CAVE BEAR METAPODIALS FROM DIVJE BABE I (WESTERN SLOVENIA)

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Abstract: The excavation of the Late Pleistocene cave site of Divje babe I (Western Slovenia) yielded several thousand cave bear metapodials. Multivariate statistical analysis of metric data for 1,598 metacarpals and metatarsals allowed these bones to be grouped according to sex. The differences in sex ratio between the samples from OIS 5a-5d and OIS 3 are explained with the increased intersexual competition for lairs in OIS 3 due to more severe climatic conditions.

Key words: Divje babe I, cave bear, metapodials, sex structure, palaeoclimate.

INTRODUCTION

The cave-bear group is by far the best represented animal taxonomic unit in the fauna of the Late Pleistocene cave site of Divje babe I. The majority of remains probably belonged to animals that died during or just after hibernation. The high number of finds enabled a detailed biometric analysis of many skeletal elements, from long bones (Jambrešić & Turk, in press) and isolated teeth (Debeljak, 2002a) to skulls (Toškan, in press (a)). The excavated material also includes several thousand metapodials. These hefty, compact bones are relatively numerous in many Late Pleistocene sites and are therefore often subject of detailed morphometric analyses (for example Rakovec, 1967; Pohar, 1981; Krklec, 1997; Gužvica & Radanović-Gužvica, 2000; Withalm, 2001; 2004; 2005). Considering their role in the biomechanics of walking (Opavský, 1990), such attention is justified in principle, though conducting such analyses without knowing the sex ratio of the sample raises many doubts. Namely, the cave bear shows well-marked sexual dimorphism (*cf.* Kurtén, 1955; Reisinger & Hohenegger, 1998; Grandal d'Anglade, 1993; 2000; Rabeder, 2001; Baryshnikov *et al.*, 2003), which was surely reflected also on the metatarsals and (particularly) on the metacarpals. For this reason, the method for sexing cave bear metapodials based on their size is presented below.

MATERIAL AND METHODS

Divje babe I is a 45 m long and up to 15 m wide horizontal cave, opening towards the north-west, and lies 230 m above the bed of the Idrijca River near Cerkno (western Slovenia; 450 m above sea level). The thickness of the Pleistocene clastic sediments exceeds 13 m. They are composed mostly of autochthonous dolomite blocks, rubble, sand and silt (Turk, 1997). There were 26 layers determined during excavation (time span: approx. 115.000 - 35.000/40.000 years B.C.), which are mostly difficult to set apart macroscopically. Turk (2003) therefore substituted the *ad hoc* delineated geological layers with new basic stratigraphic units, the so-called facies A to C. The substitution is based on the analysis of the vertical distribution of structural aggregates (0.5 - 3 mm) and bone remains (> 3 mm) along several profiles and in two blocks of sediments. More than 90 (Nelson & Ku, 1997; Lau *et al.,* 1997; Turk *et al.*, 2001; 2006; Blackwell *et al.*, in press) available ESR and ^{14}C (AMS) dates have shown that facies A and B correspond to the Oxygen Isotopic Stage 3 (= OIS 3; i.e. Interpleniglacial) and facies C to OIS 5a-5d (i.e. Early Glacial). Four U/Th dates are also available (Nelson & T.-L. Ku, 1997) but since extended gaps in sedimentation greatly influenced mobilisation and absorbtion of U, thus leading to its remobilisation, the determination of age by U series method proved inaccurate in this case (Turk *et al.*, 2003). The

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OIS 4 (i.e. Pleniglacial I) is almost not represented in the cave, since a pause in sedimentation occurred at the time. The transition between facies A and B corresponds with the former layer 7 (i.e. approx. 50.000 years B.C.) and the transition between facies B and C with the former 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.*, in press). Although the facies C begun to form already around 115,000 years B.C., the most ancient metapodials included in this study originate from the layer 16a, being dated to 75,000 - 85,000 years B.C. (Blackwell *et al.*, in press).

Although radiometric datations are not without pitfalls, the high number of available dates (>90) in combination with the methodology used (e.g. assessment of the total dose rate from external environment in ESR dating using the neutron activation analysis; *cf.* Blackwell & Blickstein, 2000) do give the assurance of a relatively reliable chronology of the site. According to latest data (Turk *et al.,* 2006; Blackwell *et al.*, in press) radiocarbon datations seem to be reliable for layers 2 - 6 (although a shift of +2-3 ka due to calibration in calendar years is necessary), while ESR datations proved trustworthy for layers 2 - 23. Nevertheless, since no radiometric method provides a chronology which is in itself of sufficient reliability for detailed archaeological interpretation, the available datations were considered also in the context of the site stratigraphy (with sedimentological, paleobotanical and paleontological data taken into account). The results, however, fully confirmed the reliability of the radiometric datations (Turk, in press).

Following the new basic stratigraphic units (= facies), the available sample of cave bear metapodials was divided into three subsamples: Db-A (includes metapodials of facies A), Db-B (facies B) and Db-C (facies C). Due to unpredictable objective reasons (*cf.* Turk, 2003), it was possible to observe the vertical distribution of structural aggregates and bone remains (whose distribution served as the basis for the substitution of *ad hoc* delineated geological layers with facies) only on a part of the excavation field. For this reason only the metapodials from that part of the excavation field were metrically analyzed. The initial sample of several thousand specimens thus decreased to 1,598 metacarpals and metatarsals, only. Nevertheless, each of the three subsamples (i.e. Db-A, Db-B and Db-C) included a sufficient number of specimens of individual skeletal elements (i.e. metacarpus I - V, metatarsus I - V) so as to enable the application of multivariate statistical methods.

Eight different measurements were taken from each metapodial (Withalm, 2001; fig. 1): greatest length (gL), medio-lateral breadth of the proximal epiphysis (pB), antero-posterior breath of the proximal epiphysis (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 epiphysis (gDB), medio-lateral breadth of the articular surface of the distal epiphysis (dB) and antero-posterior breadth of the distal epiphysis (dH). Only specimens with fused epiphyses were included in the analysis. It must be pointed out that several studies of skeletons of ungulates have indicated the possibility of a considerable growth of bone tissue also in bones with fused epiphyses (Legge & Rowley-Conwy, 1988; Payne & Bull, 1988; Luff, 1993). However, this occurred mostly on skeletal elements that ossify very early in the ontogenetic development (e.g. scapulas, distal parts of humeri, astragali), which is not the case with metapodials. Nevertheless, metacarpals and metatarsals with visible exostoses were excluded from the analysis by way of precaution.

The analyses of the X-ray images of the paws of the black bear (*Ursus americanus*) have shown that the fusion of epiphyses in metacarpals terminates when the animal reaches two years of age. In the following months the ridge of the distal epiphysis becomes fully shaped (Marks & Erickson, 1966). The metapodial development in the cave bear is though to conclude on average somewhat later (supposedly just before reaching three years of age), since the ontogenetic development of the skeleton in the cave bear is though to be slower (*cf.* Debeljak, 2002b). Beside this, the tempo of the epiphyses fusion in the study by Marks and Erickson is most probably somewhat overestimated, since their conclusions are based on the analysis of X-ray images (1966; see also Moran & O'Connor, 1994).

The analysed samples mostly include complete metapodials where all eight measurements could be taken. Partly damaged metacarpals and metatarsals, where one of the measurements could not be taken, were also analyzed. The missing data were substituted by estimates, which were obtained using forward stepwise regression (StatSoft Inc., 2001). The efficiency of the method was tested on undamaged specimens: the absence of statistically significant differences between the measured and estimated values (F-test: $p < 0.05$) indicated the appropriateness of the method used.

Metapodials were sexed based on the results of the principal component analysis (PCA). This method enables a satisfactory explanation of the variation of certain
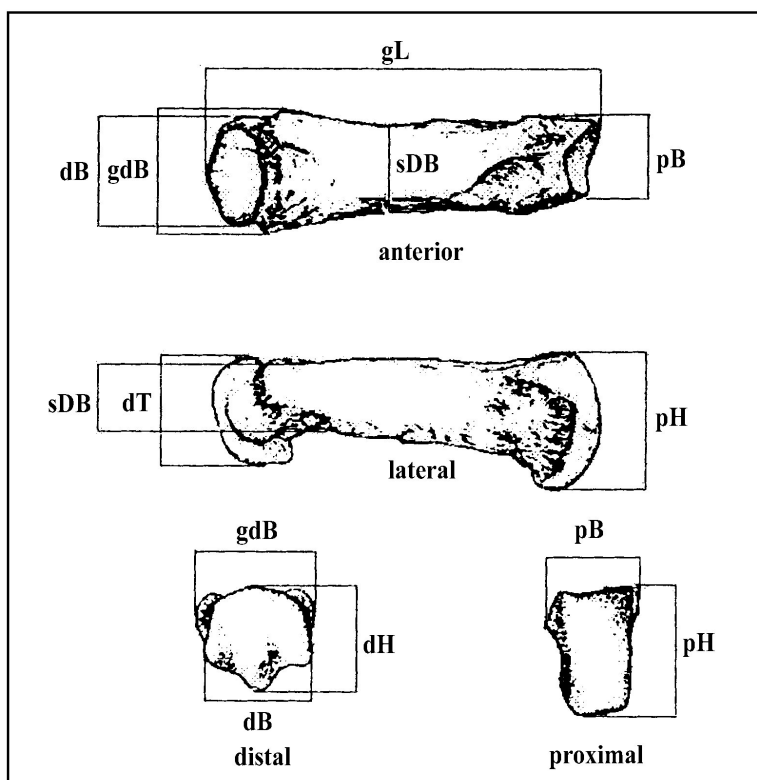
Figure 1. Cave bear (*Ursus spelaeus*) metapodial with indicated measurements. For definitions of individual measurements see the text.

number of basic *X* variables with a (considerably) smaller number of principal components (Pc$_i$), which renders the interpretation of the intrasample variability considerably easier (Manly, 1994; StatSoft Inc., 2001). Prior to the principal component analysis the available metric data were first standardized (*cf.* Albarella, 2002). Thus only the relative deviations of individual specimens from the average value of each of the eight measurements in the reference sample (deviations are expressed in standard deviations) were transferred to subsequent analyses. Consequentially, all metacarpals/metatarsals could have been pooled together to form a uniform statistical sample, rendering it considerably more representative. Metric data were standardized using the formula:

Standardized value = (x - M)/S

where x represents individual measurements to be standardized and M and S the average and the standard deviation for the same measurement in the reference sample.

In statistical analyses the StatSoft 2001, Statistica for Windows software package, version 6.0 was used. The analyzed material is held at the National Museum of Slovenia in Ljubljana.

RESULTS

The weight of the cave bear male is supposed to be a third above the weight of the female (Viranta, 1994), which indicates a well-marked sexual dimorphism. In spite of this, the analysis of 4,459 metacarpals and metatarsals of *U. spelaeus* and *U. deningeri* from eight Austrian and one Italian site has shown that sexing the metapodials on the basis of any single linear measurement is not possible (Withalm, 2001). Better results were expected by using the principal component analysis, since this method enables the simultaneous consideration of several (in this case all eight) parameters. Due to the previous standardization of metrical data it was possible to compare the variability in the size of metapodials on a unified sample of all five metacarpals/metatarsals. The metapodials from facies B were used as reference sample in standardization, since they fall between the specimens from facies A and facies C in their size.

The correlation matrix of standardized values of all eight parameters was used as input data for the PCA, separately for metacarpals and metatarsals. The first principal component accounts for 83.7 percent of the variability of the basic data set for metacarpals and 72.8 percent for
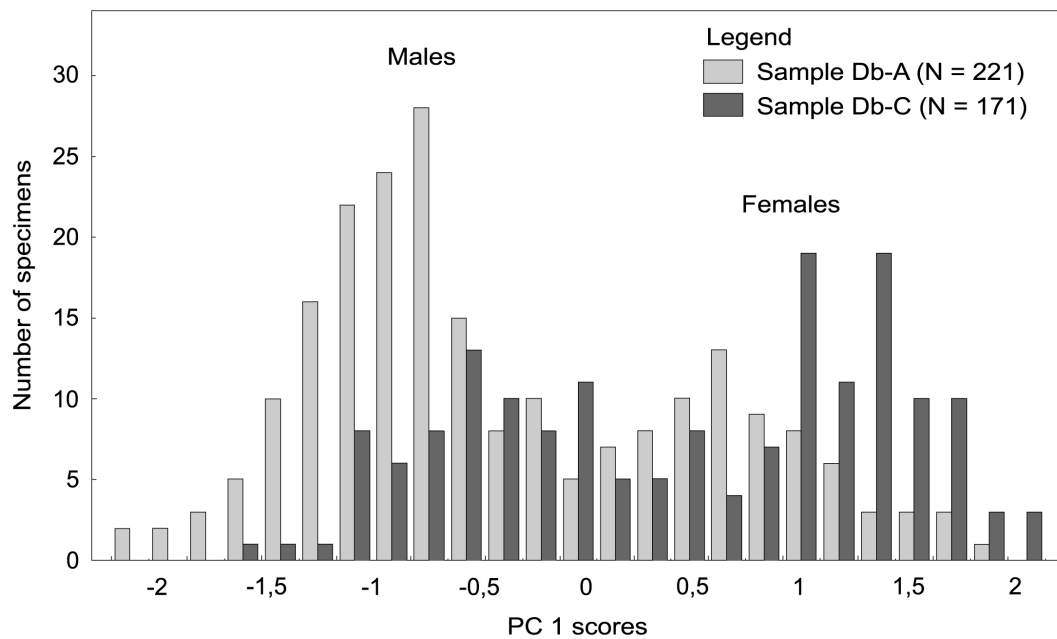
Figure 2. Distribution of the first principal component (PC 1) scores, calculated on the basis of a correlation matrix of standardized data for eight measurements of cave bear (*Ursus spelaeus*) metacarpals from Divje babe I: samples Db-A and Db-C. Scores were standardized using the data of the sample Db-B, which is thus not represented on the figure. Due to negative factor loadings, the large (i.e. male-ascribed) metacarpals form the left of the two peaks and the small (i.e. female-ascribed) metacarpals the right one.

metatarsals. Factor loadings of all eight parameters are negative and vary between the values of -0.76 and -0.94. The communalities are high and the residual correlations low. Due to the above, the major part of the basic data set could accurately be represented already with the first principal component.

The distribution of PC 1 scores is distinctly bimodal for metacarpals/metatarsals from the Db-A sample as well as for those from the Db-C sample (fig. 2, fig. 3). Such a distribution reflects the sexual dimorphism and enables at least an approximate estimate of the sex ratio. Overlapping of the scores of both sexes is slightly higher for the metatarsals than for the metacarpals. This observation is quite expected considering the constitution of the cave bear and was proven also on long bones of both pairs of limbs (REISINGER & HOHENEGGER, 1998).

The distribution of the PC 1 scores indicates that the number of metacarpals and metatarsals of both sexes was roughly equal in the sample from OIS 5a-5d (= sample Db-C). As opposed to that, the material from the OIS 3 (=sample Db-A) shows an approximate two-thirds majority of male specimens. None of the metapodials (i.e. Mc I - V, Mt I - V) show significant deviations in that sense. In three of the five metacarpals the differences in sex ratio between the samples Db-A and Db-C are even highly

statistically significant (χ^2 test: p < 0.01; tab. 1). The sex ratio was estimated without considering the anatomical orientation of specimens (i.e. without distinguishing between left and right metacarpals / metatarsals), since the available samples were not large enough. The only exception in this sense is represented by second metacarpals, which are the most numerous among all metapodials in the studied sample (Mc II: N = 96). Also in this case, however, the results confirmed the balanced sex ratio in the Db-C sample and a predominance of male-ascribed second metacarpals in the Db-A sample (tab. 2).

The results mentioned so far refer exclusively to the material from the middle part of OIS 3 (= Db-A sample) and from OIS 5a-5d (= Db-C sample), since the metapodials from the initial part of OIS 3 (= Db-B sample) were used as the reference sample in the standardization of metric data. In order to provide an estimate of the sex ratio also for the Db-B sample, metric data of the metapodials from that sample were standardized using the data of the entire fossil sample from Divje babe I (Db-A + Db-B + Db-C) as reference. The results clearly showed a predominance of males (fig. 4), thereby confirming the hypothesis made above on the majority of metapodials in the OIS 3 material being ascribed to males.

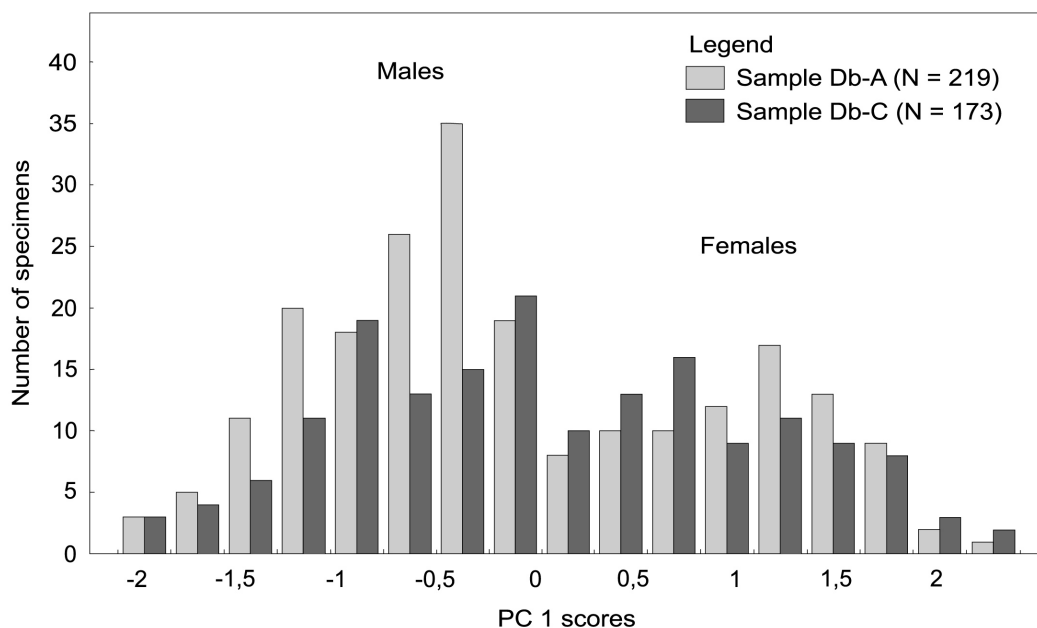The sex ratio of cave bear assemblages is usualy esti-

Figure 3. Distribution of the first principal component (PC 1) scores, calculated on the basis of a correlation matrix of standardized data for eight measurements of cave bear (*Ursus spelaeus*) metatarsals from Divje babe I: samples Db-A and Db-C. Scores were standardized using the data of the sample Db-B, which is thus not represented on the figure. Due to negative factor loadings, the large (i.e. male-ascribed) metatarsals form the left of the two peaks and the small (i.e. female-ascribed) metatarsals the right one.

Table 1

The number of male- and female-ascribed cave bear (*Ursus spelaeus*) metacarpals from Divje babe I: samples Db-A and Db-C. Statistically significant differences in the sex ratio between the two samples are shaded.

Mc	Sample Db-A		Sample Db-C		Total			χ^2 test
	♂	♀	♂	♀	♂	♀	♂ + ♀	
Mc I	22	9	9	23	31	42	73	χ^2=26.20 p= 0.00
Mc II	44	13	19	20	63	33	96	χ^2= 8.32 p= 0.00
Mc III	36	16	20	12	56	28	84	χ^2= 0.40 p= 0.52
Mc IV	19	15	18	19	37	34	71	χ^2=37.00 p= 0.54
Mc V	25	12	10	21	35	33	68	χ^2= 8.42 p= 0.00
Total	146	75	76	95	222	170	392	χ^2=18.30 p= 0.00

mated by using metric data of canines, since they show a well pronounced sexual dimorphism (e.g. KURTÉN, 1955). For the material from Divje babe I such an analysis was performed by DEBELJAK (2002b). Her results indicate a roughly equal share of male and female specimens not only in facies C, but also in facies A and B, thus contrasting the conclusions based on the study of metapodials. The discrepancy between the two approaches, however,

can be convincingly explained with the lack of canines of (sub)adult cave bears (compared to cheeck-teeth and to most postcranial elements) in certain layers from facies A and B (TURK & DIRJEC, in press; TOŠKAN, in press (b)). Namely, because of the lack of canines the sample studied by DEBELJAK was actually non-representative, making the resulting sex ratio estimates questonable.

The lack of canines is really only evident in layers with

Table 2
Statistical testing of differences in the sex ratio of all cave bear (*Ursus spelaeus*) metacarpals from the Db-A and Db-C samples on one side and only the second metacarpals (Mc II) of the same species from the same two samples (Db-A and Db-C) on the other side.

Sample Db-A	♂	♀	Total	χ^2 test
Mc II (left)	21	6	27	$\chi^2 = 1.50$
All metacarpals	146 (= 65.7%)	76 (= 34.3%)	222	p = 0.220
Sample Db-A	♂	♀	**Total**	χ^2 **test**
Mc II (right)	23	7	30	$\chi^2 = 1.35$
All metacarpals	146 (65.7%)	76 (= 34.3%)	222	p = 0.245
Sample Db-C	♂	♀	**Total**	χ^2 **test**
Mc II (left)	14	12	26	$\chi^2 = 0.80$
All metacarpals	76 (= 44.4%)	95 (= 55.6%)	171	p = 0.370
Sample Db-C	♂	♀	**Total**	χ^2 **test**
Mc II (right)	5	8	15	$\chi^2 = 0.18$
All metacarpals	76 (= 44.4%)	95 (= 55.6%)	171	p = 0.675

hearths and/or above-average number of stone artefacts. The relatively lower number of canines in these layers could thus be related to Palaeolithic man, who might have collected the larger (= male) specimens as some sort of trophies and transported them elsewhere (Turk & Dirjec, in press; Toškan, in press (b)). Such a conclusion is corroborated by the results of taphonomic analyses, showing that the lack of canines cannot be explained by differential post-depositional fragmentation (Toškan, in press (b)). In addition to this it should be emphasize that the estimated sex ratio emerging from the study of metapodials corresponds to the results of metric analyses of long bones (Jambrešić & Turk, in press) and skulls (Toškan, in press (a)).

DISCUSSION

Sexing the cave bear metapodials from Divje babe I offered an interesting point of departure for a detailed insight into the biology of the species. The accumulation of cave bear remains in caves is usually related to natural mortality during the period of lethargy (*cf.* Pohar, 1981; Stiner, 1998; Weinstock, 2000; Debeljak, 2002b). Such inferences are drawn from data on the high energetic cost of hibernation in recent bears (Watts & Jonkel, 1988) and by considering the supposed comparability of metabolisms of brown and cave bears (Nelson *et al.*, 1998; Lidén & Angerbjörn, 1999; Fernández-Mosquera *et al.*, 2001; but see also Jenkins *et al.*, 2001).

The physiological readiness for entering hibernation in recent bears is determined by the circannual rhythm tied to the seasonal cycle of vegetation (Ewer, 1973). This is responsible for an approximate timing of the beginning of hibernation, while the actual transition to the lethargic state is thought to be triggered by an interaction of certain climatic factors (amount and frequency of precipitation, dense clouds, general deterioration of weather) and smaller quantities of available food (Johnson & Pelton, 1980). What about the choice of lair? For the present-day black and brown bears it is known that the first to occupy a lair in good climatic conditions are pregnant females, which are followed by subadult individuals and finally by males (Slobodyan, 1976; Pasitschniak-Arts, 1993). Postponement (in males sometimes even a complete absence) of the beginning of hibernation can be caused by abundant crops of beech-nuts, acorns and the like (Johnson & Pelton, 1980; Germonpré & Sablin, 2001). In accordance with the above, we might infer that females have a wider choice of appropriate lair in mild winters and/or in periods of relatively large amounts of available food. A different picture emerges at the onset of severe climatic conditions and/or shortage of food. In these cases, males enter the hibernation approximately contemporaneously to the subadult individuals and pregnant females (Slobodyan, 1976; Pasitschniak-Arts, 1993), thus significantly increasing the intersexual competition for appropriate lairs (Johnson & Pelton, 1980; Stiner, 1998). Since pregnant females and females with subadult young usually avoid solitary males when choosing a lair (Slobodyan, 1976; Wielgus & Bunnell, 1994), the onset of climatically severe conditions undoubtedly favours males.

Similar behaviour was probably present also in the cave bear, as is indicated by the increased $\delta^{15}N$ values in males from the cold phases of Würm (Fernández
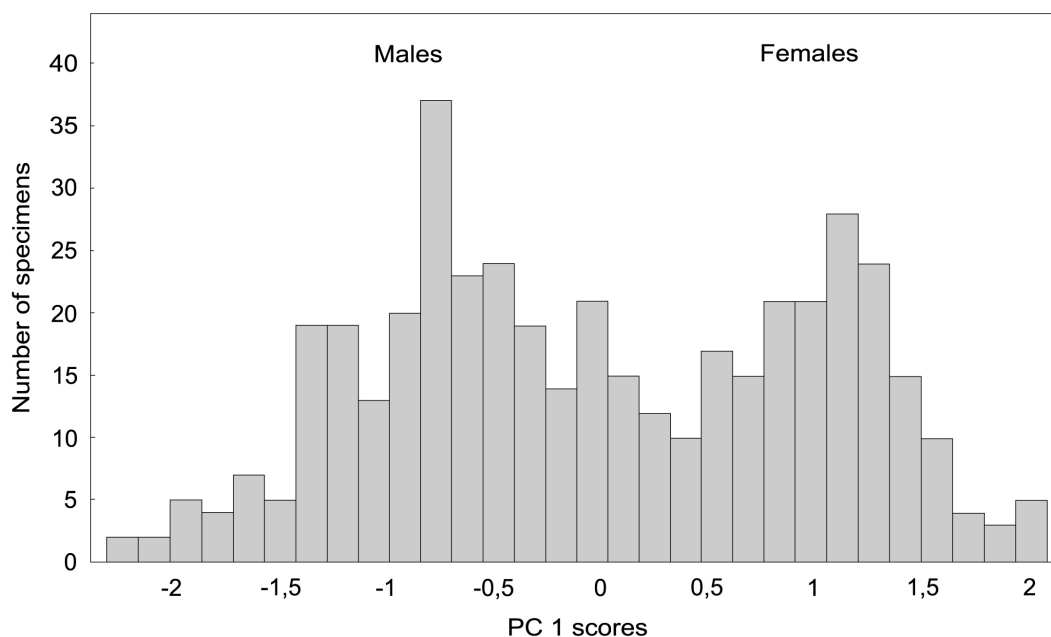
Figure 4. Distribution of the first principal component (PC 1) scores, calculated on the basis of a correlation matrix of standardized data for eight measurements of cave bear (*Ursus spelaeus*) metacarpals from Divje babe I: sample Db-B (N = 434). Scores were standardized using the data of the entire fossil sample from Divje babe I (Db-A + Db-B + Db-C). Due to negative factor loadings, the large (i.e. male-ascribed) metacarpals form the left of the two peaks and the small (i.e. female-ascribed) metacarpals the right one. PC 1 explains 77.0% of the variance accounted for by the basic data set.

Mosquera *et al.*, 2000; 2001). The increased $\delta^{15}N$ values are thought to be tied to the earlier beginning (and thereby longer duration) of hibernation, during which urea recycling in amino acid synthesis occurs. Although the metabolism in the black/brown and cave bear might well have diverged to some extent (i.e. cave bears being more tied to hibernation) the transition to the letargic state seems to have been triggered by climatic factors in cave bears, too. The presumption of a sex-specific timing of the actual beginning of hibernation in cave bears is thus to be considered as a legitimate one (*cf.* Germonpre & Sablin, 2001). This realisation is important in the context of the observed sex ratio of cave bears from Divje babe I. There is, in fact, no doubt that the climatic conditions in OIS 5a-5d south of the Alpine glaciation were significantly more favourable and more stable than those in OIS 3. This is shown by sedimentologic analysis (Turk *et al.*, 2001; 2002), palaeobotanic research (Šercelj & Culiberg, 1991) and by the study of the small mammals' remains (Kryštufek, 1997; Toškan, 2002; Toškan & Kryštufek, in press). It is therefore to be expected that pregnant females and females with subadult young went into hibernation before the males in OIS 5a-5d. This provided them with much more freedom in choosing a

lair. Namely, though in recent bears females use to avoid males when looking for a lair, males also usually do not occupy the already occupied caves, even when inhabited by females (Slobodyan, 1976; Wielgus & Bunnell, 1994). An approximately equal representation of both sexes in the Db-C sample from Divje babe I (fig. 2, fig. 3, tab. 1, tab. 2) could thus be efficiently explained with the wider choice of females in looking for a lair. Since in mild winters males of the present-day brown and black bear often make their lair in the open (for example in a thicket of young trees or in a shelter of a fallen tree; Rogers, 1981; Slobodyan, 1976; Groff *et al.*, 1998), an even lower share of male metapodials in the Db-C sample could be expected. The reasons for this not being the case are to be sought in the ethology of the cave bear, since it was supposedly more prone to hibernating in caves than the present-day representatives of the *Ursus* genus (Couturier, 1954; Fosse *et al.*, 2002).

A colder and more humid climate in OIS 3 surely contributed to a more pronounced seasonal availability of vegetable food. The winters of that period are thought to have been longer and substantially more abundant in snowfall (Turk *et al.*, 2002). For the (predominantly) herbivorous (*cf.* Bocherens *et al.*, 1994; 1997; Nelson

et al., 1998) cave bear, this environment probably led to a more or less synchronous autumnal occupation of caves from individuals of both sexes. Pregnant females or females with subadult young probably avoided solitary males in choosing their lairs and the latter probably occupied also those caves that used to be occupied by females in the warmer and less humid OIS 5a-5d. The increased share of males choosing Divje babe I as their lair in OIS 3 seems thus not to be problematic.

Lately morphological and metrical differences between several alpine cave bear associations of the same geological age were considered large enough by some authorities (Rabeder, 2004; Rabeder *et al.*, 2004a; Hofreiter *et al.*, 2002; 2004) to suspect more than one evolutionary line. Analyses of fossil DNA indicated at least three different lineages within the cave-bear group, two of these groups showing evidence of reproductive isolation (Rabeder *et al.*, 2004a; 2004b; Hofreiter *et al.* 2004; Noonan *et al.*, 2005; but see also: Peatkau, 1998; Orlando *et al.*, 2002). It was thus suggested that *Ursus spelaeus* Rosenmüller, 1794 comprised at least two species, of which *Ursus ingressus* Rabeder *et al.*, 2004 occurred in the eastern parts of the Alpine region and the Dinarids of Slovenia and Croatia. For two other morphological forms, subspecific status with *U. spelaeus ladinicus* and *U. spelaeus eremus* was suggested (Rabeder *et al.*, 2004a). In line with this thesis the appearance (or predominance) of larger individuals of cave bear in Interpleniglacial (≈OIS 3) layers of e.g. Potočka zijalka, Vindija and Gamssulzenhöhle was explained by immigration of the considerably larger *U. ingressus* (Rabeder *et al.*, 2004a; 2004b; Withalm, 2004; 2005). The latter species is assumed to have immigrated into the Alps around 50.000 years BP, subsequently replacing the other two forms of cave bears (Rabeder & Hofreiter, 2004).

According to the above the predominance of larger individuals in the upper layers (i.e. facies A) of Divje babe I could also be explained by immigration of a considerably larger cave bear species (*U. ingressus*), thus resulting in the pretence of an asymmetrical distribution between sexes. Unfortunately data about aDNA are not yet available for the cave bear from Divje babe I. Nevertheless, detailed morphometrical analysis of metapodials pointed out a complete lack of statistically significant differences between specimens from the three facies once the "size" component has been discarded (Burnaby's method) from the metric data [Toškan, in press (b)]. Since *U. ingressus* is supposed to differ from *U. spelaeus* in the metapodial bone proportions (Rabeder *et al.*, 2004a; Hofreiter *et al.*, 2004; (see supplement data available with the article

online), Withalm, 2004; 2005) the lack of such differences in the material from Divje babe I speaks against the hypothesis of the immigration of *U. ingressus*. Moreover, according to Rabeder *et al.* (2004a) the differences in the index of plumpness (Ip = gDB/gL; see fig. 1) of the first metacarpal and metatarsal bones seem to be the most striking and therefore best usable indicator for diagnostic use. It is thus important to note that the comparison of the first metacarpals and metatarsals ascribed to *U. ingressus* from Potočka zijalka (Withalm, 2004) with those from facies A (≈ 35/40 - 50 ky BP) of Divje babe I does not show statistically significant differences in *Ip* values (t-test: p > 0.05). But the same also holds true for the comparison of *Ip* values for the first metacarpal/metatarsal bones from Potočka zijalka with those from Divje babe's facies B (≈ 50 - 70 ky BP) and facies C (≈ 70 - 85 ky BP), which deposited before the assumed immigration of *U. ingressus* into the Alps (Rabeder & Hofreiter, 2004). Differences in *Ip* values of the first metacarpals between male-/female- ascribed specimens from facies A and those from facies C are not statistically significant neither (t-test): males (facies A) vs. males (facies C: p = 0,891; females (facies A) vs. females (facies C): p = 0,627), as would be expected if the predominance of larger individuals in the upper layers (i.e. facies A) would be related to the immigration of *U. ingressus*. By taking the above into account it thus seems legitimate to explain the bimodal distributions of PC 1 scores by the sexual dimorphism.

CONCLUSION

The use of multivariate statistical methods in analysing cave bear metapodials from Divje babe I enabled us to sex them. As already mentioned above, the estimated sex ratio differs somewhat from the one that is based on the metric data of canine teeth (Debeljak, 2002b), but corresponds exactly to the results of the metric analysis of long bones (Jambrešić & Turk, in press) and skulls (Toškan, in press (a)). The presented method can therefore serve, among other uses, also as an independent control of the otherwise more popular approach to estimate the sex ratio, i.e. by using metric data of canines.

A comparable share of male and female metapodials in the sample from OIS 5a-5d as opposed to the almost two-thirds majority of male-ascribed metacarpals and metatarsals in OIS 3 can be explained with a more severe climate in OIS 3. Longer and colder winters with a thick and longer-lasting snow cover caused the males to begin their hibernation more or less contemporaneously with subadult individuals and (pregnant) females, which
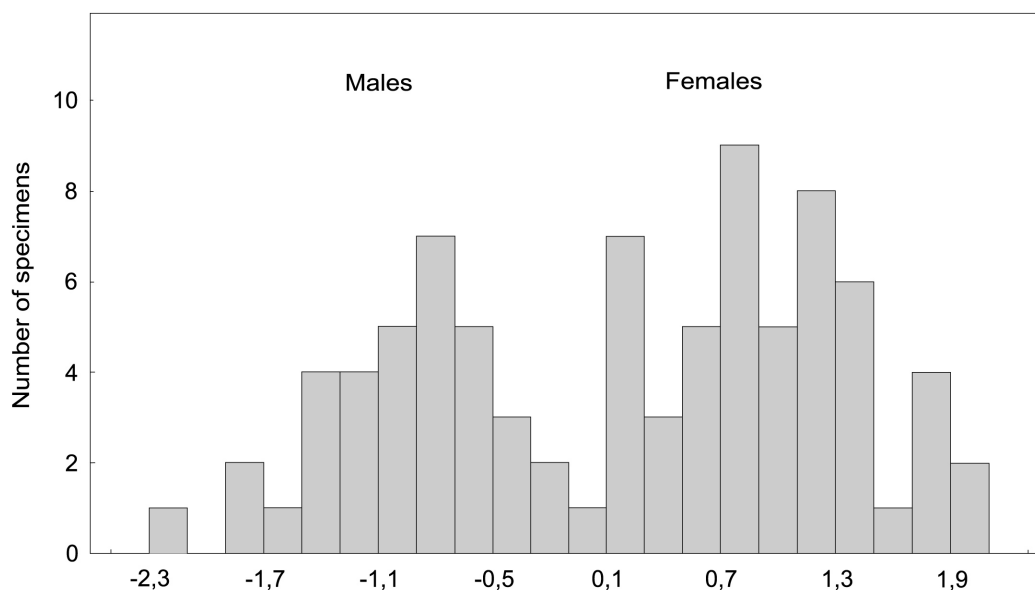
Figure 5. Distribution of the first principal component (PC 1) scores, calculated on the basis of a correlation matrix of standardized data for eight measurements of cave bear (*Ursus spelaeus*) metacarpals from Divje babe I: specimens from layers 6 and 7 (N = 85). Scores were standardized using the data of the sample Db-B. Due to negative factor loadings, the large (i.e. male-ascribed) metacarpals form the left of the two peaks and the small (i.e. female-ascribed) metacarpals the right one. PC 1 explains 72.8% of the variance accounted for by the basic data set.

substantially increased the intersexual competition for appropriate lairs. Such a thesis is corroborated by the fact that the sex ratio in metapodials from the only two relatively warm and/or arid phases of OIS 3 (i.e. the set of layers 2-5 without layers 5a and layer 6-7; *cf.* Turk *et al.*, 2001; 2002; in press) does not show a majority share of males otherwise characteristic of the rest of the material from OIS 3. Instead, the share of males in the material of the two above-mentioned phases is practically equal to the share of females, just like in the Db-C sample from the relatively warm OIS 5a-5d (fig. 5; see also fig. 2, fig. 3 and fig. 4).

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