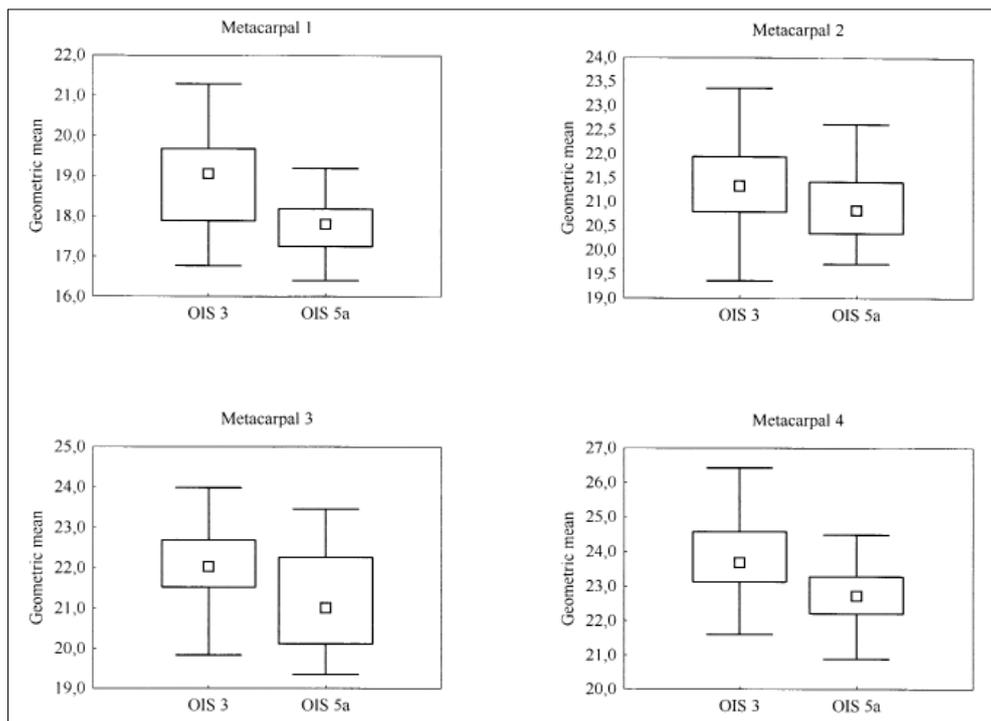


Fig. 3. Size (expressed as the geometric mean) of metacarpals 1 to 4 of female cave bears (*Ursus spelaeus*) deposited during OIS 3 and OIS 5a in Divje babe I. The smallest box in the plot (= middle point) represents the mean (central tendency) of the variable, while the dispersion (variability) is represented by ± 1 times the standard error (large box) and ± 1 times the standard deviation about the mean ("whiskers").

by the specific biomechanics of walk of the cave bear, as this relatively small metacarpal bone bears only a minimal part of the animals' weight (*cf.* Diedrich *et al.* 2008) and might have thus been relatively less influenced by its variations (Toškan, in preparation).

Caverna Generosa

The excavations in Caverna Generosa yielded a significantly lower number of completely preserved fused metacarpal bones relative to Divje babe I. Consequently, by treating each of the metacarpals 1 to 4 separately, no clear picture emerged of the relationship between the average overall size of specimens originating from a relatively temperate phase of OIS 3 (i.e. levels 0, 1, 2, 2b, A, B and I) and those from a much colder interval of the same period (i.e. levels 5, 6, 8, 9 and III) (see e.g. Fig. 5).

With this fact in mind we decided to compare the overall metacarpal size by using as a proxy the scores of

the first principal component, again calculated on the basis of standardized metric data in order to allow the pooling of all the male/female metacarpals together into a single sample. As already explained, the first principal component (PC1) accounts for as much of the variability in the data as possible, and is thus as a rule seen as (the sole) bearer of the size information. It follows that any differences in the distribution of PC1 scores emerging from the comparison of metacarpals from Caverna Generosa, associated with the two climatically differing phases of OIS 3, are to be interpreted as divergences in the average overall (body-) size.

The results are interesting as they conform to what seems to have emerged from the similar (though still preliminary) study of the material from Divje babe I mentioned above. Namely, the differences in average overall size are more evident in females, with specimens associated to the colder phase(s) being larger (Fig. 6). As a matter of fact, males from Caverna Generosa do not seem

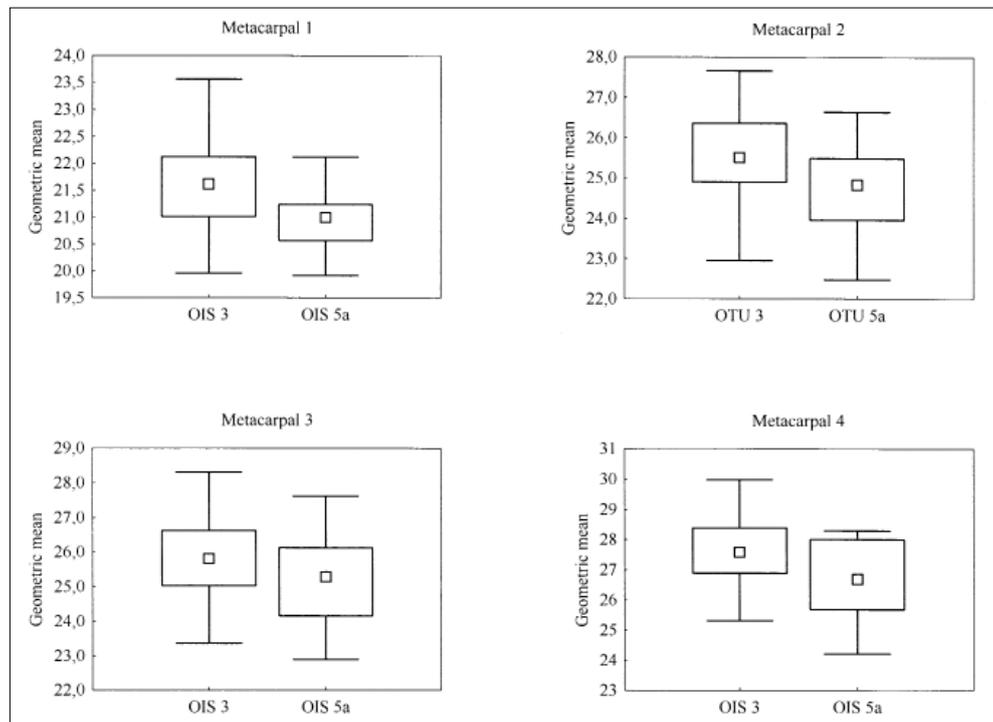


Fig. 4. Size (expressed as the geometric mean) of metacarpals 1 to 4 of male cave bears (*Ursus spelaeus*) deposited during OIS 3 and OIS 5a in Divje babe I. Legend: see captions to figure 3.

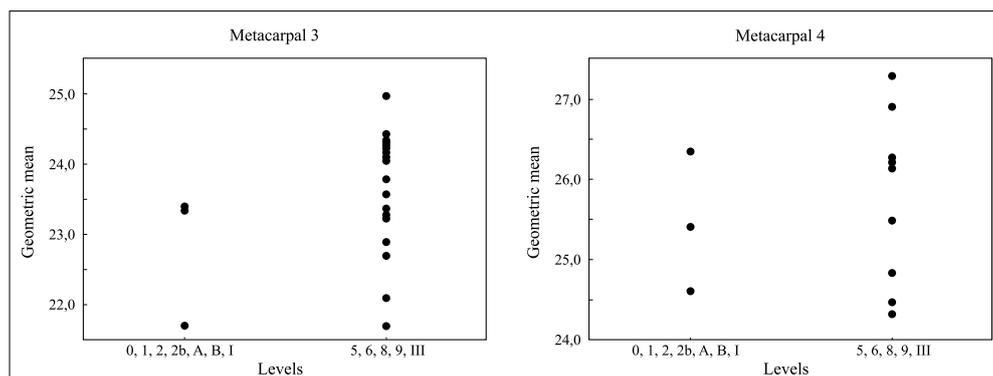


Fig. 5. Size (expressed as the geometric mean) of metacarpals 3 and 4 of female cave bears (*Ursus spelaeus*) originating from levels 0, 1, 2, 2b, A, B, I and levels 5, 6, 8, 9, III of Caverna Generosa.

to have differed in average size at all. This may even not be surprising if we consider the decidedly less pronounced size discrepancies uncovered by comparing the size of males from OIS 5a and OIS 3 relative to females from the same two periods in the case of Divje babe I (Toškan 2009, 40).

Grotta Sopra Fontana Marella

A detailed morphometrical study of cave bear remains from Grotta Sopra Fontana Marella has already been done by Perego *et al.* (2001), who report of a significant increase in the size of several cranial and postcranial skeletal elements at levels FM1 and FM2 relative to FM4 (Fig. 7). Their observations match those, which emerged from the studies of the material from Caverna Generosa and Divje babe I, as the climate during the formation of level FM4 is supposed to have been more temperate. The problem that Perego *et al.* (2001) addressed, yet have failed to solve definitively, concerns the sexing of long bones, which may potentially have important implications for the interpretation of the results. Namely, if the share of females in the material from level FM4 significantly exceeds that in FM1 and FM2, then the observed size discrepancies might well be attributable to sexual dimorphism and not to e.g. climatic oscillations. With the aim of shedding additional light on this problematic, we compared the size of individual long bones from Grotta

Sopra Fontana Marella to those from Divje babe I. As the latter sample includes male and female specimens from both temperate and cold intervals of the OIS 5 and OIS 3 periods, it should give a reasonable good framework for the assessment of the intra-species variability in body size. The results are reassuring, as in most of the cases (i.e. humeri [Fig. 7a], ulnae, radii and femora) the concerns that females might significantly predominate at level FM4 and males at levels FM1 and FM2 proved to be unfounded. With the only exception in this sense being represented by tibiae (Fig. 7b), the possibility of the observed diachronic size variability being linked (mostly) to sexual dimorphism can be effectively rejected.

DISCUSSION

Metric analysis of cave bear metacarpals from Divje babe I and Caverna Generosa, as well as of long bones from the Grotta Sopra Fontana Marella cave site, emphasized the existence of diachronic changes in body size (Figs. 3–7). Contrary to the usual view in palaeontology, these changes do not seem to be due either to cave bears becoming larger and more robust with time or to polytypism, or to sexual dimorphism. The latter reason can be ruled out right away due to the fact that the here presented analysis treated the metacarpals/long bones of the two sexes separately. Similarly improbable is the possibility of the detected variations in body size being explainable by the cave

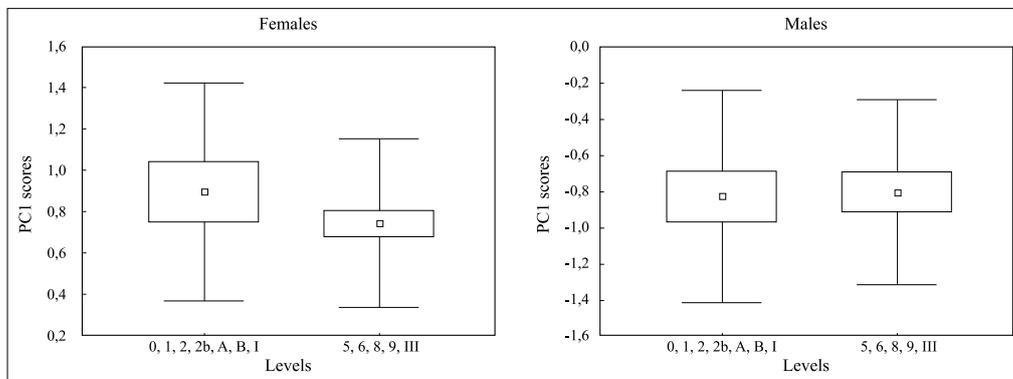


Fig. 6. Size (expressed as PC1 scores) of metacarpals 2 to 4 of female (left) and male (right) cave bears originating from levels 0, 1, 2, 2b, A, B, I and levels 5, 6, 8, 9, III of Caverna Generosa. Because of negative factor loadings, large specimens show low PC1 scores and vice-versa. Legend: see captions to figure 3.

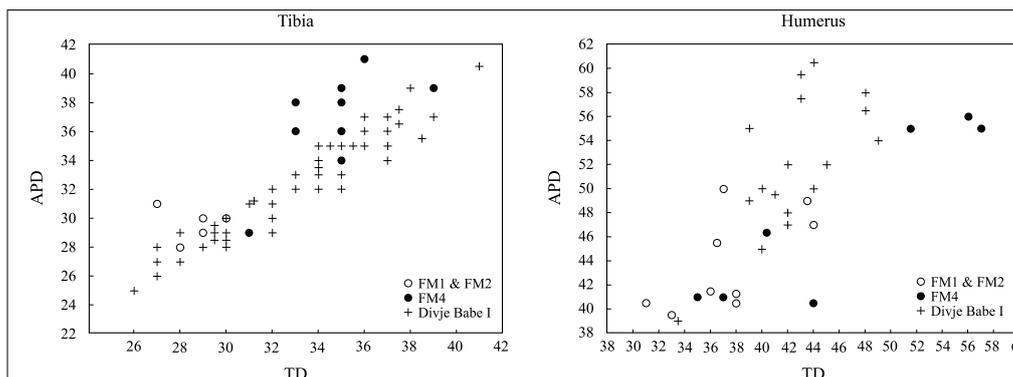


Fig. 7. The scatterplot of transversal (TD) and antero-posterior (APD) diameters of diaphysis of humerus and tibia for the material from Grotta Sopra Fontana Marella. Also shown are the data for cave bears from Divje babe I. All measurements are in mm. Modified from Perego *et al.* (2001, Fig. 7).

bears becoming larger and more robust with time. Not only do the metric data on first lower molars from Divje babe I effectively demonstrate that the temporal trend in cave bear body size was not linear (Debeljak 2002). Even more telling is the trend of the metapodial size variations observed in female cave bears from Caverna Generosa with specimens from younger geological contexts tending to be larger relative to those from older ones (Fig. 6).

The latter argument is valid also in rejecting the thesis of polytypism. Namely, if – as proposed by Rabeder and Hofreiter (2004) – a considerably larger cave bear species did indeed immigrate into the Alps approximately 50 ky ago (i.e. *Ursus ingressus* Rabeder *et al.*, 2004), progressively replacing *Ursus spelaeus* in this part of Europe, then why did the Caverna Generosa females grow progressively larger? Moreover, *U. ingressus* is supposed to differ from *U. spelaeus* in the metapodial bone proportions (Rabeder *et al.* 2004, 58; Withalm 2004, 156 ff), but Toškan (2006, 154) found no statistically significant morphometrical differences between specimens from the three facies of Divje babe I. It thus does not come as a surprise that the preliminary results of palaeogenetic investigations of cave bears from the mentioned site showed the sequenced specimens from each of the three facies to invariably fall within the same clade (Stiller *et al.* 2009, supplemental material: tab. S2).

As none of the common explanations seems to account for the observed diachronic variations in metacarpal/long bone size for cave bears from the three studied sites, we focussed our attention on the possible influence of the climate. After all, body size was observed to have increased with the onset of colder (and possibly damper) conditions in both Divje babe I (Figs. 3–4) and Grotta Sopra Fontana Marella (Fig. 7; Perego *et al.* 2001; Figs. 5–7). Analogously, the ameliorated climate conditions during the deposition of levels 0, 1, 2, 2b, A, B and I of Caverna Generosa saw (female) cave bears growing smaller (Fig. 5).

If climate is really “to blame” for the observed diachronic variations in cave bear body size, then the reason behind it is hardly Bergmann’s rule (Mayr 1956). A lower *body surface area / body volume* ratio is undoubtedly energetically economical in homeotherms. Bears are, however, known to have alternative ways of energy saving, such as a thicker winter fur (Rogers 1981, 67; Pasitschniak-Arts 1993, 4) and winter dormancy. Moreover, neither the extant brown bear (*Ursus arctos* Linnaeus, 1758), nor the American black bear (*Ursus americanus* Pallas, 1780) conforms to Bergmann’s rule (Geist 1987, 1037; Kojola, Laitala 2001). The fact that the magnitude of stored fat becomes a greater fraction of body mass as size increases (Lindstedt, Boyce 1985, 873), on the other hand, does seem to fit our results fairly well. Even more so since cave bears are known to have been herbivorous animals that spent winters in energy-saving dormancy. If smaller individuals are supposed to have depleted their energy reserves first, making them succumb to starvation before

larger-than-average cave bears, then longer winters with substantially more abundant snowfall during the colder phases of Würm understandably led to the prolongation of the dormancy period (*cf.* Fernández Mosquera *et al.* 2001; Germonpré 2004, 54 f) and thus to the need to increase autumn energy reserves in individuals of both sexes. Since the limiting factor for cave bears from colder phases to appease these augmented energetic needs had less to do with the quantity of food in general than with the extremes in seasonal food availability, the increase in body size during these periods is both feasible and likely.

What remains to be explained are the inter-sexual differences in the observed diachronic variations in body size. Namely, in the case of Caverna Generosa, the decrease in body size with the onset of more temperate climate conditions has been observed in females only. Moreover, oscillations in body size happened to be decidedly more pronounced in females relative to males also in the case of Divje babe I (see above). In trying to explain such a picture, data on the biology of extant brown and black bears were used. As noted by Ferguson and McLoughlin (2000, Tab. 1), age at maturity and interbirth interval in brown bear populations characterized by low population density increase with greater seasonality. Since mature females are liable for the energy costs of reproductive processes, their seasonal weight gain and loss exceeds that of males, both relatively and absolutely (Kingsley *et al.* 1983, 178). It thus does not come as a surprise that the (spring) weight of females levels off soon after the average age of first reproduction, while that of males continues to increase through maturity and eventually reaches nearly twice that of females (Kingsley *et al.* 1983, Fig. 1; Hilderbrand *et al.* 2000). Somewhat longer winters with substantially more abundant snowfall during colder phases of Würm most probably triggered the increase of age at maturity and interbirth interval also in cave bear females. By getting their first litter later in life, they would have the chance to prolong the investment in their own body size. Ultimately, such a scenario would have resulted in females from colder phases of the last glacial growing larger relative to individuals from more temperate phases of the same geological period, without having any direct effect on the body size of males.

CONCLUSIONS

The diachronic variations in cave bear body size which emerged from the analysis of metacarpals/long bones from Caverna Generosa and Grotta Sopra Fontana Marella (*cf.* Perego *et al.* 2001) are satisfactorily explainable by climatic oscillations during the last glacial. As is the case in extant brown and American black bears, harsher climates are supposed to have prompted cave bears to prolong the energy-saving dormancy period, which required an increase in autumnal accumulation of adipose tissue (~ size). Other factors might have contributed to

the phenomenon (cf. Perego *et al.* 2001, 460 ff), but in a supposedly minor way (cf. Turk, Dirjec 2007, Tab. 12.3.1; Bocherens 2008). Inter-sexual differences observed in the case of Caverna Generosa and – at least as far as the pronouncement of size oscillations is concerned – also in Divje babe I, do not contradict the above thesis as they are explainable with females being liable for the energy costs of reproductive processes. The results here presented are thus supporting Toškan's model developed while studying the cave bear remains from Divje babe I (Toškan 2008).

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