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LIFE AND DEATH
OF THE PLEISTOCENE CAVE BEAR

A STUDY IN PALEOECOLOGY

BY

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CONTENTS

	Page
Introduction	4
Acknowledgements	6
Age groups.....	7
The developmental sequence	7
The causes of the age grouping	8
Development stages in the dentition.....	9
Growth	14
Life table analysis	17
Reliability of the record	17
Factors of mortality	18
Method of analysis.....	21
Comparison with Cotencher and Cueva del Toll.....	24
Mortality from birth to adult age	25
The complete Life table	26
Testing the Life table	28
Mortality and selection	31
The descendance of the species	31
The life history of an <i>Ursus spelaeus</i> cohort	33
Selection	34
A selection complex in the second molars	36
Width relationships of second lower molars.....	39
The extinction of the cave bear	42
The degeneration theory	42
Sex ratios	44
Man's role in the extinction of the cave bear	48
The last survivors	49
Survival of isolated populations	52
Summary.....	56

INTRODUCTION

In previous studies of mortality rates in fossil mammal populations (KURTÉN, 1953, 1954a, 1954b) it has been noted that information on mortality among juveniles is uncertain and ambiguous even when fairly good estimates for adult age groups can be made. Some tentative conclusions formed by me (Kurtén, 1953, pp. 83—87) had a slender factual basis on account of the almost universal under-representation of juvenile remains in samples of fossil mammals. The methods used were (a) estimates of the probable productivity of the population, and (b) such corrections for the bias in representation that were suggested by the data (tying up the oldest juvenile age class with the youngest adult one by extension of adult rates of mortality, used for the Pontian ovibovines *Plesiaddax* and *Urmiatherium*). Both methods, although independent of each other, certainly introduce speculation and personal bias. The former method can only be used if birth rates are known or can be safely inferred, and even then the potential productivity may not be completely realized, whereby an unknown factor remains. The latter method has other defects. For both the Pontian ovibovines mentioned, there is a one-year hiatus between the two sets of data — for juveniles and adults — and a half-year hiatus before the youngest age class. Both gaps were bridged by extrapolation backward; but both probably coincide with marked changes in the rate of mortality. As records of juvenile mortality these are not satisfactory, and it would be desirable to obtain survivorship data for juveniles from unbiased samples.

In several studies of the age grouping in cave bears (*Ursus spelaeus* Rosenmüller and Heinroth) EHRENBERG (e.g. 1935a, 1935b) has drawn attention to the frequent occurrence of juvenile individuals. The percentages of immature specimens in most samples are much larger than in fossil or recent mammalian samples generally. Moreover the available collections are large, sometimes representing hundreds or thousands of individuals. Finally, the time represented is very short, geologically speaking, and the samples are thus unusually homogeneous. For all these reasons the cave bear appears to be an exceptionally promising species in a study of mortality and survival, as well as for other kinds of quantitative investigation (KURTÉN, 1955).

The present study is mainly based on the large cave bear collection from Odessa (VON NORDMANN, 1858—60; see also KURTÉN, 1955a, 1955b), but data on other collections studied by me have also been used, as well as published information. The results are naturally liable to a certain bias, and factors possibly conducive to distortion will be discussed. Nevertheless, even if the

actual figures are somewhat off the mark, it appears that the "concave" survivorship pattern (i.e. mortality decreasing with increasing age) in the young age classes can be proved. There is no hiatus requiring extrapolation, and rates of mortality can be estimated directly from the sample in an unbroken sequence from birth to adult age. The survival of the adults can also be evaluated, but the results are more speculative, and more liable to distortion by personal bias, than those for the young.

The survival data thus obtained are used as a framework for a general discussion of the ecology of the species, its evolution and extinction. Only a few evolutionary aspects will, however, be discussed in the present contribution; I hope to return to the topic in another connexion.

The student of cave bear collections in various museums will find that much of the material is biased in one way or another, and gives a spurious representation of the population properties. Two most remarkable examples are the collections from the caves Hohlestein and Sibyllenhöhle, preserved in the Natural History Museum of Stuttgart. I am most grateful to Dr. K. D. ADAM, of Stuttgart, for giving me the explanation of the singular conditions of these samples.

The Hohlestein sample, from the later Würm, consists of about 90 per cent males and 10 per cent females. This fantastic disproportion is of the highest statistical significance, but it is probably entirely spurious. The cave was excavated in 1862—1866 by O. FRAAS. A great number of specimens were apparently distributed to private collectors — perhaps as a premium for services in the excavation — the selection being made by the museum authorities, apparently with an eye to keeping the finest specimens for the museum itself. This simply meant the large ones, or the males. Most of the females were lost to science and there is now no way of establishing the true sex ratio in this cave, which would be most important as the Hohlestein bear was among the last survivors of the species. Recently a Hohlestein specimen was acquired by the museum from a private collection. Characteristically, it was a female jaw.

The sample from the Sibyllenhöhle, in contrast, comprises about 77 per cent females and 23 per cent males! The cave was excavated in 1898 by E. FRAAS and the Schwabischer Höhlenverein. Here, too, specimens were distributed to private collectors. But in this case the selection was made by the Society members, the natural result being that the less spectacular female specimens were left in the possession of the museum. Here, too, most of the distributed specimens are irretrievably lost to science, and much of the value of the collection has been destroyed.

Exploitation of caves for phosphate has also seriously impaired the value of some collections. Even the otherwise magnificent Mixnitz collection is

unusable for some purposes, including the study of mortality rates, because only a small part of the specimens actually present could be collected — an observation in no way intended to implicate the scientists concerned, who surely tried to save as much material as possible. The result is, however, that *isolated teeth*, relative to jaws and skulls, and *sound specimens* relative to pathological ones, are exceedingly under-represented. Most juvenile age classes are predominantly represented by isolated teeth, and hence are under-represented in the Mixnitz collection. By carefully collecting the pathological bones, ABEL and his collaborators have given us exceedingly interesting and important information on the health of the Mixnitz bear, but no figures on the relative incidence of maladies can be obtained, and no valid comparison with other samples can be made (see also ZAPPE, 1954).

Apart from predatory exploitation, the simple fact that cave bear material is plentiful at many sites has frequently fostered an unscientific attitude. Selection has been made of suitable museum specimens, oddities, freaks, or whatever the investigator found particularly interesting, whereas much material was refused, left to destruction or distributed to the public. Naturally, any refusal of specimens and any selection, on any grounds, automatically results in a biased sample and distorts the scientific value of the collection. Even when all the material is saved, collectors frequently omit to make field records for other than the most complete specimens.

It is to be hoped that the time of predatory exploitation is now ended; there is not an unlimited number of bear caves. Authoritative and competent work is now being done by many students fully aware of the unique interest of the cave bear for population studies, as, for instance, EHRENBERG and MÖTTL in Austria, KOPY in Switzerland, and DE VILLALTA in Spain. The excavation of the Cueva del Toll at Moyá (Barcelona), for instance, continued under the auspices of Dr. de Villalta, with careful field records for every scrap of material, will undoubtedly result in one of the finest and most useful collections in existence; the deposits are very rich.

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AGE GROUPS

THE DEVELOPMENTAL SEQUENCE

One of the most striking features of every larger cave bear collection which I have studied is the clear-cut separation of the younger individuals into a series of discrete stages of development, identical or nearly so for all the samples. The phenomenon was carefully studied by EHRENBURG (1922) for the Mixnitz collection, and his conclusion was that the cave was inhabited only during the hibernating season. The result is that we have growth stages one year apart, and these are easily recognizable for the younger stages on the basis of size, progression of tooth replacement, deposition of dentine in the pulp cavities, and initiation of wear of the tooth crowns.

The youngest specimens are neonates, equal in size to newborn cubs of *Ursus arctos*. Good fossils are rare, on account of the extreme fragility of the bones; the presence of such newborn individuals is generally revealed by bone fragments and the enamel caps of the milk teeth. Various stages intermediate between this age class and the succeeding one are also present in an unbroken series, illustrated, for instance, by the milk teeth in the Odessa sample, to be described below. Occasional more complete finds show random stages in early ontogeny: jaws with milk teeth being cut; with milk teeth in position and the germs of the permanent teeth forming; with permanent teeth pushing up and the roots of the milk teeth being resorbed.

Following this there comes a well-defined ontogenetic stage, which is the predominant one in many samples. In this stage, all permanent teeth are already formed, but only a few of them are in place. In the lower cheek dentition, M_1 is in its permanent position or almost so, P_4 and M_2 have emerged and are nearly but not quite in position, whereas M_3 is still turned sideways and partly concealed in the ascending ramus; only part of the crown is visible through an opening in the wall of the jaw. The tip of the permanent canine may just protrude out of its alveolus. The last milk teeth have just been shed.

COUTURIER (1954, pl. XXX) published an excellent X-ray photograph of the skull and jaw of a brown bear cub of three months. The stage there pictured is slightly less advanced than that seen in the cave bears. The first molars are almost in place, but the milk molars are still retained in the jaws, and the second lower molar has only emerged with the tips of the anterior cusps. Judging from the rate of development thus indicated, the somewhat more advanced stage in the cave bear would seem to represent an age of about 4 months or slightly more, in round numbers 0.4 years. The great preponderance of specimens in this stage, with very slight variation in both directions, indicates a mortality peak of fairly short duration.

The stage is represented by numerous jaws in the Mixnitz collection; in most others it is predominantly represented by isolated teeth, which make up a large fraction of the total.

With this stage the hibernation evidently came to a close, for there is a very wide ontogenetic gap between it and the following one.

In the next stage, which is evidently that of roughly 1.4-year-olds, growth has proceeded and all teeth are in place except M^2 , which is still at an angle to the rest of the tooth row, M_3 , which is partly to the side of the coronoid process and not fully emerged, and the canines, which have their crown bases almost flush with the alveolar border. Nearly all teeth are still unworn, but the first molars may show small attrition facets, and some of the peculiarities of wear in the anterior dentition may occasionally be seen.

Growth proceeds and wear of the teeth is initiated during the following stages, until, at about four years of age, the bears have attained fully adult stature. The processes of growth can be studied in some detail, and I return to them below.

THE CAUSES OF THE AGE GROUPING

It has been noted that the young of the year are predominantly represented by remains indicating an age of 4–5 months, this in fact being the largest single homogeneous group or age class in most samples. After that there follows a hiatus apparently representing one year. How is this concentration to a very short period to be explained?

These are individuals which were born during hibernation and which evidently died towards the end of the winter. It might be anticipated that in early spring, before the thaw set in and before the mothers could restore their vigour with fresh food, the cumulative hardships of wintering would take their maximum toll. This would be the time when the stores of fat and vitamins gathered during the preceding late summer and autumn would have been giving out. Consequently, the nutritive components of the mothers' milk would have been ebbing, and moreover some of the mothers may have died from undernourishment and cold and left their offspring doomed to death. Thus a mortality peak in late winter, just before the bears left their lairs, is to be expected.

It is also clear that mortality in the older age groups was largely concentrated to the end of the hibernation, because heavy mortality earlier in winter would be reflected in the young of the year, which were dependent on their mothers.

An additional point worth mention, concerning the young of the year, is the strain imposed by the replacement of the dentition. The large size of

the permanent teeth necessitates almost a rebuilding of the jaw in this process; that this may have been an important mortality factor has been pointed out by EHRENBERG and others.

If the bears left their lairs in April — a date not uncommon in brown bear populations — this would mean that parturition occurred in December or perhaps at the end of November. This would be slightly earlier than in *Ursus arctos*. Of course it is also possible that hibernation was extended to May and that the young were born in December—January, as in the brown bear.

DEVELOPMENT STAGES IN THE DENTITION

Milk teeth. The milk canines predominate in numbers among the deciduous teeth in the Odessa collection. They show a continuous series in age from germs (in the youngest individuals) up to shed teeth with resorbed root. They may be artificially grouped in a series of stages, though it should be remembered that these stages are linked up by intermediates.

(a) Germs with hollow enamel caps and root walls only beginning to form; neonate stage. 13 specimens.

(b) Root almost fully formed, but still open at the apex. 9 specimens.

(c) Root closed at the apex, no signs of wear or resorption. 17 specimens.

(d) Faint traces of beginning resorption, crown sometimes slightly worn. 8 specimens.

(e) Root partially resorbed, crown often worn. 17 specimens.

(f) Root completely resorbed. These teeth are either shed or just about to be shed. 140 specimens.

Permanent teeth. The annual stages in the development of the permanent teeth in the Odessa collection are denoted below by Roman numerals. Stage I is recognizable for all teeth; the specimens invariably have open roots and there is a very wide gap between this stage and the succeeding one. Very frequently the specimens in this stage may be told at a glance from the colour of the enamel, for the crown is stained, the darker the less advanced. Some of the M^2 and M_3 , consisting of little more than enamel caps, are almost black, and the predominant colour is a rich chestnut brown.

The number of specimens within each stage, recorded in the text for the milk canines, has been separately tabulated (table 1) for the permanent teeth. From top to bottom, the number of specimens in each stage as labelled is given; the lowermost entry gives the total of older specimens, which has not been divided into age groups. Cumulative frequencies are given in table 2, counting from the oldest to the youngest.

TABLE 1.

Frequencies of permanent teeth of *Ursus spelaeus* (Odessa sample) in the developmental stages indicated by Roman numerals (left) and described in the text. The lowermost entry in each column gives the total of specimens in the given stage plus older ones.

Stage	I ¹⁻²	I ₁₋₂	I ³	I ₃	C	P ⁴	P ₄	M ¹	M ²	M ₁	M ₂	M ₃	Σ ¹
I	83	75	45	47	38	43	35	75	82	55	114	51	743
II	88	32	22	28	22	6	72	25	24	18	28	32	237
III	—	120	15	11	128	5	—	43	12	10	25	24	102
IV	—	—	11	10	—	30	—	—	8	81	18	10	57
V	—	—	5	5	—	—	—	—	7	—	66	7	24
VI	—	—	44	5	—	—	—	—	5	—	—	43	10
VII	—	—	—	33	—	—	—	—	25	—	—	—	—

TABLE 2.

Cumulative frequencies of the data given in table 1.

Stage	I ¹⁻²	I ₁₋₂	I ³	I ₃	C	P ⁴	P ₄	M ¹	M ²	M ₁	M ₂	M ₃	Σ ¹
I	171	227	142	139	188	84	107	143	163	164	251	167	1946
II	88	152	97	92	150	41	72	68	81	109	137	116	1043
III	—	120	75	64	128	35	—	43	57	91	109	84	515
IV	—	—	60	53	—	30	—	—	45	81	84	60	302
V	—	—	49	43	—	—	—	—	37	—	66	50	179
VI	—	—	44	38	—	—	—	—	30	—	—	43	68
VII	—	—	—	33	—	—	—	—	25	—	—	—	—

First and second upper incisors. I¹ and I² are very similar in morphology, and their size variation overlaps widely. It is therefore not possible to distinguish between the two. In ontogeny I¹ is somewhat more precocious, but even in this trait there is sufficient age variation in stage I to obliterate the distinction. It was not considered practicable to carry the age grouping beyond separation of the initial stage.

Stage I: The roots are formed about halfway to their apices, rather more so in I¹ and rather less in I², as the modal condition.

All remaining specimens are lumped as "older". A few incisors are worn down to the root. In some instances no clear separation could be made between upper and lower ones; the questionable specimens have been apportioned *pro rata*.

First and second lower incisors. I₁ and I₂ are morphologically distinct, but older specimens in which most or all of the crown has worn away cannot always be classified.

The two initial stages could be fairly well distinguished from the rest. Possibly the grouping could be carried further by sectioning all teeth and studying the deposition of

1) Excluding the lowermost entry of each column; that is, including only the specimens demonstrably belonging to the given ontogenetic group.

2) Excluding the lowermost entry of each column. Note that the successive shrinkage of numbers in the Σ column does not as such portray the mortality; mortality rates are obtained from tables 1 and 2 together, as described later on in the text.

dentine in the pulp. Judgment on the basis of wear appears unreliable; the wear starts early and is often erratic.

Stage I: The roots are about as far developed as for the corresponding teeth in the upper jaw.

Stage II: The roots are closed; the crown is generally unworn, but in some specimens, apparently belonging to this group as indicated by the thinness of the root wall, traces of attrition are found.

Older groups were not distinguished.

Third upper incisor. The analysis was carried to stage V.

Stage I: The enamel cap is fully formed, the root walls are beginning to develop; up to 1—1½ cm. are laid down and paper thin.

Stage II: The root wall is fully formed, but the apex is still open. The thickness of the root wall about halfway to the tip could be measured in a number of specimens; the frequency distribution, and that for the following stage, is given in table 3.

Stage III: The root is closed and its walls are thicker. The crown may show faint traces of wear in the form of a polishing of the enamel surface at the tip.

Stage IV: A seemingly homogeneous group of specimens all in the same stage of slight wear. The enamel on the tip of the crown has been pierced and the attrition facet has a mean width of 2.6 ± 0.24 mm. ($N = 8$, standard deviation 0.7 ± 0.17 mm.). The group is distinct from the older specimens, as shown by the frequency distribution of this dimension in table 4. The root wall is thicker than in stage III; it could be measured at the same point (halfway to the apex) on two specimens, where it was 5.3 and 5.7 mm

TABLE 3. Thickness of I³ root wall halfway from enamel base to apex in stages II—III.

Millimeters	II	III
1.6 — 1.7	1	—
1.8 — 1.9	2	—
2.0 — 2.1	4	—
2.2 — 2.3	4	—
2.4 — 2.5	4	—
2.6 — 2.7	1	—
2.8 — 2.9	1	—
3.0 — 3.1	—	—
3.2 — 3.3	—	1
3.4 — 3.5	—	2

TABLE 4. Width of wear facet on tip of I³ crown from stage IV on.

Millimeters	IV	V (= first peak and older)
2	4	—
2 ½	1	—
3	1	—
3 ½	2	—
4	—	—
4 ½	—	3
5	—	2
5 ½	—	—
6	—	4
6 ½	—	4
7 and over	—	32

Stage V: A group represented by a second peak in the frequency distribution of table 4, and appearing to be distinct from the older specimens, is tentatively considered to represent 4.4-year-olds.

The older individuals are lumped together.

Third lower incisor. The analysis is for the moment carried to stage VI.

Stage I: Germs with open roots, modally as I³ in stage I or slightly more advanced.

Stage II: Roots closed, crown unworn, pulp cavity large.

Stage III: Very small attrition facets have formed on the main cusp; their diameter is in the order of $1\frac{1}{2}$ —2 mm. There is no indication of heterogeneity, and the group is clearly separable from the succeeding one.

Stage IV: The facets are larger, and there is often a small facet on the lateral cusps. Again, the group appears homogeneous, and there seems to be a gap between this stage and the next one.

Stage V: The facets on both cusps are larger, but still separate. This stage also appears to form a distinct mode, and to be separated from the next one by a hiatus.

Stage VI: This is the last group with separate attrition facets on main and lateral cusps. The aspect of this group is also homogeneous, and it appears to be separable from the older ones.

There is a certain possibility that the wear may be erratic and that different individuals may reach the same stage of wear at different ages. But the grouping appears to be a natural one, and the frequencies within the successive groups do not indicate any discrepancies.

Canine teeth. Upper and lower canines may generally be distinguished on complete material. For young germs and fragments, however, as well as for some senile specimens, this is quite impossible. All permanent canines are therefore treated as one group.

Stage I: The root walls are partially formed; the stage is about similar to that seen in the most immature specimens of I³.

Stage II: The root is open at the apex: the root wall is thickened.

The somewhat erratic wear of the canines precluded a study of the older age groups, which are lumped.

Fourth upper premolar. Only three stages could be well distinguished.

Stage I: The roots are almost fully developed, except for the apex: the crown is unworn.

Stage II: The roots are closed, the crown is unworn.

Stage III: The root wall is thicker, the crown is slightly worn.

The older groups are not clearly recognizable.

Fourth lower premolar.

Stage I: As in P₄.

The wear of P₄ begins later than that of most other teeth. Several age classes therefore have a similar external facies. They might perhaps be distinguished by means of sectioning the roots; here all P₄ older than stage I have been lumped.

First upper molar. Like M₁, M¹ begins to wear very early, and the age when attrition begins seems to vary. Groups older than II could not be distinguished.

Stage I: The roots are almost fully formed, but still open at the apex. The crown is unworn.

Stage II: The roots are closed, the root walls are thicker, the crown is frequently somewhat worn.

Second upper molar. This tooth is one of the latest to be incorporated in the dentition, and the wear begins rather late and appears to be particularly regular. The age groups are easily separated.

Stage I: The roots are in a stage of development about as in M₃ or slightly more advanced; the walls are formed somewhat less than halfway.

Stage II: The roots are almost fully developed, but still open at the apices. The crown is unworn.

Stage III: The roots are closed and the walls thickened. The crown is unworn or slightly polished on the summits of the internal cusps.

Stage IV: The pulps are like pinpricks, and there is a very narrow attrition facet along the anterior part of the internal ridge.

Stage V: The facet is somewhat larger.

Stage VI: The facet is more enlarged, but the tip of the protocone is still intact.

The older specimens are lumped together for the present purpose.

First lower molar. The wear appears to be somewhat erratic, and it begins early. Only three groups could be distinguished.

Stage I: The roots are almost fully formed; the posterior root is open at the apex, but the anterior one is generally closed. The summit of the protoconid is frequently slightly polished by abrasion.

Stage II: The roots are closed, but their walls are still fairly thin; the crown is mostly unworn, but sometimes the protoconid is visibly abraded.

Stage III: Slight wear, root walls thicker than in preceding stage.

Older specimens are lumped.

Second lower molar. The wear appears to be more regular than that of M^1 and M_1 , but less than in M^2 .

Stage I: About three-quarters of the roots have formed, the apices being wide open; the crown is unworn.

Stage II: The roots are fully formed, but the posterior root is not entirely closed in all specimens. The crown is unworn or very slightly polished on the protoconid rim.

Stage III: All roots are closed, their walls being about 4 mm. thick as against about 2 mm. in the preceding stage. The crown has small localised wear facets on the protoconid, the hypoconid being sometimes slightly polished; slightly polished interstitial facets may also occur.

Stage IV: The enamel is pierced by local attrition facets on the protoconid and the hypoconid; also polishing of metaconid and metaconid-protoconid ridges.

The older specimens, in which the facets are noticeably larger, are lumped.

Third lower molar.

Stage I: This tooth lags after all the others in development. In the present stage the converging proximal parts of the root walls are developed in many specimens, but some are even less advanced and consist practically only of the enamel cap.

Stage II: The roots are open at the apex and the walls are thin. The crown is unworn.

Stage III: The roots are closed, but the pulp cavity is still wide. The protoconid ridge is slightly polished by wear.

Stage IV: The crown is slightly worn, the enamel being pierced on the protoconid.

Stage V: The occluding surface is polished and the enamel is pierced along the external ridge.

Older specimens are lumped for the moment.

As a rule, the usefulness of the teeth for age grouping appears to be correlated with the sequence of their emergence. The teeth which emerge early generally show more erratic trends of wear; those that come late wear more regularly and form more clear-cut age groups.

GROWTH

The growth was studied for samples of lower jaws from Mixnitz, Odessa and Dachstein. The dimensions used were (1) length of jaw from anterior face of canine to centre of posterior surface of condyle; (2) depth of ramus at diastem C—P₄; (3) depth of ramus at M₁.

The material from Odessa was arranged into age groups one year apart, from the age 0.4 years to 3.4 years; the remainder were grouped as adult. It is quite probable that the growth continued after the age of 4 years, and the last segment of the growth curve is likely to be somewhat too steep. The earlier parts are based on true annual groupings, but the material is so small that irregularities may well have been induced by chances of sampling.

The material from Mixnitz could be divided into annual groups from 0.4 to 2.4 years. These groups give results identical with the same groups from Odessa. The older specimens are grouped as subadults and adults, since

TABLE 5.

Growth of lower jaw in *Ursus spelaeus* from Mixnitz, Odessa, and Dachstein.

Age		Mixnitz		Odessa		Dachstein	
		♂	♀	♂	♀	♂	♀
Length C-condyle	0.4	M	8		1		5
		M	167.4		170		139.2
		σ	10.7				16.2
		V	6.4				12
1.4	N	11	8	0	1	0	1
	M	203.8	203.2		208		190
	σ	7.2	8.4				
	V	3.5	4.1				
2.4	N	9	9	1	1	0	3
	M	251.9	244.2	a250	a250		232.7
	σ	13.4	13.9				
	V	5.4	5.7				
Sub- adult	N	5	7	1	1	0	1
	M	326.6	278.4	a297	a265		258
	σ	5.5	8.5				
	V	1.7	3.1				
Adult	N	27	13	5	2	1	2
	M	326.8	282.8	321.2	287	a260	259
	σ	14.3	12.9	4.8			
	V	4.4	4.6	1.5			

		Age		Mixnitz		Odessa		Dachstein	
				♂	♀	♂	♀	♂	♀
Height diastema	0.4	N		9		1		5	
		M		40.00		38		32.8	
		σ		2.08				3.8	
		V		5.2				12	
	1.4	N	33	20	2	1	0	1	
		M	50.11	45.20	48.5	44		39 1/2	
		σ	2.37	2.70					
		V	4.7	6.0					
	2.4	N	23	17	1	1	1	2	
		M	55.67	49.79	57	53	50	44.5	
		σ	3.41	2.73					
		V	6.1	5.5					
	Sub- adult	N	10	12	3	2	0	1	
		M	68.30	56.17	63.0	56.5		50	
		σ	4.94	2.81					
		V	7.2	5.0					
	Adult	N	44	16	10	4	1	2	
		M	69.18	57.38	65.7	54.2	58	46	
		σ	4.48	2.92	5.2	2.5			
		V	6.5	5.1	8.0	4.6			

my notes do not permit greater accuracy; the former group is not necessarily equivalent to the 3.4-year group from Odessa. The results, in fact, indicate that it probably includes some specimens older than 3.4 years.

A few jaws from the Schreiberwandhöhle of Dachstein give some information on growth, mainly in females. The grouping is the same as for Mixnitz.

Table 5 gives the statistics. The growth in jaw length is shown in fig. 1. The main part of the Mixnitz 1.4-year group could be sexed from the size of the canines and alveoli (see Kurtén, 1955b). Surprisingly, there is no trace of any sex dimorphism in this dimension at 1.4 years of age. At 2.4 years, some sex dimorphism is probably in existence, but it is much less pronounced than in the adults, and cannot be shown to be significant. The difference between male and female mean is about 3 per cent (male mean = 100); in the adults it is 14 per cent. The seeming difference in growth pattern through the stage labelled "subadult" probably results from contamination in the Mixnitz sample, and has no significance.

The depth of the jaw at the diastem shows dimorphism much earlier in ontogeny, at 1.4 years in the Mixnitz and Odessa samples. This is natural, as the depth is influenced by the size of the canine tooth. The dimension thus gives valuable clues for the sexing of very young individuals when the

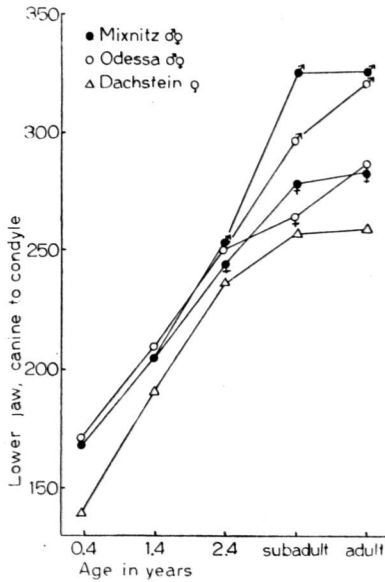


Fig. 1.

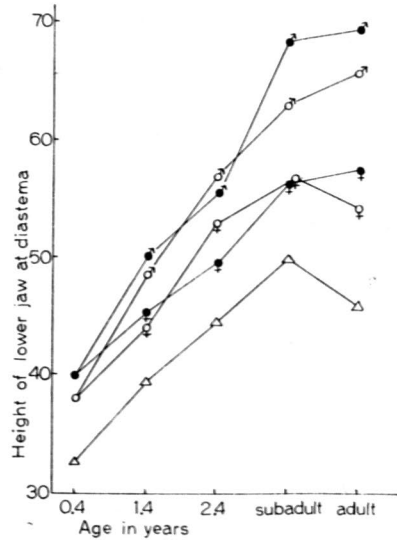


Fig. 2.

Fig. 1. Growth in length of the lower jaw (from canine to condyle) of cave bears from Odessa and Mixnitz (both sexes) and Dachstein (females only).

Fig. 2. Growth in jaw depth at the diastema between canine and P_4 ; samples and symbols as in fig. 1.

canine itself has been lost. The difference between males and females is in the order of 11–12 per cent both at 1.4 and 2.4 years. In the next interval the difference increases and rapidly approaches the adult type of sex dimorphism, in the order of 17 per cent. The exact trend of growth through the three-year-stage is uncertain, because of the contamination of the Mixnitz "subadult" group, but the few Odessa specimens available indicate that the sex dimorphism becomes well established before 3.4 years.

In some instances the depth of the jaw appears to decrease in old individuals. This — and probably also to some extent, individual variation in small samples — is probably the reason for the reduction from subadult to adult in two instances seen in fig. 2 (females from Odessa and Dachstein).

The depth of the jaw below M_1 has about the same trend as the depth at the diastema, but the sex dimorphism sets in later, at about 2.4 years. In the fully grown adult it is about 18 per cent.

The curves for the Mixnitz and Odessa samples are largely similar, though the Odessa jaws appear on an average to be slightly shallower than those from Mixnitz. The Dachstein females show about the same trends, but growth was retarded somewhat earlier, and the dimensions are somewhat smaller at all ages. Study of larger samples of this small form, *Ursus spelaeus her-*

cynica, will be necessary for the determination of whether there are significant differences in the growth patterns.

The variation in the earliest groups (expressed by the Pearsonian coefficient *V*) is relatively high, apparently a result of sampling during a period of very rapid growth.

From an ecological point of view, the most important results are those concerning the development of sex dimorphism. It begins as early as in the first year of life for the dimensions that are influenced by the size of the canine teeth, but otherwise it seems to become pronounced during the third year. The indication is thus that puberty occurred at some time in the third year, being then accompanied by increased growth-rates in males relative to females.

LIFE TABLE ANALYSIS

RELIABILITY OF THE RECORD

Do the remains of the cave bear individuals in different stages of development give a reliable record of the distribution of mortality in the population? There seem to be four main factors influencing the analysis, and I enumerate them beginning with the one nearest at hand to the investigator.

- (1) Bias in interpretation of individual age,
- (2) Bias in collecting,
- (3) Bias in fossilization,
- (4) Bias in the distribution of cave mortality.

The fourth factor merits a section of its own; the other three will be discussed initially.

(1) This factor is covered by the description of the ontogenetic stages. The possibility of bias is more important for older age classes than for younger ones, and practically non-existent for the initial stages (neonate and 0.4-year stage).

(2) There will be a tendency to bias in collection, insofar as small teeth and small fragments escape notice. This is difficult to judge. My main sample, that from Odessa, was collected more than a hundred years ago; but the evidence, as far as it goes, indicates that this bias would not be very important. There is every reason to infer that ALEXANDER VON NORDMANN was a most competent and careful collector, as well as a most skilled anatomist. Even the smallest teeth, shed milk canines without roots and the like, are represented by abundant material, and the indication is that von Nordmann was fully aware of the importance of a quantitative collection, in contrast with too many later investigators. As will be shown later on, the age distributions in the collection from Cotencher and in the material to date excavated in the Cueva del Toll agree in all essentials with that in the Odessa sample.

After he had concluded his studies, von Nordmann caused some specimens to be distributed to other museums. Odessa teeth were studied by me in the Zoological Institute of the University of Lund; their age distribution is random. No other Odessa samples have been tracked down.

(3) The tendency to bias in fossilization would appear to be the same as in (2). The fact that so much of the cave bear material consists of fragments, that whole skulls and undamaged mandibles, as well as complete long bones, are scarce, and articulated skeletons or parts of such almost unknown, has been convincingly explained by Koby (1943) in his theory of the »charriage à sec». The bones of the bears that had died in spring, and presumably had been scraped clean and partially disarticulated by scavengers during summer, were then still more scattered, trampled and broken when the bears returned to their lair in the autumn. Abiotic factors similarly conducive to disarticulation were mentioned by Schadler (in Abel and Kyrle, 1931; for a discussion, see Ehrenberg, 1956). In these processes it would seem likely that the juvenile teeth, consisting mostly of enamel caps without much dentine deposited, would suffer more than the teeth of mature individuals. Thus we might expect a more or less pronounced juvenile under-representation, as in so many other instances. Curiously enough, there is no correlation between stage of development and relative frequency (see below, p. 22), and no suggestion of a juvenile under-representation. As Koby has observed, the charriage à sec is much more pronounced in caves with a sand floor than in such with a loamy one; the Odessan deposits are of the latter type, which affords the remains better protection.

FACTORS OF MORTALITY

So far we have considered the processes introducing bias by postmortal selection of the remains up to their inclusion in the mortality census. Perhaps the most important question, however, is whether the individuals that died in the caves make up a random representation of the distribution of mortality in the population. This necessitates a preliminary excursion into cave bear ecology and an attempt to sum up the probable causes of death.

The closest living relative of the cave bear is the brown bear, *Ursus arctos* L., of Eurasia and North America. Unfortunately but little is known of the factors of mortality in this species. A summary on enemies in nature is given by Couturier (1954, pp. 547–549). Enemies are few, the wolf apparently being the most dangerous one; a wolf pack may attack and kill even adult bears. The great cats might also be powerful enemies, but observations indicate that they generally avoid conflict with brown bears. There is a record from the Ussuri basin of tigers attacking brown bears (Couturier, *loc. cit.*), but this

seems to be highly exceptional. These and other carnivores are, naturally, a menace to unprotected cubs. Bear cubs are also sometimes killed by adult male bears. The bear's most dangerous adversary is however man.

Other biotic factors in mortality include disease and senescence, and possibly lack of food; abiotic factors mainly cold. The relative importance of these factors has not been evaluated.

Turning now to the cave bear, we may initially consider the biotic factors, beginning with enemies. Here the great size and probably immense strength of the animal must be remembered. It is not likely that any one of the contemporary carnivores constituted a very serious enemy to the adult bears. The largest true carnivore of Europe in the late Pleistocene was the great cave lion, *Felis leo spelaea*. Even this powerful beast must have been inferior in strength to a cave bear, and it is quite likely that the two species habitually avoided combat, like the great cats and bears of the present day.

A pack of cave hyenas (*Crocuta crocuta spelaea*) may have been more dangerous, as the living members of this species, hunting in packs, are actually able to kill solitary lions; but such occurrences must have been as exceptional then as now. The same was probably true for the Pleistocene wolf, which was hardly larger than its living descendant; and for the dhole (*Cuon alpinus europaeus*), sparsely represented at a few sites.

As to the fierce larger ungulates (bison, aurochs, boar, and others) and the mammoth, it is to be presumed that the cave bear, which was evidently almost exclusively herbivorous in habits, went out of their way.

The relationship between man and cave bear is harder to evaluate, and current opinion is much divided. It seems however clear that much of the evidence earlier adduced to show that Pleistocene man, particularly Mousterian man, was habitually a cave bear hunter, must now be viewed critically. That there remain some instances in which it can be reasonably assumed that a cave bear was killed by man, is not to be denied; but it now seems clear that the direct influence of man was of slight importance in the mortality of the species (SOERGEL, 1940). That man, through indirect influence, may have been a very important factor in the extinction of the bear, is a different proposition, and one which must be seriously considered; I shall return to it later on.

None of these enemies would seem to have been an important factor in adult mortality. Most of them were probably dangerous to young individuals, if unprotected.

Among biotic factors, disease may have been of great importance, as suggested by many studies. The relatively high frequency of diseased individuals in many samples has been repeatedly stressed, and the list of maladies diagnosed is a long one. Many of these (rheumatism, etc.) point to the effects of the unfavourable climate, and in particular the moist and unwholesome

microclimate of the caverns. Probably some of the diseased individuals more easily fell a prey to enemies such as lion, hyena, wolf and man, but only if in very enfeebled condition; a cave bear suffering from pain, but with its strength little impaired, must have been an exceedingly ugly customer, and one to be avoided rather than engaged in combat. Diseased individuals are probably likely to have succumbed more readily than others to the rigours of a long hibernation, and thus may be expected to be sampled with a high frequency among those that died in their lairs and became fossilized. There is then a possibility that the record may be somewhat biased in favour of diseased individuals, as compared with the population as a whole.

The influence of lack of food is difficult to evaluate as long as the feeding habits of the species are unknown. The cave bear may have been omnivorous, but almost certainly with a stronger vegetivore bias than its living ally, evidenced by the excessive wear of the dentition. Occasional grazing has been suggested by EHRENBERG (1935). The variety of possible diets seems to suggest that lack of food was not of prime importance in mortality, apart from the time of hibernation.

Finally we have the abiotic factors, which, directly or indirectly, seem to be responsible for the main part of the sampling in the cave deposits. By elimination these factors seem to have been the most important ones, or at least to have had a great influence on the population. Of abiotic factors, winter cold probably affected the population most strongly, and, as we have seen, the cumulative hardships of wintering resulted in a mortality peak near the end of the winter.¹ It appears most probable that this was the peak of mortality for the whole year. It follows that the record, being sampled in the season of peak mortality, must also represent a very important fraction of the total mortality in the population.

To infer from this that the distribution of deaths as recorded by the fossils is a valid representation of the actual total distribution of deaths in the population, is of course somewhat speculative. It is possible that young bears more frequently died in caves than old ones, or vice versa; but there is no clear reason why this should be so. With the knowledge that the record represents sampling during the winter half of the year, and making the reasonable assumption that the main part of the mortality occurred during this season, we shall proceed on the working hypothesis that the chances for a young and an old individual to die in a cave and become fossilized were equal. If this leads to incongruous results, we must reconsider the hypothesis; if not, the burden of proof is shifted away.

¹ Other important mortality factors in caves are stone-fall and, particularly, natural traps (see ZAPFE, 1954, for a most illuminating discussion).

METHOD OF ANALYSIS

There are two possible kinds of analytic approach to the data, and the selection between them depends on inferences about the way in which the fossil remains represent the population. They may be interpreted as a census of the living population; for instance, if a local population was destroyed simultaneously by some extraordinary environmental agency (if this occurred repeatedly, it might result in a great accumulation of fossils). The analysis should then be time-specific, i.e. the successive frequencies are entered under l_x in the Life table, and the other functions of the table are computed accordingly.¹ On the other hand, the sample may represent a normal mortality record, and the proper method of analysis is then the dynamic one: the frequencies are entered under d_x , and the other functions computed on this basis. The previous ecological discussion definitely suggests the dynamic approach.

This may, however, be carried out in several ways. An entirely logical method would be to calculate the minimum number of individuals which can be represented in each age class (for the method, see e.g. EHRENBERG, 1950). It has the drawback that the ensuing figures would be almost completely dominated by the frequencies of the second lower molar, which is more abundantly represented than any other tooth. Even though it may be granted that this tooth will give better estimates than any other one, just because it is most frequently found, and the large number of specimens will tend to reduce random fluctuation, it is clear that a weighting of the total evidence will be more valuable.

The only way is then to disregard entirely the actual number of individuals and base the calculations only on the frequencies of all age-determined teeth within successive age classes. This implies that each tooth in a jaw must be counted separately as well, though this certainly means counting the same individual over and over again; the same will naturally happen many times for isolated teeth where the connexion cannot be demonstrated.

The results have nothing to do with the absolute number of individuals, but they take in the evidence of each part of the dentition and give weighted averages which should yield better estimates than the results for a part of the dentition only. Moreover, this system has greater flexibility. For some teeth, groupings throughout the period of growth and even beyond it could be obtained; for others only the first age group could be distinguished.

The procedure is to compare (a) the total number of teeth demonstrably belonging to a given age group (representing number of deaths) with (b) the

¹ For a detailed discussion of these methods, and the principles of Life table treatment of fossil samples, see KURTÉN (1953, 1954b).

sum of these and all older homologous teeth (representing the strength of the cohort when entering the given stage), thus obtaining the rate of mortality within the given interval.

We may take, as an instance, the mortality rate between stages I and II, or between ages 0.4 and 1.4 years. From tables 1 and 2 it may be seen that the values of (a) and (b), adding the rows for stage I in both tables, are 743 and 1946, respectively. The rate of mortality estimated from these numbers is 38.2 per cent.

This is a weighted mean, taking in all the available evidence. The values for the separate teeth show a variation around this mean (see table 6). For instance, the values for P_4 are (a) 35 and (b) 107 (from tables 1 and 2 respectively), giving a mortality rate of about 33 per cent; for M_1 , (a) 55 and (b) 164, giving 34 per cent; and so on.

TABLE 6.

Variations in the estimates of the rate of mortality, obtained from the age distributions of different teeth. (Rates in per mil.)

Interval	I^{1-2}	I_{1-2}	I^3	I_3	C	P^4	P_4	M^1	M^2	M_1	M_2	M_3	All
I—II	486	331	317	338	202	512	327	524	503	335	454	303	382
II—III		211	227	304	147	146		368	296	165	204	276	227
III—IV	—	—	200	172	—	143	—	—	211	110	229	286	198
IV—V	—	—	183	189	—	—	—	—	178	—	214	167	189
V—VI	—	—	102	116	—	—	—	—	189	—	—	140	134
VI—VII	—	—	—	132	—	—	—	—	167	—	—	—	147

Our next objective is to see if these relative values are influenced by the stage of development of the tooth in stage I. Some teeth in this stage consist of practically nothing but the enamel cap of the crown; in others the roots are almost fully formed. If there is any tendency to bias in fossilization, correlated with the presumably greater fragility of the partially formed germs, it should be detectable here; hence the results will also indicate whether the representation of the juveniles is likely to be biased.

One of the least advanced teeth in this stage is M^2 , which consists practically only of an enamel cap and very thin root walls formed less than halfway to the apex. Yet this tooth gives a rather high value (50 per cent), contrary to what might be expected. M_3 , on the other hand, which is also in the early germ stage, gives a deviation in the expected direction (the value being 30 per cent), but this deviation is smaller than that in the opposite direction for M^2 . If the values for M^2 and M_3 , the two teeth latest to emerge in the cheek dentition, are combined, we get the value 40 per cent, which is still slightly

above the mean. None of these differences from the mean can be shown to be statistically significant.

Other comparisons indicate a similar randomness. M_1 is one of the most precocious teeth, almost fully formed in stage I, and a high value might be expected; yet the figure is slightly below the mean (34 per cent). M_2 is less advanced than M_1 , and yet the figure is higher, 41 per cent. On the other hand, the figure for M^1 , which is as precocious as M_1 , is still higher, 52 per cent.

There appears to be one exception, viz. the canine teeth, for which the figure is as low as 20 per cent. This deviation is significant, and stage I seems to be under-represented in the canines. This may be a result of the peculiar shape of the crown, which makes the canine germ exceptionally liable to destruction. The distribution of the canines has little effect on the total result, and part of the deviation may be random; for this reason the canines were included in the computations.

The question whether the found rates of mortality show more than random variation may be answered by a chi-square analysis (see SIMPSON and ROE, 1939). If the mortality rates between 0.4 and 1.4 years in all the 12 groups of teeth of tables 1–2 are compared, the value of χ^2 is found to be 79. There are 11 degrees of freedom, and the value is significant ($P < 0.01$); the variation is not random. However, if the canines are left out, the chi-square value for the remaining 11 groups, with 10 degrees of freedom, is only 9.0, which is far from significant ($P > 0.05$). The variation is apparently random except in the canines, and it may be concluded that, as a rule, postmortal selection in fossilization has little importance for the age distribution in the Odessa sample.

Analogous results were obtained for the same age interval in two other samples, those from Cotencher and the Cueva del Toll, to be discussed in more detail below. For the cheek teeth from Cueva del Toll (6 degrees of freedom), $\chi^2 = 17$, and $P = 0.01$; there may be some non-random variation, and inspection of the data (table 7) indicates that the distribution of M_2 may be slightly biased, but the value may only mean that the hundredth chance has come off. For Cotencher (5 degrees of freedom) $\chi^2 = 12.1$, and $P > 0.05$; the variation is not significant.

For the succeeding intervals, no significant deviations were found in the ratios for different teeth. As an example may be taken the rate of mortality between stages III and IV. Group III could not be distinguished for P_4 , I^{1-2} , I_{1-2} , C, and M^1 , and only the remainder of the teeth can be used. The figures appear in table 6; they vary between 11 and 28 per cent. All deviations can be attributed to random variation. The totals are (a) 102 and (b) 515, and the rate of mortality is 19.8 per cent; this estimate is again a weighted mean, taking in all the available evidence.

COMPARISON WITH COTENCHER AND CUEVA DEL TOLL

The collection from the famous Mousterian station of Cotencher (DUBOIS and STEHLIN, 1933) was studied in the Geological Institute of the University of Neuchâtel. A few teeth were moreover seen in the Natural History Museum in Basel. The material of M_2 was deficient in the sample available to me; there are only a few specimens of this tooth (which is otherwise the most common tooth in bear collections), and they were not included in the study.

The collection from the recently discovered Cueva del Toll, near Moyá, was studied in Barcelona. The excavations are not yet concluded, and more cave bear material will be forthcoming. The material excavated until July, 1956, was at my disposal, including a few teeth found during a visit to the cave and graciously donated to Helsingfors University by the leader of the excavations, Dr. DE VILLALTA. All cheek teeth were used in the study.

TABLE 7.

Distribution into stage I (0.4-year-olds) and older in cheek teeth of *Ursus spelaeus* from the caves of Cotencher and Cueva del Toll.

<i>Cotencher</i>	P^4	M^1	M^2	P_4	M_1	M_2	Total	
Stage I	21	22	36	21	20	11	131	
Older	42	31	39	38	38	45	233	
Σ	63	53	75	59	58	56	364	
Mortality rate	33.3	41.5	48.0	35.6	34.5	19.6	36.0	
<i>Cueva del Toll</i>	P^4	M^1	M^2	P_4	M_1	M_2	M_3	Total
Stage I	18	31	23	15	28	23	20	158
Older	16	27	30	20	56	63	49	261
Σ	34	58	53	35	84	86	69	419
Mortality rate	53.0	53.4	43.4	42.9	33.3	26.7	29.0	37.7

The distribution into stage I and older, for these two samples, is given in table 7. Time did not permit a study of the older age groups, but a comparison between the mortality rates for the interval 0.4—1.4 years in these samples and that from Odessa will indicate whether the results for the Russian bear are likely to be of general validity for the species.

The values found are highly consistent. For Cotencher, a rate of 36.0 per cent is indicated; for Cueva del Toll, 37.7 per cent. In both instances the deviation from the Odessa figure, 38.2 per cent, is extremely slight, and a chi-square test shows it to be devoid of significance ($P > 0.05$). If the data for the three localities are added together, the grand total gives a mortality rate of 37.9 per cent, with the standard error 0.93 per cent, which may be taken as the best estimate of this rate now available.

The results also indicate that the dynamics of the cave bear population was of the same pattern in different parts of its range (and probably at different times). The three samples represent a marginal western, a central, and a marginal eastern population, and thus cover the whole range of the species from extreme west to extreme east.

MORTALITY FROM BIRTH TO ADULT AGE

The record can be extended from stage I (which is taken to represent a modal age of about 0.4 years) back to birth with the aid of the milk teeth. In its mode the 0.4-year stage roughly coincides with the shedding of the milk canines. To take in its total range of age variation, however, it is also necessary to include some of the slightly younger stages. It seems probable that all the milk canines which show resorption marks on the root, thus indicating the existence of germs of permanent teeth, should be included in the milk-tooth equivalent of the permanent-tooth stage I.

The milk canines younger than that stage (a—c in my tabulation p. 9) number 39, whereas the total of milk canines is 204. This gives a mortality rate of 19.1 per cent from birth up to the age of 0.4 years.

We now have a series of mortality rates from birth up to the age of 5.4 years, and on this basis it is possible to compute a truncated Life table (table 8). The mortality rates are entered under the heading $1,000 q_x$ (and are given on a per thousand basis to avoid the use of decimals), and the other functions are computed from them. Of the Life table functions, e_x (expectation of life) must be left out for the present, since the history of the cohort after 5.4 years is unknown.

TABLE 8.

Partial Life table (from birth to 6.4 years) for *Ursus spelaeus*, Odessa, based on mortality rates indicated by milk canines (see the text) and permanent teeth (table 6).

Age	d_x	l_x	$1,000 q_x$
0.0 — 0.4	191	1,000	191
0.4 — 1.4	309	809	382
1.4 — 2.4	113	500	227
2.4 — 3.4	76	387	198
3.4 — 4.4	59	311	189
4.4 — 5.4	34	252	134
5.4 — 6.4	32	218	147
6.4 —	—	186	—

The table clearly demonstrates the decrease in mortality rates from the newborn to the adult. This is then an example of the highly elusive "concave" survivorship pattern. Its existence in natural populations can be theoretically

postulated, but its actual demonstration meets with great difficulties (DEEVEY, 1947; KURTÉN, 1953). In the first 4—5 months, the mortality is 19.1 per cent, which is equivalent to 41 per cent in one year. This rate is successively reduced, finally sinking below 15 per cent in the young adults.

From birth up to 4.4 years the mortality is almost exactly 75 per cent. The cave bear was fully adult at about four years of age. The mortality up to that age, or the total juvenile mortality, is about 70 per cent. It would seem to be more than a coincidence that this figure, 70 per cent, was reached by KURTÉN (1953) as an estimate of the average rate of juvenile mortality in a number of natural mammal populations.¹

THE COMPLETE LIFE TABLE

The grouping of some teeth could be carried beyond the limit set in the previous discussion, or stage VI. It is clear that the role of personal judgment, and hence the possibility of bias, becomes increasingly important the further the grouping is carried. Nevertheless an attempt seems to be legitimate, and the results may at least give some idea of the pattern of survivorship in older cave bears.

Grouping was attempted for I_3 , M^2 , and M^3 , all of which normally seem to be characterized by fairly regular attrition. Exceptions do occur, and I have seen instances of abnormal wear, for example skulls with markedly worn teeth on one side and almost intact tooth crowns on the other. Such individuals do not however seem to be frequent enough to distort the results in a serious way.

The analysis was made by arranging the teeth in a series of increasing attrition, and grouping together those which showed identical wear. This primary grouping was thus entirely morphological. The grouping obtained was tested in various ways. Regarding the molars, for instance, measurements of the height of the crown as worn were taken at some fixed points, and a mean was computed for each tooth, giving a "mean height" of the crown. To minimize the influence of individual size variation, this mean can be expressed as a percentage of the length or width of the tooth. Group means were computed and compared. A fairly regular decrease would be expected, and was also found, though the trends become erratic for the older groups, in which the crown tends to wear very irregularly, so that the facet locally may extend far down onto the roots.

¹ A rather similar figure was computed by KENYON, SCHEFFER and CHAPMAN (1954) for juvenile mortality in the Alaska fur-seal, *Callorhinus ursinus*.

TABLE 9.

Attempted grouping of the total available material of I_3 , M^2 and M_3 from Odessa into age groups.

Stage	Group frequencies				Cumulative frequencies			
	I_3	M^2	M_3	Σ	I_3	M^2	M_3	Σ
I	47	82	51	180	139	163	167	469
II	28	24	32	84	92	81	116	289
III	11	12	24	47	64	57	84	205
IV	10	8	10	28	53	45	60	158
V	5	7	7	19	43	37	50	130
VI	5	5	6	16	38	30	43	111
VII	4	5	6	15	33	25	37	95
VIII	2	3	4	9	29	20	31	80
IX	3	2	5	10	27	17	27	71
X	2	2	4	8	24	15	22	61
XI	3	2	3	8	22	13	18	53
XII	3	2	3	8	19	11	15	45
XIII	5	2	3	10	16	9	12	37
XIV	4	3	3	10	11	7	9	27
XIV	4	1	2	7	7	4	6	17
XVI	2	1	2	5	3	3	4	10
XVI	1	1	1	3	1	2	2	5
XVIII	0	1	1	2	0	1	1	2

A quite different kind of test is also possible. From the relationships found in the younger groups, which are particularly clear-cut morphologically, we know the average annual mortality in young adults. Numerous analyses (see KURTÉN, 1953) give grounds for the expectation that the rate of mortality would be approximately constant during the next few years in the life history of the cohort. The grouping gave the expected result: the apparent mortality in the following years fluctuated around 10–15 per cent. Later on, a gradual increase in mortality rates was indicated, and the last survivors would appear to have attained an age of 15–20 years.

Is this apparent maximum age at all likely to be near the truth, or, in other words, can it be taken as a good estimate of the potential natural longevity¹ of the cave bear? We have no information on the potential natural longevity of the living bears; data on longevity in captivity were discussed in KURTÉN (*op.cit.*), where it was shown that the longest records give averages between 20 and 30 years. There is reason to suppose that these figures for bears, which thrive excellently in captivity, are somewhat in excess of the potential natural longevity. If the cave bear was almost exclusively herbivorous — a widely accepted conclusion — a limitation to some 15–20 years

¹ Maximum potential life span in natural conditions, not optimal conditions.

would seem a not unrealistic estimate. SOERGEL (1940) was definitely of the opinion that the cave bear was not as long-lived as the brown bear, and emphasized that a "senile" dentition did not necessarily reflect great age. Thus for the cave bear, as for many other mammals (see FLOWER, 1931; KURTÉN, *op.cit.*), the potential longevity under natural conditions would be limited, first and foremost, by the wear of the dentition.

A Life table, based on this analysis, and recast with round-year intervals (except for the first year, which is divided into two intervals, 0—0.4 and 0.4—1.0), is given as table 10. The expectation of life (e_x) is calculated on the assumption that all the mortality (except for the 0—0.4 interval) was concentrated to early spring.¹

TABLE 10.

Total Life table (from birth) for the cave bear, *Ursus spelaeus*, based on the Odessa sample.

x	x'	d _x	l _x	1.000 q _x	e _x
0—0.4	—100	191	1.000	191	3.41
0.4—1	—88	201	809	249	3.76
1—2	—71	179	608	294	4.30
2—3	—41	98	429	228	4.94
3—4	—12	58	331	175	5.28
4—5	17	43	273	158	5.32
5—6	47	27	230	117	5.24
6—7	76	27	203	133	4.88
7—8	105	23	176	131	4.57
8—9	135	20	153	131	4.20
9—10	164	18	133	135	3.77
10—11	193	16	115	139	3.30
11—12	223	17	99	172	2.77
12—13	252	17	82	207	2.37
13—14	281	23	65	354	1.75
14—15	311	16	42	381	1.50
15—16	340	12	26	462	1.17
16—17	364	8	14	571	0.83
17—18	399	6	6	1.000	0.4

TESTING THE LIFE TABLE

There are some possibilities for testing the intrinsic consistency of the Life table, as well as its consistency with data of other types. The first question is whether the population structure of the table is in balance with the productivity of the species.

¹ Normally the mortality is assumed to be evenly distributed over the interval, which in calculation means that it is centred at $x+0.5$ years; here $x+0.4$ was used. For the method of calculation, see DEEVEY (1947).

The productivity of the recent brown bear has been studied by several zoologists. COUTURIER (1954, p. 463) has compiled a number of data, the most precise of which are those given by KAZEFFF and KREMENZ. According to KAZEFFF, out of ten litters with newborn, six or seven comprised 2 cubs, two or three 3 cubs, and one 4 cubs. This gives a mean productivity per female of 2.5 or 2.4. KREMENZ gives a total of 43 cubs for 16 births, the mean here being still somewhat higher or 2.69. From this it may be assumed that 2.5 is the more probable figure for KAZEFFF's sample, and the two may be combined. This gives 26 litters and 68 cubs, or a mean of 2.62.

The female bear commonly has two litters in three years. This would mean an average annual productivity of 1.67 per adult female. As some of the oldest females may be sterile, the youngest ones may have smaller litters, and some may not find mating partners, this figure is slightly too high.

The productivity of the cave bear is only known from a few litters (EHRENBURG, 1922). The suggestion is that twins may have been common and single births not infrequent in the later Mixnitz population, but the evidence is not conclusive.

In our cohort it may be assumed that the 4-year group of young adults constitutes the initial parent class, since puberty seems to have been attained during the third year. There are records of female brown bears pregnant in their third year, and this may also have happened in the cave bear population, but it was probably exceptional. The part of the population which is 4 years old and older, that is the sum of the l_x values from age group 4.0–5.0 on, is 1,948, as against 2,846 younger individuals (sum of l_x entries from 0.0–0.4 to 3.0–4.0, excluding the entry for 0.4–1.0). Of these 1,948, about one half, or 974, should represent females.¹ The annual productivity of these 974 females should be 1,000 newborn, which is the initial age class of the cohort. This means an average annual productivity of 1.03.

This figure is lower than the estimate for the living brown bear. Such a difference may be expected. The true mean for *Ursus arctos* is likely to be somewhat lower than 1.67, because it is not probable that the potential productivity is fully realized, for reasons given above. A value approaching 1.03 is possible; but it is also possible that the productivity of the cave bear was slightly lower than that of the brown bear. Larger mammals have on an average smaller litters.

Taking all this into account, it seems that the estimate gives a very reasonable value. A population structure like that of the Odessa bear in table 11 would appear to be stable, with mortality and productivity in metabolic balance, a steady state.

¹ The sex ratios will be discussed below.

This test giving a positive result, we may now proceed to a quite different kind of check of the Life table. It will be assumed that this population structure is essentially the same as that of the Mixnitz cave bear — an assumption which is warranted by the similarity of the mortality records from Odessa, Cueva del Toll and Cotencher. The total number of individuals represented in the Drachenhöhle at Mixnitz has been estimated at some 30,000 (see SOERGEL, 1940, for a discussion). This immense accumulation of remains was sampled during a relatively long period. If the period began during the Eem Interglacial and was extended during the main part of the Würm, it may have been up to 60,000 years long; more probably it was somewhat shorter, and settlement may have been intermittent; some 30,000 years may perhaps be taken as the minimum length. It may thus be tentatively estimated that the deposition proceeded at an average rate of $\frac{1}{2}$ —1 individual per annum.

What population size is presupposed by a mortality of one individual per annum? This question is answered by the Life table. The total population of the table, obtained by adding together all entries under l_x (except for the 0.4—1.0 interval), is 4,794 individuals. Of these 1,000, or 20.9 per cent, died annually (the "crude" mortality rate). The death of one individual annually would thus presuppose a population size of 4—5 individuals, that is, a single bear family, or a small group of solitary bears. The cave was big enough to house such a number of individuals; ABEL (1929) thinks it possible that up to six families, exceptionally, might have used it as a lair.

Young individuals are relatively rare at Mixnitz, and among the adult ones the males predominate; reasons will be given below for the conclusion that the Drachenhöhle was preferred by solitary adults to a greater extent than by bear families. The crude death rate for the adults is lower than that for the whole population, for instance 17.0 per cent from 4 years up. The annual death of one individual would then presuppose a population of about 6 individuals. The true figure would probably lie somewhere between these estimates, say 5 individuals.

It is not probable that all the individuals of the Drachenhöhle population died in the cave and became fossilized; thus the real figure would be higher than 5. On the other hand, the time span may have exceeded 30,000 years, and the rate of deposition may have been lower than 1 individual per annum. If so, the population figure should be lowered. The two factors thus counteract each other. At most, it can be suggested that the stationary population was on the order of some 4—10 individuals, both solitary and bear families; and this is in accordance with the estimate of the capacity of the cave. The results, incidentally, indicate that a large fraction of the individuals that died, did so in the cave and became fossilized; which strengthens the basis of the Life table.

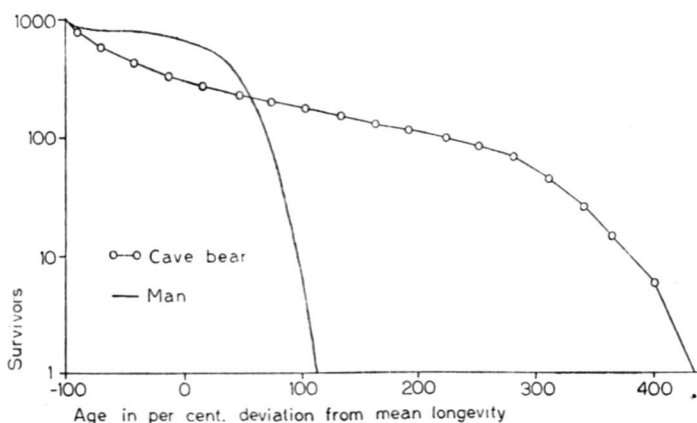


Fig. 3. Survivorship curves (from birth) for *Ursus spelaeus* (Odessa; original data) and *Homo sapiens* (white males, continental U.S.A.; data from ALLEE *et al.*, 1949), superimposed by means of PEARL's method.

The juvenile mortality was discussed above, and shown to agree with that in some other natural mammal populations. The mortality in the adults is slightly higher than what might be expected from my results in 1953. It was then shown that there is a relationship between gross size and annual rate of mortality in adult mammals, the correlation being inverse, and that a sigmoid curve of the logistic type could be used to express this relationship. It was however also pointed out that the curve probably was no more than an approximation of a general trend, and emphasized that significant deviations from the norm might be expected. According to the logistic curve, the average annual mortality of adult cave bears in their prime would have been on the order of 7–8 per cent. The Life table suggests a somewhat higher value, some 12–13 per cent. The difference may well be real.

No extensive comparison with other populations is at present feasible, because few complete Life tables for natural populations have been constructed. Fig. 3 shows the survival curve for the cave bear, compared with that for human males, using x' to denote time according to PEARL's well-known method. A population pyramid for the cave bear is shown in fig. 4.

MORTALITY AND SELECTION

THE DESCENDENCE OF THE SPECIES

The record of the species *Ursus spelaeus* extends from the Holsteinian Interglacial (Mindel/Riss, Elster/Saale) to the end of the Würm. Finds from the Holsteinian include specimens from Steinheim and the Heppenloch in Germany, and from Swanscombe in England. There are only a few finds from this interglacial, but this is not necessarily any indication that the population

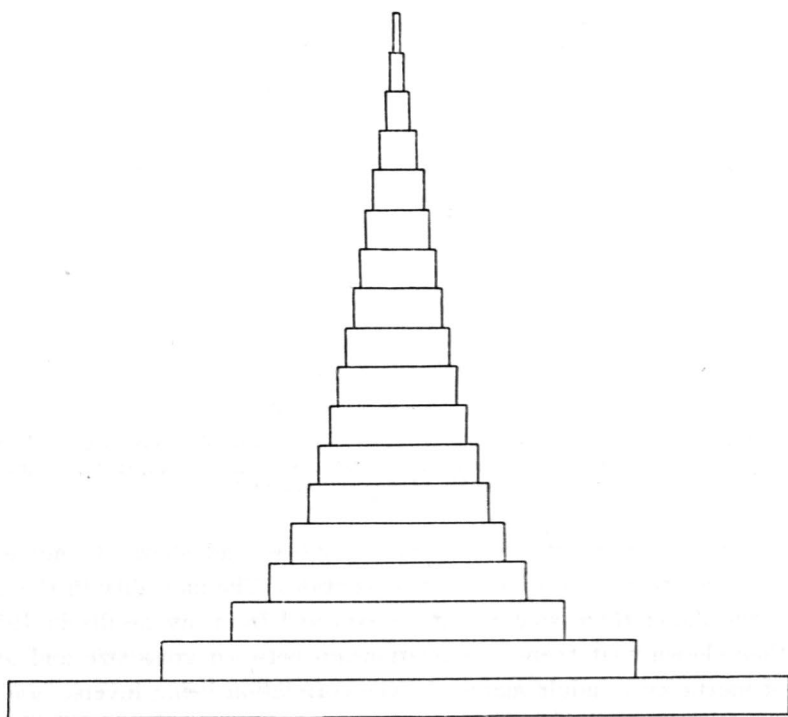


Fig. 4. Population pyramid for *Ursus spelaeus*, Odessa.

was particularly small. The mammalian faunas from the Holsteinian are, in general, rather poorly recorded. It is noteworthy, however, that the large sample of bears from Grays Thurrock, apparently of Holsteinian date, does not to my knowledge include any cave bear specimens; whereas, at Heppenloch, both species occur associated, and at Steinheim and Swanscombe, only *spelaeus* is known.

Ursus spelaeus evidently arose from the Cromerian *U. arctos deningeri*. It is likely that the western European part of the Cromerian population became isolated from the remainder of the *arctos* population in eastern Europe and Asia by the ice sheets of the Mindel (Elster) Glaciation, and the tundras between Alpine and Scandinavian glaciers, and evolved into *U. spelaeus*. That the two species, *arctos* and *spelaeus*, were distinct in the Holsteinian is clear from the fact that both then existed in Europe, even in the same area (Heppenloch), without merging together. For an outline of the evolution and stratigraphy of the Pleistocene bears, see KURTÉN (in the press).

The cave records become frequent in the Eemian Interglacial and continue up to the final cold oscillation of the Würm (the Pomeranian). Possibly future

research will give more details on the earlier, Holsteinian history of the cave bear; most caves from this time were probably closed long ago, and remain unknown. Occasionally, the brown bear acts as a vicar of its sibling. Such is the situation in most British caves, where *Ursus arctos* occurs in the great numbers characteristic of bear caves, and with an age grouping which suggests hibernation. The cave bear is occasionally present in some British bear caves, but only a few specimens are known, and they probably represent strays outside of the settled territory of the species. The northern boundary of the cave bear range presumably coincided roughly with the English Channel of the present day, then dry land; large samples of the species are known from Belgian sites.

THE LIFE HISTORY OF AN *URSUS SPELAEUS* COHORT

In the evolutionary history of the cave bear, the population we are studying occupies a relatively late position. It belongs to the nominate subspecies, *Ursus spelaeus spelaeus* (to date only one valid subspecies apart from this seems to be known, the small Eemian *U. spelaeus hercynica* Rode), and lived in the eastern marginal zone of the species range, in the outskirts of the great south Russian loess belt, probably during the early Würm. There is no trace of a competing *Ursus arctos* population; if there were brown bears in this region, they at least did not normally hibernate in caves.

The relationships between the two species suggest that the absence of *U. arctos* records in caves may actually be due to the activity of *U. spelaeus*. In England, where the cave bear was not regularly present, the bear caves are full of *arctos*; and in the uppermost strata of many Continental caves, after the disappearance of *U. spelaeus*, *U. arctos* is often found (for instance Mixnitz, Gailenreuth, Muggendorf). Moreover, the presence of brown bears in cave bear territories is sometimes revealed by a few *arctos* remains among the wealth of *spelaeus* bones. Such intrusions have been recorded, for instance, by DUBOIS and STEHLIN (1933) at Cotencher, and by KOPY (1944) in two caves in the Jura, St.-Bras I and II. I have seen typical *arctos* specimens from the *spelaeus*-caves of Steeden an der Lahn and Hohlefels.

It may perhaps be suggested that the ranges of the two species overlapped to a great extent, but that the larger and more powerful *U. spelaeus* generally ousted its smaller ally in the competition for caves as winter lairs. Intra- and interspecific territoriality is practised by many carnivores; as signs, urination marks etc. may be used. After the extinction of *U. spelaeus* the prize fell to *U. arctos*, which was able to settle at the sites not meanwhile conquered by man. Outside of the range of *U. spelaeus*, *U. arctos* habitually hibernated in caves — not only in Britain, but also as far away as, for instance, at Choukoutien.

In our Odessa population, the young apparently were born in December or January, the mothers then hibernating. The expectation of life at birth was only about $3\frac{1}{2}$ years. Some six per cent were stillborn or died soon after birth; about five per cent of the remaining probably died before one month of age. The total toll of death during the first month of life was apparently about 11 per cent. Many of the cubs that died in this early stage may have been afflicted with hereditary diseases; this is the time when selection weeds out the grossly inadaptive factors, lethal and semilethal genes. In the following period mortality was reduced; of the cubs attaining about one month of age, some 91 per cent survived to three months.

At this time the permanent teeth were being formed and began to emerge, and the milk teeth were being shed. At the same time, the strains of the long hibernation were beginning to tell. Once more mortality rose, reaching a peak close to the end of hibernation. When finally the surviving cubs made their first excursion into the outside world, almost one-half of the cubs born, and some seventeen per cent of the mothers, had died.

The summer world would have been more friendly to the young bears, unless they strayed too far from the protection of their mothers. The following winter took a less heavy toll; yet only some forty per cent of those initially born survived it. With continued growth in size, strength and experience, the mortality was continuously reduced, and expectation of life for the survivors increased; and at the age of 5–10 years, when the bears were at the height of their strength and prowess, annual mortality fluctuated close to ten per cent.

After these peak years, symbolized in the survivorship curve by its point of inflection — its precise location is uncertain — senescence slowly assumed importance. It was mainly exogenous senescence, induced by the environment. Many years of wintering in cold and moist caves would leave their mark in reduced resistance to disease. The dentition, not particularly well adapted to an almost herbivorous mode of life, was heavily taxed. Mortality was gradually augmented; at fifteen years of age there is only a frazzle left of the initial cohort, in a few years more even the roots of the teeth are wearing down. The enfeebled state of the dentition impedes feeding, and the last survivors die, emaciated, during hibernation.

SELECTION

A successful hibernation was mainly the result of a successful season in the preceding summer and autumn. A well-nourished bear stood a better chance to survive the winter than one which entered its winter quarters in a wasted condition. Winter mortality, thus, predominantly reflects the ecological success of the bears during summer and autumn; it is selective.

Differential survival or mortality is one aspect of selection, not the only one but of great importance; this is so-called Darwinian or "stabilizing" selection. Such differential survival may favour variants close to the population mode, while weeding out more extreme variants. This is the "centripetal" selection of SIMPSON (1953), and a population in this situation is, on an average, well-adapted; the selection tends only to promote the central or "normal" type in the population. On the other hand, variants at one end of the population range may be favoured, at the cost of other ones; this "linear" selection is directed towards an optimum outside of the range, and the population is ill-adapted. A combination of these two, centripetal selection with a linear component, is directed towards an optimal value within the total variation range, close to but distinct from the population mode.

Instances of differential survival affecting mammalian teeth have been given in KURTÉN (1953, 1955b), and other data will be published elsewhere. The study of differential mortality is particularly easy with mammalian tooth crowns, because variation caused by growth does not occur. Any depletion of variability or change of mean in a cohort, with increasing age, is therefore due to differential survival, or Darwinian selection. Naturally, the measurements of young and old should be taken in the same way, and care should be taken to avoid measurements affected by wear. In the cited papers, the study was based on absolute dimensions of teeth. For the bears it was necessary to use sexually homogeneous samples, in order to avoid the effects produced by sex dimorphism. The study is thereby limited to sexable material, and this approach is not practicable for the Odessa sample, which consists mainly of isolated teeth; these cannot be sexed, except the canines and some incisors. Other methods must be devised for a study of differential mortality in this population.

Regression analysis was found to be useful and highly illuminating; but for the present purpose, the less laborious and more easily understood quotient method will be used. This reduces the possibilities for study, insofar as only dimensions with an isometric or nearly isometric interrelationship can be used. The method is to express one of the dimensions in per cent of the other, and study the changes in the variation and average value of this index with increasing age in the cohort.

The selection may also be represented graphically. If there is no Darwinian selection on a numerical character, the rate of mortality will be precisely the same regardless of the value of the variate. Graphically, this may be represented as in fig. 5a, where any value of x (the variate) corresponds with the same invariable mortality rate. Centripetal selection will give a survival peak for the central (proximal) variants, whereas the rate of mortality is higher for the extreme (distal) variants (fig. 5b). A moderate linear component

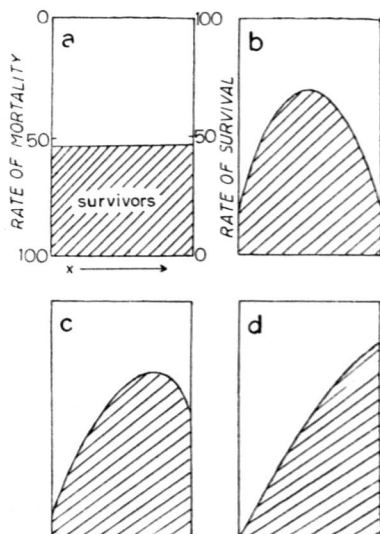


Fig. 5. Diagrammatic representation of differential survival affecting the distribution of a given variate (x) in a cohort. (a), no selection; all values of x have the same survival value. (b), centripetal selection; central variants have higher survival rates than extreme ones. (c), centripetal selection with a linear component; highest rate of survival for individuals somewhat above the central value, very low survival rates for small variants. (d), predominantly linear selection; largest variants have the highest, and smallest variants the lowest, rates of survival. Discussion in the text.

gives a skewed survival distribution, with a peak not coincident with the central value, but still with reduced survival for distal variants on both sides of the optimum (fig. 5c). Finally, extreme linear selection will move the survival peak wholly to one end of the realized range, and give a pattern of the type shown in fig. 5d. The position of the peak in b and c indicates the value towards which the selection is directed, that is the optimum; the optimum in d may coincide with the extreme end of the variation range, or be wholly outside of the range.

A SELECTION COMPLEX IN THE SECOND MOLARS

The index 100 (length of M^2 paracone/total length of M^2 crown) was computed for the Odessa material. It expresses the length of the paracone, or anterior external cusp — the largest cusp of the second molar — as a percentage of the total crown length. The dimensions could be adequately and consistently measured on most of the material except a few specimens in excessive stages of attrition.

The change in the mean and standard deviation for this index with increasing age is shown in table 11. The standard deviation (σ' , see SIMPSON and ROE, 1939) shows a slow but steady reduction of variation throughout

TABLE 11.

Parameters for the index, 100 (paracone length/crown length) of M^2 in the Odessa *Ursus spelaeus* cohort, at successive ages. The material is cumulative from old to young, the 0.4-year group thus comprising the total material.

Age	N	M	σ
0.4	109	28.87 \pm 0.16	1.70 \pm 0.11
1.4	43	28.27 \pm 0.26	1.69 \pm 0.18
2.4	27	27.50 \pm 0.27	1.39 \pm 0.19
4.4	18	27.33 \pm 0.31	1.30 \pm 0.22
6.4	10	27.30 \pm 0.36	1.14 \pm 0.25

the series, perhaps not statistically significant but nevertheless, as a trend, highly suggestive. That Darwinian selection did occur is however conclusively proved by the fact that the mean also changes in the cohort, and this change is highly significant. The mean for the group that died at 0.4 years is 29.26 \pm 0.20, and differs from, for instance, the mean for the cohort at 2.4 years (see the table) with the highest significance ($P < 0.001$). There is a continuous reduction in the mean index with increasing age, particularly strong during the first interval, but continuing up to the last stage recorded (cohort at 6.4 years).

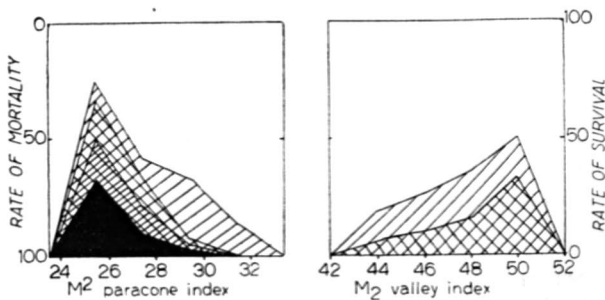


Fig. 6. Centripetal selection with a linear component simultaneously acting on the relative paracone length of M^2 (left) and the relative length of the valley between protoconid and hypoconid in M_2 (right) in *Ursus spelaeus*, Odessa. Grouping as in tables 11–12.

This means that there was strong linear selection in favour of a relatively smaller paracone than the average. The result cannot be spurious (for instance, due to the wear of the tooth), because the paracone remains practically unworn during the first years of life, or precisely the time when the selection is particularly strong. The individuals with a relatively large paracone had much higher rates of mortality than those with a small paracone; this is clearly depicted in fig. 6a, which also shows that an index on the order of 26 — close to one end of the range but still inside of it — was optimal.

What is the cause of this intense selection, and why does it begin so early?

The interval 0.4—1.4 years is the time when M^2 begins to emerge; at the end of the interval, the tooth is wholly erupted, but still at an angle to the tooth row, and not completely in function. However, the paracone is the first part of the tooth crown to emerge, and it enters into functional occlusion before 0.4 years. Therefore, if a large paracone is actually inadapative, it is natural that selection will begin at this early date, and be particularly strong until most of the inadapative variants have died.

For an explanation we may look to the interaction between M^2 and M_2 ; the latter occludes with the anterior part of the former. The paracone of M^2 bites between the protoconid and hypoconid of M_2 , and corresponds with the valley between these two cusps. Possibly the inadapitiveness of a large paracone may result from a disturbance in the occlusion.

TABLE 12.

Parameters for the index, 100 (distance between summits of protoconid and hypoconid/crown length) of M_2 in the Odessa *Ursus spelaeus* cohort, as in table 11.

Age	N	M	σ
0.4	137	44.19 \pm 0.22	2.55 \pm 0.15
1.4	36	45.00 \pm 0.34	2.06 \pm 0.24
2.4	15	45.53 \pm 0.52	2.03 \pm 0.37

This was tested by means of an analogous study of M_2 . Here, the distance between the summits of the protoconid and hypoconid was measured; this measurement gives a numerical expression of the size of the valley into which the paracone of M^2 occludes. Again, an index was computed: 100 (distance between tips of protoconid and hypoconid of M_2 /total crown length of M_2).

This index could be obtained for the three initial age groups only, because the tips of the cusps become obliterated by attrition in later groups. The trend for the series 0.4—2.4 years is, however, definite (table 12). There is a marked change in the mean of the index, and the difference between the individuals that died at 0.4 years (mean = 43.90 \pm 0.26) and the survivors at 1.4 and 2.4 years is significant ($P < 0.01$). There is also a reduction in the variation, showing centripetal selection; but the shift of the mean, and the asymmetry of the survival (fig. 6b) reveals the existence of a strong linear component in selection. Again, selection is directed toward an optimum within the total range, but distinct from the mode.

In this instance, the selection acts in favour of a greater than average distance between the summits of the cusps, or in other, a large valley between the cusps. The significance of this becomes fully clear when it is remembered that selection on M^2 favours a small paracone. Obviously, the average condition in the population was one of imperfect adaptation: the paracone of M^2 was, on an average, somewhat too large to fit well into the corresponding

valley of M_2 . Selection will then act simultaneously on both teeth, favouring on one hand second upper molars with relatively small paracones, on the other hand second lower molars with relatively large valleys between the external cusps.

The most surprising fact is perhaps the very early stage in which the individuals with slightly maloccluding teeth were weeded out. Darwinian selection started immediately when the teeth entered into function, and was extraordinarily effective: in two or three years most inadaptable variants were weeded out, and later on (to judge from M^2) the selection on the survivors became almost purely centripetal.

This situation must have persisted for a very long time, or else it would not have been statistically detectable in the sample. In other words, even this strong Darwinian selection had no effect on the population, despite that most inadaptable variants were eliminated very early in life, and hence could not partake in reproduction. This suggests that the variation in these indices was phenotypic only; it only represents random modification around a single genotypic regression line. Genetic variation in favour of a smaller paracone in M^2 , or larger valley in M_2 , would have been at a premium, and would have been strongly favoured by selection. But the population did not adjust; and the conclusion is that no such variation was available. Apparently, these characters were not governed by polygenes in the cave bear.

WIDTH RELATIONSHIPS OF SECOND LOWER MOLARS

The widths of the anterior and posterior lobes of the second lower molars have a nearly isometric relationship in bears. M_2 is particularly common in most bear collections, and it was possible to make a study of the Darwinian selection on the width index, 100 (anterior width/posterior width), in numerous populations. These include not only local samples of *Ursus spelaeus* itself, but also fossil and living *Ursus arctos*, among them the Cromerian *U. arctos deningeri*, progenitor of the cave bear.

Apart from the Odessa sample, the following collections have been used:

Ursus arctos deningeri, Mosbach (Natural History Museums of Mainz and Wiesbaden; Hessisches Landesmuseum in Darmstadt; the Geological Museum in Frankfurt). The sample was divided into three groups: young (unworn or slightly worn), adult (medium worn) and old (much worn).

Ursus arctos deningeri, Forest Bed (British Museum and the Geological Museum in London, and the Castle Museum in Norwich). Two groups: young (as above) and adult (medium worn or more).

Ursus spelaeus, Mixnitz (Paleontological Institute of Vienna University). Four groups, as in table 13.

Ursus spelaeus, Sloup Cavern (Paleontological Institute of Vienna University). Grouping into young (about 0.4–1.4 years) and adult.

Ursus spelaeus, Gailenreuth (British Museum). Grouping as for Sloup.

Ursus spelaeus hercynica, Schreiberwandhöhle, Dachstein (Paleontological Institute of Vienna University). Grouping as for Sloup.

Ursus arctos taubachensis, Kent's Cavern (British Museum). Grouping as for Sloup.

TABLE 13.

Darwinian selection on the index 100 (anterior width/posterior width) of M_2 in different bear populations (as in table 11).

	Age	N ¹	M	σ
<i>Ursus arctos deningeri</i>	Young	19	95.42 ± 0.67	2.94 ± 0.48
Mosbach	Adult	13	95.77 ± 0.86	3.10 ± 0.61
	Old	5	97.20 ± 1.00	2.23 ± 0.70
<i>Ursus arctos deningeri</i>	Young	19	94.68 ± 0.81	3.55 ± 0.58
Forest Bed.....	Adult	11	93.91 ± 0.93	3.08 ± 0.66
<i>Ursus spelaeus</i>	0.4	207	96.31 ± 0.27	3.88 ± 0.19
Odessa.....	1.4	100	95.90 ± 0.37	3.71 ± 0.26
	3.4	71	95.75 ± 0.41	3.45 ± 0.29
	~ 7	30	95.62 ± 0.70	3.83 ± 0.49
	~ 12	12	94.45 ± 1.11	3.84 ± 0.78
<i>Ursus spelaeus</i>	0.4	146	97.84 ± 0.29	3.55 ± 0.21
Mixnitz	2.4	63	97.51 ± 0.39	3.06 ± 0.27
	~ 4	32	97.73 ± 0.60	3.37 ± 0.42
	~ 10	4	98.95 ± 0.96	1.91 ± 0.68
<i>Ursus spelaeus</i>	Young	25	96.40 ± 1.04	5.19 ± 0.73
Sloup Cavern.....	Adult	12	96.17 ± 1.25	4.34 ± 0.89
<i>Ursus spelaeus</i>	Young	22	96.14 ± 0.83	3.91 ± 0.59
Gailenreuth	Adult	7	95.71 ± 1.27	3.35 ± 0.90
<i>Ursus spelaeus hercynica</i>	Young	23	96.17 ± 0.62	2.98 ± 0.44
Dachstein	Adult	7	96.00 ± 1.00	2.65 ± 0.71
<i>Ursus arctos taubachensis</i>	Young	11	97.73 ± 1.40	4.65 ± 0.99
Kent's Cavern	Adult	6	94.83 ± 1.01	2.48 ± 0.72
<i>Ursus arctos arctos</i>	Young	42	96.90 ± 0.56	3.62 ± 0.40
Finland	Adult	22	96.05 ± 0.52	2.46 ± 0.37
	Old	14	96.07 ± 0.60	2.24 ± 0.42

¹ Here as elsewhere, cumulative from older to younger.

Ursus arctos arctos, Recent, Finland (most in the Zoological and Anatomical Institutes of Helsingfors University). Grouping as for Mosbach.

The trends for this index are shown in table 13 and fig. 7. A reduction of the variation with increasing age in the cohort is very common, though not

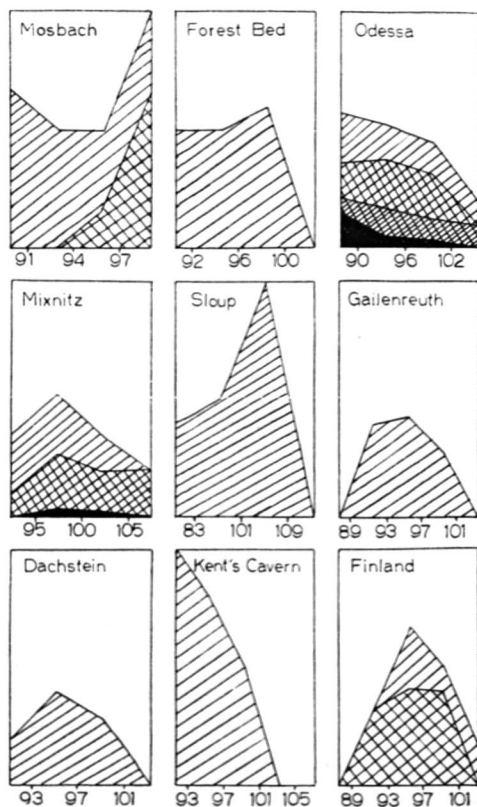


Fig. 7. Selection patterns (as in figs. 5–6) for the index 100 (anterior width/posterior width) of M_2 in nine bear populations (for specification and grouping, see table 13).

universal (exceptions in the oldest age groups from Odessa, in one age group from Mixnitz, and one from Mosbach). At least it seems that selection has been at work at some time or other in each of the populations, and the graphs, accordingly, show survival peaks. Mostly, the optimal value seems to have been close to the mode, with the peak almost in a central position, and the survival values diminishing to both sides. Moderate asymmetry is exemplified by the Odessa and Mosbach populations, indicating selection in favour of lower and higher indices respectively; the trends for the means are consistent in both cases (table 13), and a linear component is suggested, but the differences are not highly significant.

In one instance, however, a linear trend is practically certain. This is the brown bear from Kent's Cavern, where the index is radically reduced with increasing age (i.e., selection in favour of a relatively narrow anterior lobe and a relatively broad posterior one). The mean index for the individuals that died when young is 101.20 ± 1.93 , and the difference from the mean for the older (see table 13) is almost surely significant ($P < 0.02$). The graph shows the extreme trend of the differential survival; the mortality for individuals with a high index is in the order of 100 per cent, and approaches zero for those with a low index.

This comparison indicates that the Darwinian selection on a dental character may differ from place to place, from time to time, and from species to species. The cause of these differences must, in the present instance, remain obscure. The character discussed here — relationships between anterior and posterior widths of M_2 — is functionally important in the occlusion with not only one but two other teeth. The anterior part of M_2 occludes with M^1 , the posterior part with M^2 . The width relationships between the occluding teeth react on the "fit" of the numerous cusps into the corresponding valleys. The interaction thus becomes quite intricate, and the selection probably acted simultaneously on all three teeth, favouring the survival of variants with perfect occlusion.

The results show that Darwinian selection may act very strongly on seemingly trivial dental characters. The longevity of a cave bear tooth cusp is not great; in a few years it wears down, and henceforth selection has little effect. But in the initial years selection may be intense. The fact that the work of selection is mainly done in the juvenile year classes means that its effect on reproduction and hence evolution may be very great, provided that suitable genetic variation occurs. No wonder that, in most species, the intricate cusp patterns occlude flawlessly, and that centripetal selection, signaling high average adaptation, is much more common than linear selection. Moreover this gives an insight into the causes of the evolutionary plasticity and intraspecific stability of mammalian dental patterns — qualities arising from intense and subtle selective control.

THE EXTINCTION OF THE CAVE BEAR

THE DEGENERATION THEORY

The impressive series of studies on the Mixnitz collection, which were published by many collaborators in ABEL and KYRLE (1931), led ABEL to the formulation of a new theory of the extinction of the cave bear. Paraphrased from ABEL (1929), its outline is as follows.

During a long time the species lived under optimal conditions. In this situation, natural selection was relaxed, and thus the survival and reproduction of inferior variants was possible. The population finally became saturated with degenerative strains, which, together with the deterioration of the environment, led to extinction. Symptoms of the degeneration are mainly (1) the increasing number of diseased individuals; (2) a differential birth-rate with increasing excess of males; (3) the appearance of stunted individuals, the "Mixnitz dwarfs"; (4) a general increase of variability.

SOERGEL (1940), accepting Abel's conclusions, discussed the topic, starting with the assumptions (a) that the productivity of the cave bear was lower than that of the brown bear, (b) that the rates of mortality were higher in the cave bear, (c) that the natural potential longevity of the cave bear was inferior, and (d) that there was a differential birth-rate. He concluded that the metabolic balance of the cave bear population was a precarious one, and that the species was more liable to rapid extinction than *Ursus arctos*.

The theory, as formulated by ABEL, had a Lamarckist tinge, now only of historical interest, and deliberately not stressed in the present discussion. Abel did give selection a role in ecology and evolution, that of "stabilizing selection"; it plays an important part in his theory.

Relaxation of selection in populations, leading to an increase of non-adaptive variants, has been found in recent populations. It occurs however only in fluctuating populations and then in the phase of increase in the population cycle; the subsequent contraction of the population is always accompanied by severe selection. The theory presupposes an "optimal" phase of very long duration. During this time, selection could only be completely relaxed in connexion with a boundless increase of the population; any population control by environmental agencies introduces selection. This would lead to an enormous multiplication of cave bears. Such an "Überschwemmung" was, in fact, postulated by PENCK (1938) to account for the great number of remains found, but SOERGEL (1940) showed that the fossil accumulations result from intensive sampling out of a constantly small population.

Moreover it has been shown (above, and by KURTÉN, 1955 b) that measurable and even strong stabilizing selection acted on the cave bear population, including that of Mixnitz. The theory of a relaxed selection is also contradicted by the relatively high juvenile mortality, the frequency of diseased individuals, and other evidence of population control. The theory cannot be accepted.

SOERGEL's inference that the cave bear population was more vulnerable than that of the brown bear is certainly warranted, if his assumptions are true. But at present there is no definite evidence in favour of any one of his assumptions, although (a) and (c) probably are correct; and one of them (d) is, in my opinion, demonstrably false. Furthermore, the species survived,

apparently without decline, from the Mindel up to Würm I, after which the decline seems to have begun; during this long time the population must have been essentially stable, or secularly decreasing and increasing. To make this at all possible, any effect of factors (a) and (c) must necessarily have been counterbalanced by an opposing trend of (b), or the species would have become extinct immediately.

After these general remarks, the symptoms of the supposed degeneration will be considered. This was partially done in KURTÉN (1955b), where it was shown that the alleged Mixnitz dwarfs are quite normal females, an opinion also given by THENIUS (1954). The sex ratios will be discussed initially; remarks on the other degenerative symptoms will be found later on.

SEX RATIOS

The great variation in size among cave bears from a single population has been shown to be due mainly to sex dimorphism. The canine teeth are particularly characteristic (BACHOFEN VON ECHT in ABEL and KYRLE, 1931; RODE, 1935; KOBY, 1949), and a combination of various quantitative characters permits the sexing of almost all the canines, skulls and mandibles in a collection (KURTÉN, 1955b).

BACHOFEN VON ECHT (*op.cit.*) drew attention to the fact that the number of males at Mixnitz, in particular in the upper strata, exceeded that of females; later, EHRENBURG (1935b, 1950) has found similar abnormal sex ratios at some other sites. KOBY (1949) found females to outnumber males at some sites, and equal frequencies of both sexes were recorded for other sites by KURTÉN (1955b).

ABEL (1929) concluded that the excess of males was due to a differential birth-rate, reflecting racial degeneration. This interpretation was endorsed by EHRENBURG, SOERGEL, and others.

KOBY (1949) suggested that the apparent preponderance of males at Mixnitz might reflect bias in collecting; the smaller female canines would tend to be overlooked. He also stressed the genetical improbability of a change in birth-rates producing such an excess of males.

Koby's suggestion does not, however, explain the change in sex ratios encountered by BACHOFEN VON ECHT, and it seems to be negated by the fact that a strong excess of males appears not only among the isolated canine teeth, but also among the jaws and skulls. Of 172 jaws from Mixnitz studied by me in the Paleontological Institute of Vienna University, 104 were male and 68 female; and out of 61 skulls, 40 were male and 21 female. In both instances the excess of males is significant ($P < 0.01$ and < 0.02 respectively). Yet female jaws and skulls are surely too large objects to be overlooked by

a collector. There can be no reasonable doubt that the excess of males in the Drachenhöhle at Mixnitz is real.

A tabulation of sex ratios from data known to me (table 14) shows that these are highly variable. The "normal" ratio, not significantly different from 50:50, is most frequently encountered (Odessa, Schreiberwandhöhle of Dachstein, Cotencher, Cueva del Toll, Vacluse, Hastière), but significantly greater numbers of females are found in several caves (Gondenans, Montolivot, Saint-Bras), and some show significant excess of males (Mixnitz, Trou du Sureau, Salzofen). As curiosities I have included data on the two heavily biased

TABLE 14.
Sex ratios in cave bear samples from different sites.

Site (Author)	Material used	Group	Absolute frequencies			Percentages		P ¹
			♂	♀	Total	♂	♀	
Mixnitz (Kurtén)	Canines, jaws, skulls	Young	103	92	195	52.8	47.2	~ 0.1
		Old	243	138	381	63.8	36.2	< 0.001
		Total	346	230	576	60.1	39.9	< 0.001
Odessa (Kurtén)	Canines, jaws, skulls	Total	74	87	161	46.0	54.0	> 0.1
Dachstein (Kurtén)	Canines, jaws, skulls	Young	9	6	15	60.0	40.0	> 0.1
		Old	9	9	18	50.0	50.0	1
		Total	18	15	33	54.6	45.4	> 0.1
Cotencher (Kurtén)	Canines	Young	18	22	40	45.0	55.0	> 0.1
		Old	38	38	76	50.0	50.0	1
		Total	56	60	116	48.3	51.7	> 0.1
Cueva del Toll (Kurtén)	Canines, jaws, skulls	Young	19	18	37	51.3	48.7	> 0.1
		Old	54	50	104	51.9	48.1	> 0.1
		Total	73	68	141	51.8	48.2	> 0.1
Gondenans (Koby)	Canines	Total	201	255	456	44.2	55.8	~ 0.01
Montolivot (Koby)	Canines	Total	18	36	54	33.3	66.7	< 0.02
Vacluse (Koby)	Canines	Total	16	28	44	36.3	63.7	~ 0.02

¹ P, probability value.

Site (Author)	Material used	Group	Absolute frequencies			Percentages		P ¹
			♂	♀	Total	♂	♀	
Saint-Bras (Koby)	Canines	Total	21	55	76	27.6	72.4	<0.001
Hastiere (Ehrenberg)	Canines	Total	—	—	76	60	40	~ 0.1
Trou du Sureau (Ehrenberg)	Canines	Total	—	—	94	63	37	~ 0.01
Salzofen (Ehrenberg)	Individuals, minimum	Total	—	—	107	67	33	~ 0.001
Hohlestein ² (Kurtén)	Canines, jaws, skulls	Total	36	4	40	90.0	10.0	(<0.001)
Sibyllenhöhle ² (Kurtén)	Canines, jaws, skulls	Total	5	17	22	22.7	77.3	(~ 0.02)

collections from Hohlestein and the Sibyllenhöhle (see p. 5). Statistically, the deviations from the normal sex ratio are highly significant in both instances, but as noted the deviations probably arose from bias in sampling. That only a small fraction of the total material from these caves is now available is evident; for instance, there are practically no isolated teeth, which otherwise constitute the dominant element in all complete cave bear collections. No conclusion on sex ratios can be based on the samples from Hohlestein or the Sibyllenhöhle.

In my opinion the variation of the sex ratio can be readily explained on ecological grounds (KURTÉN, 1955b). It is most probable that some caves were more suitable for females with their young, whereas others were less frequently used by bear families and more often by solitary individuals, usually males. The fact that the brown bear male is frequently dangerous to its offspring is highly suggestive. The female would prefer to hibernate in a cave not occupied by other bears, and in an easily defended position. Thus there is a very great excess of females in the relatively small cave of Saint-Bras. The enormous Drachenhöhle at Mixnitz, which probably served as winter quarters for several individuals, would be generally avoided by more

¹ P, probability value.

² Heavily biased collections.

experienced female bears in gestation. With the evolution of the cave itself, conditions may have changed from time to time, and at some times it may have presented suitable, easily defended winter quarters for females with newborn cubs; thus changes in relative frequencies of the sexes at different levels could arise, even as a result of minute, now hardly detectable changes in the cave.

In the medium-large Cueva del Toll at Moyá, both sexes occur in equal numbers.

The ecological theory can be tested. If it is correct, then the following situation should be encountered in the Mixnitz collection:

(1) Among the fully adults, male individuals should predominate, as most of the adult females would be in gestation or have half-grown young, and only occasionally would accept this cave as winter quarters.

(2) Among the young individuals, the sex ratio should be around 50:50, because cubs of both sexes were born in about equal numbers, and subadults of both sexes would be solitary. Actually, a very slight excess of males may be expected, since male juvenile mortality in mammals (in man, for instance) is a shade greater than that of females.

The frequencies as actually found, both in the Mixnitz sample and in some others which I have examined, appear in table 14. The division between young and adult was made on the basis of the wear of the dentition; the "young" group includes the subadults of the growth study (pp. 14-16). The young individuals show the expected sex ratio, near 50:50 but with a very slight excess of males, not significant but possibly real and if so a result of differential mortality.¹ On the other hand, the adults show a great disproportion between the sexes, and the difference between the sex ratios in the two groups is significant. This evidence agrees perfectly with the ecological theory, and is definitely incompatible with the theory of a differential birth-rate.

Similarly, in other caves where the juvenile sex ratio may be studied, distributions not significantly differing from 50:50 were found. We may conclude that the birth-rate of the two sexes was constant and as in other mammals. Other evidence adduced by Abel, such as the fractures of the os penis, suggesting pairing fights, does not necessitate the assumption of an excess of males. A similar fracture was described by Koby (1946) from Saint-Bras, where the females outnumber the males.

¹ At one level and locality in the cave, EHRENBERG (in ABEL and KYRLE, 1931) found a juvenile ratio of 3 males to 1 female. Small samples will tend to vary around the 50:50 ratio, and in a few of them a marked excess of one sex is to be expected, without this being significant.

MAN'S ROLE IN THE EXTINCTION OF THE CAVE BEAR

The cave bear survived to the last cold oscillation of the last glaciation (the Pomeranian, Würm III). The last survivors are associated with late Magdalenian industries, or may be otherwise dated as from this level (ANDRÉE, 1931, 1939¹; HESCHELER and KUHN in TSCHUMI, 1949). However, there are very few records of such late date, and it is clear that a decline in numbers had begun much earlier. In most caves with a long stratigraphic succession the cave bear disappears well before the Magdalenian, and the majority of cave bear fossils apparently date from the Eemian interglacial, the early Würm and the Göttweig interstadial. Unfortunately, many cave collections are inadequately dated, and at present no exact figures on the temporal and geographic distribution of the species can be given. If full data were available, charts giving the number and distribution of occupied sites at successive points in time would give excellent information on the extinction of the species.

It is improbable that the warming of climate towards the end of the Pomeranian was more than a subsidiary factor in this process. The decline had begun earlier; and on the other hand, the species survived two interglacials from the great Mindel glaciation to the Würm; during these the climate was as mild as that of the present day, or milder.

It may be suggestive that the decline of the species seems to have begun after Würm I. This is the time when Aurignac Man, *Homo sapiens*, enters Europe. The hypothesis that predation by man formed a main factor in the extinction of the bear must be rejected; particularly because most of the evidence of such predation (much of it controversial) dates from the Mousterian, before the beginning of the decline. But it was noted that the indirect influence of man may have been of importance.

The evidence clearly suggests that the presence of Neanderthal Man did not affect the cave bear population to any marked extent. With the invasion of Aurignac Man and the subsequent increase of human populations, however, more and more caves were probably occupied by man. Human occupation of a former bear-cave is likely to have been a peaceful process. If new settlers took possession in summer or early autumn, they would probably find the cave empty. The bear returning for hibernation would find the cave occupied and might be scared off without actual fighting.

In this way the distances between unoccupied caves suitable to bears would increase gradually. Sooner or later this would lead to a fragmentation of the population into many semi-isolated local groups; and, as the distribution of caves is patchy — cave formation being possible only in certain types

¹ Not seen; cited by ZEUNER (1945). The sites are Balve and Hohler Stein in Westphalia.

of rock — the isolation of some such demes or local population "islands" may have become virtually complete.

Such population "islands" may be thought of as consisting of smaller or larger groups of bears, from perhaps a single family to larger panmictic units of some tens of individuals or more, inhabiting single caves or clusters of sites not regularly occupied by man, and separated from other groups by impassable terrain, glaciers, wide areas devoid of caves, or human-occupied territory. Every now and then such population "islands" would spill an overflow of individuals into their surroundings; young adults would leave the territory of their parents and search for a habitat of their own. With approaching winter the caves in the territory would be occupied by man or beast. The ousted bears would be compelled to seek some inferior shelter, with highly raised mortality as a result. The best chance of prolonged survival would be stood by individuals that were able to reach the site of a small former population "island" which had died out.

In this way, without much actual fighting between man and bear, a rise in the human population would automatically lead to a decline in the bear population.

It has been pointed out (e.g. by Koby, 1944) that at numerous sites the cave bear becomes extinct without there being any trace of human occupation, and this has been advanced as evidence that the activity of man has had no connexion with the extinction of the bear. This is however fallacious. An isolated site cannot support more than a few individuals, and such a small population is extremely vulnerable. The effect of isolation on a population "island" will be discussed below; but before that we must answer the question, is there any real evidence for such a fragmentation of the population as here suggested?

THE LAST SURVIVORS

Relatively few sites are known to have been occupied by the cave bear after the middle Paleolithic. In a tabulation of Swiss caves compiled by HESCHELER and KUHN (in TSCHUMI, 1949), fifteen are stated to contain *U. spelaeus*, but only two of these postdate the Mousterian. They are the Schlossfelsen of Thierstein at Büssenschach, where the cave bear is said to be associated with late Magdalenian industries, and the Köhlerhöhle, with similar associations. In both instances, *U. spelaeus* is said to be associated with *U. arctos*, and the possibility of mistaken determinations should be kept in mind. From outside Switzerland the same authors cite an occurrence in the Sirgenstein Cave (Swabian Alps), associated with the Magdalenian; the Sirgenstein bear is indubitably *U. spelaeus*. This can also be definitely stated about the bear from the Tischoferhöhle at Kufstein in Tyrol, which according to AMPFERER

(cited by ZAPPE, 1954) would even postdate the Pomeranian, and thus be the latest cave bear sample on record¹. Two Westphalian sites have been mentioned (p. 48 n.) However, the only late-Würm sample of adequate size available to me is that from Hohlestein (Lontal, Swabian Alps; see WETZEL, 1954, fig. 21 V). It was studied in the Stuttgart Natural History Museum.

A study of these Swabian late-Würm cave bears will give us some idea of the population, as it were, on the verge of extinction. The variation found in the sample, compared with that in earlier populations, may be indicative to some extent of the size of the population. A constantly small population is characterized by strong inbreeding and gene loss, resulting in genetic uniformity. This is to a certain degree reflected in the phenotype, which shows depleted variation (but extreme inbreeding again increases the phenotypic variability; for experimental demonstration and discussion see BADER, 1956).

Cave bear demes in general, even from the heyday of the species in Mousterian times, are less variable than brown bear demes; this was the somewhat surprising result of a quantitative analysis (KURTÉN, 1955b) which showed that the "enormous" variability commonly ascribed to the species is spurious, and results from a confusion between interdeme variation and sexual dimorphism on one side, and individual variation on the other, as well as uncritical use of observed ranges of variation as a measure of variability. The low intrademe variation indicates that migration between demes, even in the optimal period, was lower than in the recent *Ursus arctos*. Thus the cave bear population seems to have been to some extent disjunct, with relatively low intermigration and reduced panmixia, even during the Eemian interglacial and in the early Würm. With progressive disjunction later on, the genetic effects of inbreeding should become more and more conspicuous.

The Hohlestein collection consists of practically nothing but adult males; the source of this bias was discussed above (pp. 5, 46). The material is however rich enough to give reliable information on the variation in adult males. The coefficient of variation was computed for a number of variates, and comparison is made with similar material from Mixnitz and the Cueva del Toll (table 15). Only adult males were used. The coefficient of variation is based on σ' (see SIMPSON and ROE, 1939), and calculated with the correction $V = V' \left(1 + \frac{1}{4N}\right)$ suggested by HALDANE (1955).

¹ LACAILLE (1954) mentions *U. spelaeus* from the postglacial cave at Inchnadamff in Scotland, but this is a *lapsus calami*; in NEWTON's (1917) report on the fauna, only *U. arctos* is mentioned (a lower canine, figured *op. cit.* pl. iv).

In the great majority of cases the coefficient of variation is higher for the samples from Mixnitz and Cueva del Toll than for that from Hohlestein (plus signs in the right columns). None of the minus-sign differences are significant, but for several variates the V is significantly lower in the Hohlestein sample than in that from Mixnitz. A sign test, as in BADER (1955), also indicates probable significance of the difference between Mixnitz and Hohlestein. The comparison with Cueva del Toll shows similar differences, though the material from the Spanish cave is somewhat smaller and does not give surely significant results. In particular the extremely low variation of the Hohlestein M_1 and M_2 should be noted.

TABLE 15.

Coefficients of variation (the Pearsonian V, emendated by HALDANE) for adult males of *Ursus spelaeus* from the sites of Hohlestein, Mixnitz and Cueva del Toll.

	Hohlestein	Mixnitz	Toll	Deviation from Hohlestein	
				Mixnitz	Toll
Width C_1	4.77 ± 0.90	5.68 ± 0.61	5.30 ± 0.75	+	+
Length P_4	8.31 ± 2.08	5.53 ± 0.82	6.24 ± 0.22	—	—
Width P_4	6.80 ± 1.70	6.34 ± 0.93	5.22 ± 1.84	—	—
Length M_1	1.86 ± 0.40	3.08 ± 0.37	3.07 ± 0.69	+	+
Width M_1	2.90 ± 0.62	5.61 ± 0.72	5.23 ± 1.40	+	+
Length M_2	3.58 ± 0.68	3.75 ± 0.37	4.93 ± 0.82	+	+
Anterior width M_2	3.23 ± 0.86	4.76 ± 0.54	5.46 ± 0.97	+	+
Posterior width M_2	3.94 ± 0.84	5.21 ± 0.59	4.41 ± 0.78	+	+
Length M_3	4.61 ± 0.82	7.52 ± 0.75	6.65 ± 1.21	+	+
Width M_3	3.98 ± 0.75	5.91 ± 0.64	5.17 ± 0.92	+	+
Length P^4	7.72 ± 1.82	4.75 ± 0.69		—	
Width P^4	6.70 ± 1.93	5.24 ± 0.76		—	
Length M^1	4.54 ± 1.44	5.19 ± 0.66		+	
Anterior width M^1	4.77 ± 1.69	4.91 ± 0.70		+	
Posterior width M^1	3.03 ± 1.07	4.59 ± 0.66		+	
Length M^2	5.70 ± 1.27	4.36 ± 0.53		—	
Width M^2	3.53 ± 1.12	6.23 ± 0.81		+	
Jaw, C-condyle	2.81 ± 0.50	3.98 ± 0.49	2.31 ± 0.78	+	—
Height at diastema ...	4.53 ± 0.67	6.42 ± 0.61	5.17 ± 1.10	+	+
Height below M_1	5.69 ± 0.95	7.27 ± 0.76	3.15 ± 0.70	+	—
Skull, prosthion-basion	3.42 ± 0.91	4.01 ± 0.51		+	
Muzzle width at M^2 ...	5.49 ± 1.23	5.70 ± 0.68		+	
Muzzle width at C.....	6.35 ± 1.70	6.25 ± 0.80		—	
Palatal length	4.01 ± 1.07	4.20 ± 0.51		+	
Mean V, 24 variates ...	4.67	5.27		+	
Mean V, 13 variates ...	4.38	5.47	4.79	+	+

The reduced variability also appears in the morphology of the Hohlestein bears — the specimens look very much alike, more so than usual in cave bear samples, though it is difficult to express this numerically. It may thus be concluded that the bear of Hohlestein was less variable than those from Mixnitz and Moyá, and this result points to a smaller population, reduced panmixia, and stronger inbreeding. It is also contrary to the opinion that the later cave bears would be more variable than the earlier ones, one of the alleged symptoms of degeneration.

SURVIVAL OF ISOLATED POPULATIONS

The number of individuals within a population "island" would be restricted by the number of suitable winter quarters in the region, and would thus tend to be held constant for long periods of time.

Doubtless it did not very often happen that all the members of such a local population died without issue; but if the situation persisted during many generations, such local extinction would be probable for the smaller populations.

An estimate of the probability of extinction may be based on our knowledge of the mortality of the cave bear. As a model we may initially select the smallest self-reproducing unit, a single pair. The assumed situation is a single cave or a couple of small caves, which can only support one family at a time; the effective breeding population will then be held constant at the level $N = 2$.

In the cave bear population, there are on an average three juveniles per two adults (cumulative frequencies of the l_x column in the Life table; see also p. 29), and our adult pair, therefore, is accompanied by three cubs.

The total number of individuals is five. Obviously extinction is certain if all the five individuals at any time happen to be of the same sex; immigration is assumed not to occur. The probability that all will be females is 0.0375; the probability that all will be males is the same, and the sum is 0.0750. Thus, in $7\frac{1}{2}$ per cent of all such cases, the population will be doomed to extinction.

The remaining $92\frac{1}{2}$ per cent of the populations of this type, which do contain individuals of both sexes, are nevertheless also liable to extinction. For instance, extinction would seem to be practically certain if all the females in the population died within a relatively short time, that is, before a new female cub is born and reared. Thus it would seem to be impossible for the population to survive, if all its females (numbering from one to four) died within two years.

What is the probability of such an occurrence? This may be estimated from the known mortality rates. We here use the crude death rate, or the

average rate for the whole population regardless of age. It is 20.9 per cent annually, and the biennial crude rate is then about 37 per cent.

This is an average figure. For any given couple of years, the actual rate tends to vary around this value (apart from the fact that the exact rate of 37 per cent cannot be realized in a population of one to four individuals, where it would give fractional values). The probability can be ascertained by studying the distribution around the mean for samples of the given sizes. For a population of two, for instance, it is 0.1314; for a population of four, only 0.0217.

These probability values are entered as P_2 in table 16. P_1 gives the probability for the presence of the given number of females in the population, or in other words, the frequencies of populations with 0, 1, 2, 3, 4 and 5 females. Those with 0 or 5 females will certainly become extinct, and the corresponding value of P_2 is 1.

TABLE 16.

Probabilities for the extinction of a cave bear population of the size $N = 2$ (2 adults and 3 young) by the death of all females within two years or random disappearance of one sex. P_1 , probability for the presence of the given number of females; P_2 , probability for extinction of a population with the given number of females; $\Sigma (P_1 P_2)$, total probability of extinction.

No. of females	P_1	P_2	$P_1 P_2$
0	0.0375	1.0000	0.0375
1	0.1492	0.4794	0.0742
2	0.3133	0.1314	0.0412
3	0.3133	0.0823	0.0258
4	0.1492	0.0217	0.0032
5	0.0375	1.0000	0.0375
			Σ 0.2194

$P_1 \times P_2$ gives the probability that a population of the given type will occur *and* will become extinct. For instance, the probability for the occurrence *and* extinction of a five-individual ($N=2$) population with three females is 0.0258. 2 1/2 per cent of the populations will be of this type and have this fate.

The sum of $P_1 P_2$ gives the total probability of extinction within 2 years for all populations with $N = 2$ and five individuals. It is 0.2194, or in round numbers 0.22. Thus, out of ten populations consisting of a single pair and their young, two will, within two years, happen into a situation which will lead to extinction unless the isolation of the population is broken.

The remaining eight populations, or more precisely 78 per cent, are not, however, on the safe side. In two years, individuals may have died, and new cubs may have been born; the turnover has occurred, and the population is

once more at the starting point, and beset by the same hazards. Again, 22 per cent of the remaining populations are likely to become extinct in the following couple of years.

With the passage of time, the probability for the initially rather improbable event — extinction — becomes greater. The changes in the values of p (probability of extinction) and q (probability of survival) with increasing time are given in table 17. In little more than six years, the chances for survival and extinction in a population of the size $N = 2$ are about even; or in other words, out of ten populations of this type, only five will survive for more than six years. In twenty years the probability is overwhelmingly in favour of extinction, and practically no population will survive up to forty years.

TABLE 17.

Probabilities of extinction (p) and survival (q), with the passing of time, for small isolated cave bear populations, the size of which is held constant and = N (number of breeding individuals).

Years	N = 2		N = 4		N = 6	
	p	q	p	q	p	q
2	0.22	0.78	0.0045	0.9955	0.0007	0.9993
4	0.39	0.61				
6	0.53	0.47				
10	0.71	0.29	0.02	0.98	0.0035	0.9965
20	0.92	0.08				
40	0.993	0.007	0.09	0.91		
100			0.20	0.80	0.03	0.97
200			0.36	0.64	0.07	0.93
400			0.59	0.41		
1,000			0.90	0.10	0.29	0.71
2,000			0.97	0.03	0.50	0.50
4,000					0.75	0.25
10,000					0.97	0.03

Thus it is clear that extinction will be very rapid if the size of the population is constantly held down to one pair. Similar computations have been made for populations comprising two and three pairs (with $N = 4$ and 6 respectively), and the results appear in table 17. The extinction of a population of two pairs in two years is highly improbable, the odds being about one to two hundred. In spite of these long odds, extinction becomes probable with the passing of time; if such a population is held isolated and constant for about 300 years, the odds for extinction and survival are about even, and hardly any population of this type will survive for more than 2,000 years. Even a population of three pairs will almost certainly become extinct in ten

thousand years, though the probability for extinction in two years is extremely low (odds less than one to two thousand); and only about a half of such populations will survive for more than 2,000 years.

Practically all the smallest isolated populations, with number of breeding individuals fluctuating between $N = 2$ and $N = 6$, will thus become extinct in a very short time. The probability for this is enhanced by the fact, not taken into account in the above computations, that populations are not stable in numbers, but fluctuate in size; for instance, the normally $N = 6$ -population may at times have counted much fewer heads than the average 15, and would in such a phase have been more vulnerable.

Larger populations would not be liable to extinction as a result of this factor within the available time span, if held constant; but some such populations may, from time to time, have fluctuated sufficiently in numbers to bring them down to the critical size. In this way, some of the slightly larger populations may also have become extinct.

The smaller populations would have been characterized by extreme inbreeding, with random fixation of deleterious genes and consequently increased mortality as an occasional result. This would hasten the extinction of many such populations.

However, there were probably many populations in existence up to Magdalenian time with N constantly much greater than the critical size, and probably great enough to insure effective selection, preventing more serious genetic drift. These populations would survive, whereas the smaller ones became extinct.

The situation in Magdalenian times may perhaps be visualized as shown diagrammatically in fig. 8. The population has been fragmented into a number of larger and smaller units, of which most of the smaller have become extinct. This extinction of the smallest populations may account for the disappearance of the cave bear in many caves, particularly Alpine ones, without any evidence of human occupation.

Between the remaining larger units — the three ones in the diagram



Fig. 8. Diagrammatic representation of the distribution of cave bears in Magdalenian times. Filled-in areas represent extant population «islands», empty symbols represent habitable sites and areas vacated by local extinction.

might, for instance, symbolize the Magdalenian populations of Westphalia, the Swabian Alps and Switzerland — some intermigration could occur. Initially, the smaller interjacent population "islands" could be used as stepping-stones in such migration, but after their extinction, a certain repression of such migration might be expected. Migrants would tend to repopulate such vacated sites and start small new populations, which would survive for some years and again become extinct, instead of moving on to another larger population unit. In this way, intermigration of individuals and genes between the larger units would be intercepted, and the isolation of the remaining populations would be enhanced.

The cause of the final extinction cannot be determined. Perhaps the last cave bears fell victims to the raids of late Magdalenian man with his evolved weapons and hunting methods. Perhaps, again, the depletion of available variability in the population made it impossible to adjust to the climatic change at the end of the Pomeranian. There are several possible causes and combinations of causes, and no good clues to the real solution.

SUMMARY

The cave bear remains from the caves at Odessa exhibit an annual age grouping, interpreted as representing winter mortality during hibernation with a mortality peak at the end of winter. Rates of mortality (M) for each annual interval were determined from the expression $M = a/b$, where a = the total number of teeth in a given age class, and b = the sum of these and all older homologous teeth. Earliest juvenile mortality was estimated on the basis of the milk canines. The analysis is less accurate for the older than for the younger stages. The ensuing Life table is given as table 10 (p. 28). Checks of its validity include a comparison of early mortality at Odessa, Cotencher (Switzerland) and Cueva del Toll (Spain), which gave identical results; ascertaining that the population was in metabolic balance with a productivity equal to or lower than that of the recent brown bear; and showing that the suggested rates of mortality may account for the great accumulation of fossils in the Drachenhöhle at Mixnitz, when the number of fossilized individuals and the lapse of time represented, and the carrying capacity of the cave, are given.

The Life table shows decreasing rates of mortality in the youngest age groups, stable rates for bears in their prime, and increasing rates for the old; consequently, the survivorship curve (fig. 4) is of the sigmoid type suggested as a general pattern in natural populations by KURTÉN (1953).

Strongly differential mortality for several characters show the existence of Darwinian selection not only in the Odessa population but also in other bear populations. Linear selection was found in some cases. Very strong linear selection acted on the paracone of M^2 and the external valley of M_2 in the Odessa population, evidently because a slight malocclusion was the average condition in the population. That this condition persisted for thousands of years, as it must have done to become recorded in the sample, suggests that no favourable genetic variation was available.

The theory of ABEL, suggesting that the extinction of the cave bear resulted from a degeneration due to lack of selection, differential birth-rates, etc., is rejected. The excess of males at some sites (and of females at some others) is explained on ecological grounds, females in gestation preferring winter quarters which were easily defended against male intruders. It is suggested that the increasing numbers of human cave-settlers in Europe during the last glaciation would lead to a reduction and fragmentation of the cave bear population. Smaller, isolated population "islands" would become extinct rapidly, whereas the larger populations, not liable to extinction from sheer accidents, would suffer to some extent from gene loss. The great homogeneity of the late-Würm population from Hohlestein accords with this suggestion. The factor or combination of factors that dealt the final blow to the last remnants of the population can probably not be identified.

ADDENDUM

After this paper had reached the proof stage, the sequence in Cueva del Toll was dated by J. J. DONNER and myself; a joint report will be issued shortly. It is sufficient here to note that the mass occurrence of the cave bear is here in the Göttweig interstadial, whereupon there is a rapid decrease in numbers. This population should thus, as suggested, be older than that of Hohlestein. On the other hand it is slightly younger than the main Cotencher sample.

REFERENCES

- ABEL, O. 1929. Paläobiologie und Stammesgeschichte. Jena, Fisher.
- ABEL, O. and G. KYRLE (ed.) 1931. Die Drachenhöhle bei Mixnitz. Speläol. Monogr. 7—9: 1—953.
- ALLEE, W. C., A. E. EMERSON, O. PARK, TH. PARK and K. P. SCHMIDT 1949. Principles of animal ecology. Saunders, Philadelphia.
- ANDRÉE, J. 1931 Die frühmesolithische Fauna aus dem Hohlen Stein bei Callenhardt. Abh. westf. Prov.-Mus. Naturk., 2; 1—11.
- 1939. Der eiszeitliche Mensch in Deutschland und seine Kulturen. Stuttgart.
- BADER, ROBERT S. 1955. Variability and evolutionary rates in the oreodonts. *Evolution*, 9: 119—140.
- 1956. Variability in wild and inbred mammalian populations. *Quart. Jour. Florida Ac. Sci.*, 19: 14—34.
- COUTURIER, M. A. J. 1954. L'Ours brun. Grenoble.
- DEEVEY, EDWARD S. 1947. Life tables for natural populations of animals. *Quart. Rev. Biology*, 22: 283—314.
- DUBOIS, A. and STEHLIN, H. G. 1933. La grotte de Cotencher, station moustérienne. *Mém. Soc. paléont. Suisse, Bale*, 52, 1—178; 53, 179—292.
- EHRENBERG, KURT 1922a. Die bisherigen Ergebnisse der Untersuchungen über die frühesten Entwicklungsstadien (Embryonen und Neonaten) und über die Fortpflanzungsverhältnisse des Höhlenbären aus der Drachenhöhle bei Mixnitz. *Anz. Akad. Wiss. Wien, Math.-nat. Kl.*, Jahrg. 59: 189—191.
- 1922b. Die bisherigen Ergebnisse der Untersuchungen über die ontogenetische Entwicklung des Skeletts des Höhlenbären aus der Drachenhöhle bei Mixnitz. *Ibid.*, Jahrg. 59: 215—217.
- 1935a. Die Pleistozoen Baeren Belgiens. I. Teil. Die Baeren von Hastiere. *Mém. Mus. Roy. d'Hist. nat. Belgique*, 64: 1—126.
- 1935b. Die Pleistozoen Baeren Belgiens. II. Teil. Die Baeren vom »Trou du Sureau« (Montaigle). *Ibid.*, 71: 1—97.
- 1950. Berichte über Ausgrabungen in der Salzofenhöhle im Toten Gebirge. V. Erste Ergebnisse der Sichtung des Fundmaterials in der Sammlung Körper in Bad Aussee. *Anz. Öst. Akad. Wiss., Sitz. Math.-nat. Kl.* 29: 262—271.
- 1956. Über Höhlenbären und Bärenhöhlen. *Verh. Zool. Bot. Ges. Wien*, 95: 19—41.
- FLOWER, S. S. 1931. Contributions to our knowledge of the duration of life in vertebrate animals. V. Mammals. *Proc. Zool. Soc. London*.
- HALDANE, J. B. S. 1955. The measurement of variation. *Evolution*, 9: 484.
- KENYON, K. W., V. B. SCHEFFER and D. G. CHAPMAN 1954. A population study of the Alaska fur-seal herd. *Special Sci. Rept., Wildlife No.* 12: 1—77.
- KOBY, F.-ED. 1943. Les soi-disant instruments osseux du paléolithique alpin et le charriage a sec des os d'ours des cavernes. *Verh. Naturf. Ges. Basel*, 1943, 59.
- 1944. Über das gleichzeitige Vorkommen von Höhlenbären und Braunbären im Jura. *Ber. schweiz. paläont. Ges.*, 36: 258—259.
- 1946. Fracture de l'os pékien chez *Ursus spelaeus* et sa guérison spontanée. *C. R. Soc. Paléont. suisse, Ecl. geol. Helv.*, 39: 17.
- 1949. Le dimorphisme sexuel des canines d'*Ursus arctos* et d'*Ursus spelaeus*. *Revue suisse de zool.*, 56: 675—687.
- KURTÉN, B. 1953. On the variation and population dynamics of fossil and recent mammal populations. *Acta Zool. Fennica*, 76: 1—122.
- 1954a. Population dynamics and evolution. *Evolution*, 8: 75—81.
- 1954b. Population dynamics — a new method in paleontology. *Jour. of Paleontology*, 28: 286—292.
- 1955a. Contribution to the history of a mutation during 1,000,000 years. *Evolution*, 9: 107—118.

- KURTÉN, B. 1955b. Sex dimorphism and size trends in the cave bear, *Ursus spelaeus* Rosenmüller and Heinroth. Acta Zool. Fennica, 90: 1—48.
— (In the press). The bears and hyenas of the interglacials. Quaternaria.
- LACALLE, A. D. 1954. The stone age in Scotland. Oxford.
- NEWTON, E. T. 1917. Notes on bones found in the Creag nan Uamh Cave, Inchnadamff, Assynt, Sutherland. Proc. Roy. Soc. Edinburgh, 37: 344—349.
- NORDMANN, ALEXANDER VON, 1858—60. Palaeontologie Südrusslands. Helsingfors.
- PENCK, A. 1938. Säugetierfauna und Paläolithikum des jüngeren Pleistozän in Mitteleuropa. Abh. Preuss. Akad. Wiss., Phys.-math. Kl., Jahrg. 1938.
- RODE, K. 1935. Untersuchungen über das Gebiss der Bären. Monogr. Geol. Palaeont., ser. 2, H. 7, Leipzig.
- SIMPSON, G. G. 1953. The major features of evolution. Columbia Univ. Press, New York.
- SIMPSON, G. G. and ANNE ROE, 1939. Quantitative zoology. McGraw-Hill, New York.
- SOERTEL, W. 1940. Die Massenvorkommen des Höhlenbären. Ihre biologische und ihre stratigraphische Deutung. Fischer, Jena.
- THENIUS, E. 1954. Das Problem der Kleinformen und die Paläontologie. Mitt. Anthropol. Ges. Wien, 83: 98—101.
- TSCHUMI, O. (Ed.) 1949. Urgeschichte der Schweiz, Bd. I. Frauenfeld.
- WETZEL, R. 1954. Quartärforschung im Lonetal. Eiszeitalter u. Gegenwart, 4/5: 106—141.
- ZAPPE, H. 1954. Beiträge zur Erklärung der Entstehung von Knochenlagerstätten in Karstspalten und Höhlen. Geologie, Berlin, Beiheft 12/1954: 1—60.
- ZEUNER, F. E. 1945. The Pleistocene period. Ray Soc., London.

