Dental sex dimorphism in European lions (Panthera leo L.) of the Upper Pleistocene: palaeoecological and palaeoethological implications.

Alan Turner

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Recently proposed metrical and geographic evidence for the presence of two sub-species of lions (*Panthera leo* Linnaeus 1758) during the Upper Pleistocene in Europe is examined in comparison with measurements made on modern specimens of known sex and a consideration of the sexual composition of modern adult lion groups. On the basis of these comparisons, the bimodal distributions observed in measurements made on fossil specimens and the presence of single size groups at certain sites are argued to support sexual dimorphism rather than sub-speciation as a preferred interpretation. Potential palaeoecological and palaeoethological insights likely to be obscured by incorrect interpretation of bimodality and size-group temporal and geographic distributions are discussed.

Alan Turner, Department of Palaeontology, Transvaal Museum, P.O. Box 413, 0001 Pretoria, South Africa.

1. Introduction

Kurtén (1968: 86) remarked on the confusion which sexual dimorphism had produced in earlier systematic studies of the large felid of the European Pleistocene. This felid, often referred to as the cave lion, appears to have been no more than a large, sexually dimorphic representative of the extant lion, *Panthera leo* (Linnaeus 1758) . Sexual size dimorphism in modern lions is quite marked (Schaller 1972), and specimens above 2 years old may be readily sexed on the basis of skull and canine-tooth measurements (Smuts et al. 1978).

In a recent publication discussing the Upper Pleistocene mammal fauna from the French cave of Jaurens, Corrèze, Ballesio (1980) has returned to the view that two sub-species of lion were present in Europe at that time, on the basis of bimodal size groupings in large-felid material from this and other European sites. Ballesio shows that the material from Jaurens falls into two clear size groups in both dental and post-cranial specimens, and asserts that these distributions cannot be explained by either individual or sexual variation: "De l'étude présente il ressort qu'il existe dans le gisement de Jaurens deux morphotypes se distinguant par la taille et qui ne sont pas la conséquence de la variation individuelle ou sexuelle."

In support of his assertion, Ballesio (1980: 65) argues firstly that the size differences between the two groups at Jaurens and elsewhere exceeds that observed to separate extant male and female lions. Secondly, he argues that the existence of specimens conforming only to his larger Jaurens size group at the sites of L'Herm in France and Gailenreuth in Germany points to the presence of a distinct sub-species. This latter argument is based upon the expectation that both males and females should always be found together, and that if the two Jaurens size groups did indeed represent sexual dimorphism then all sites containing lion remains should produce specimens falling into both size categories.

I believe that these arguments can be refuted on a number of grounds, based on observed sexual dimorphism in modern lions and on considerations of known patterns of lion behaviour. The purpose of this paper is therefore two-fold. First, to reiterate the case for sexual dimorphism as the preferred explanation for observed size distributions, and to show that Ballesio's data can be best interpreted in this way. For this purpose I shall examine size variation in a sample of extant lions of known sex and then compare the results with distributions seen in a number of fossil samples. I shall also show that the presence of a single lion size group at a site does not conflict with an interpretation of sexual dimorphism.

The second purpose of the paper is to stress the misunderstandings which may stem from a wrong interpretation of bimodal size distributions, and to illustrate some of the potential insights into aspects of past behaviour and ecology which a correct interpretation may permit. Such insights are necessarily more speculative than the discernment of sexual dimorphism on which they are based, but the approach reflects my belief that the palaeontologist must aim at more than a catalogue of specimens.

2. Size variation in modern and fossil lion dentitions

2.1. Methods

Smuts *et al.* (1978) found that specimens of modern lion could be sexed using cranial and canine-tooth dimensions in specimens over 2 years old. Since fossil lion material is seldom sufficiently complete to permit many cranial measurements to be taken, tooth dimensions are a more useful basis for comparison in the present instance. A series of modern southern African lion skulls held in the Transvaal Museum, Pretoria, presented an adequate sample of teeth for this purpose. Only skulls of known sex were included in this study, and the measurements were taken to the nearest 0.1 mm using engineering vernier callipers capable of reading to the nearest 0.01 mm.

Length and breadth measurements of the teeth were recorded. Length is the term used to describe the mesio-distal dimension and breadth the term used to describe the buccal-lingual dimension. For canine teeth these measurements were taken at the base of the crown enamel, and for the lower first molar tooth at the cingulum. Each measurements therefore expresses a maximum dimension for the base of the tooth crown, and can be taken equally well on both isolated and *in situ* teeth. (See von den Dreisch (1976) for a general guide and discussion).

The measurements which I have personally taken have been made consistently as described. However, comparisons with results published by other workers raise the question of compatibility. Ballesio (1980) gives no details of the precise method of measurement adopted, but is unlikely to have used vastly different landmarks on the teeth since lion dentition is not morphologically complex. Results should therefore be reasonably comparable, and the same holds true for other measurements quoted in this study published by Wojtusiak (1953) and Dietrich (1968). Measurements employed here which were provided by Kurtén are known to be compatible.

Smuts et al. (1978) used a somewhat different set of measurements in their study of modern lions. They took a crown height and a root maximum mesio-distal width for upper and lower canines, and found that these adequately separated male and female specimens when used univariately. Unfortunately, these measurements are not appropriate for fossil material, since the tooth crown must be unbroken and the specimen either freed from the jaw or amenable to radiographic examination. However, the results of their mesio-distal root measurement have a direct bearing on the present discussion, and will be considered further below.

It is to be expected that sexual dimorphism will also be observable in elements of the postcranial skeleton. Unfortunately such material is very much harder to come by in museum collections than skulls, particularly when one requires specimens of known sex. The discussion which follows will therefore employ only dental measurements as a basis for discerning sexual size dimorphism in modern lions, although variations in dimensions of fossil postcranial remains will then be discussed in the light of the results of this analysis.

2.2. Results

Fig. 1 shows a scatter diagram of lower M1 length and breadth measurements. Although there is no clear point of distinction between the known male and female specimens, neither is there significant overlap in either measurement. On the same diagram are shown a series of measurements made on lion M1 specimens of last glaciation age from a number of British sites. These latter specimens exhibit the same general spread as those of the modern individuals, but extend slightly beyond the maximum of the extant lions in length and breadth. A sensible interpretation of this moderately large British sample would be that both male and female lions are present and that the range of sizes, together with the average size, slightly exceeds that in the modern sample.

The material from Jaurens, listed by Ballesio (1980: tables 1 and 3), falls within the modern dispersal in Fig. 1. However, the most interesting observation is that the smaller Jaurens group falls at the top of the modern female range while the larger Jaurens group falls towards the top of the modern male range. The Jaurens sample is small, but the size dimorphism is clear and when examined against the background of the modern-day dispersal the most logical interpretation of the pattern would appear to be sexual variation. Whether on this evidence one should also conclude that the average size of the Jaurens lions exceeded that of the modern sample is a little more problematic.

The third group of fossil specimens shown on Fig. 1 is of lion teeth from the southern Polish cave of Wierzchowska Górna (Wojtusiak 1953), kindly made available to me from his own records by Professor B. Kurtén. This larger sample clearly separates into two size groups which Kurtén (1968: 86) emphatically described as male and female. The Polish specimens exhibit a similar size range to those of the British last glaciation, but are somewhat larger.

Fig. 2 repeats the exercise depicted in Fig. 1 but in this case shows the scatter of length and breadth measurements taken on lower canines. The dispersals of modern males and females are now seen to be better separated, and the British specimens are also drawn into two distinct size groups. On this evidence the British material again appears to be composed of both sexes and to average a little larger than the modern sample, although that latter interpretation is by no means clear cut. The Jaurens specimens, although
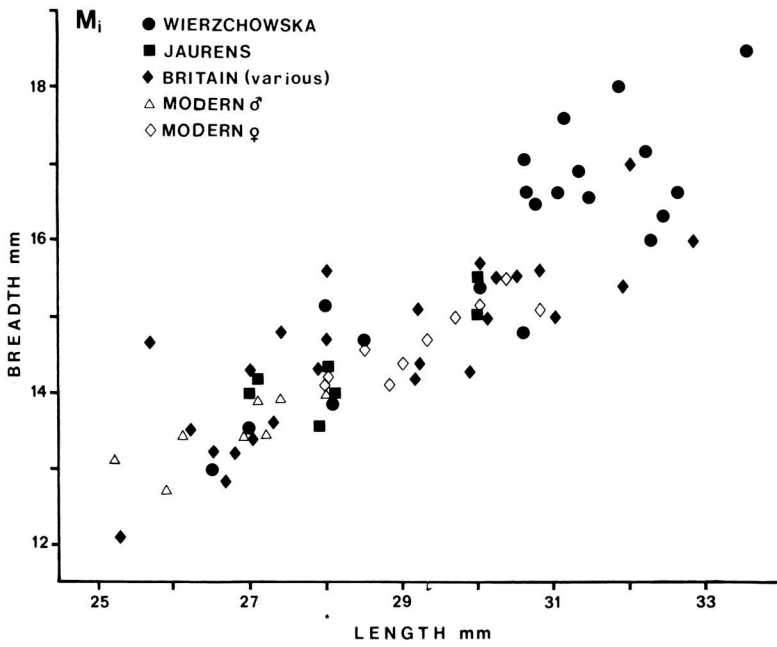
Fig. 1. Scatter diagram of lion lower molar 1 length and breadth. Sources: Wierzchowska Górna, Kurtén (in lit.); Jaurens, Ballesio (1980); British last glaciation and modern Transvaal Museum, author.
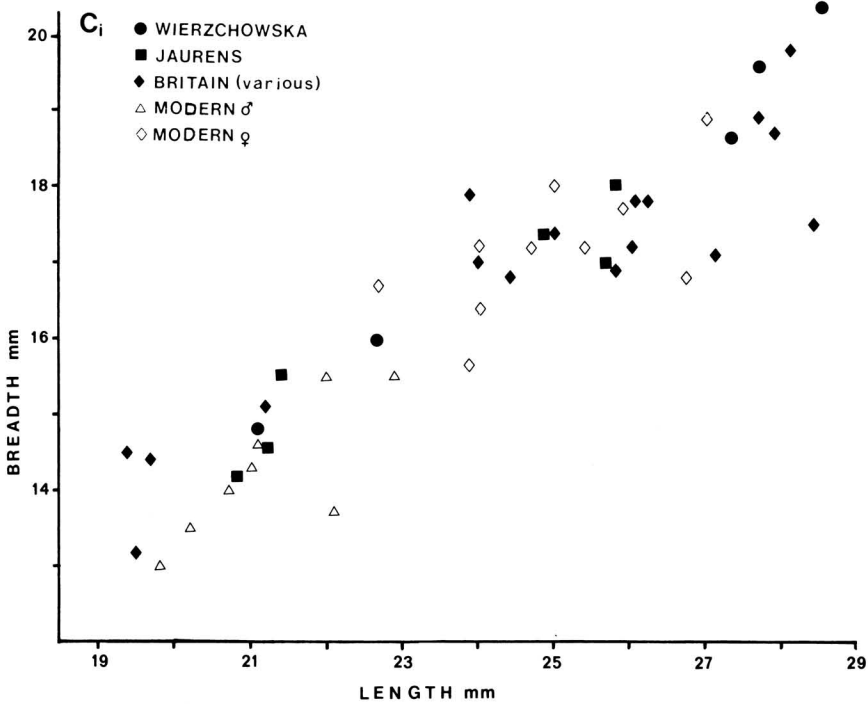

Fig. 2. Scatter diagram of lion lower canine length and breadth. Sources: Wierzchowska Górna, Kurtén (in lit.); Jaurens, Ballesio (1980); British last glaciation and modern Transvaal Museum, author.

Fig. 3. Scatter diagram of lion upper canine length and breadth. Sources: Wierzchowska Górna, Kurtén (in lit.); Jaurens, Ballesio (1980); British last glaciation and modern Transvaal Museum, author.
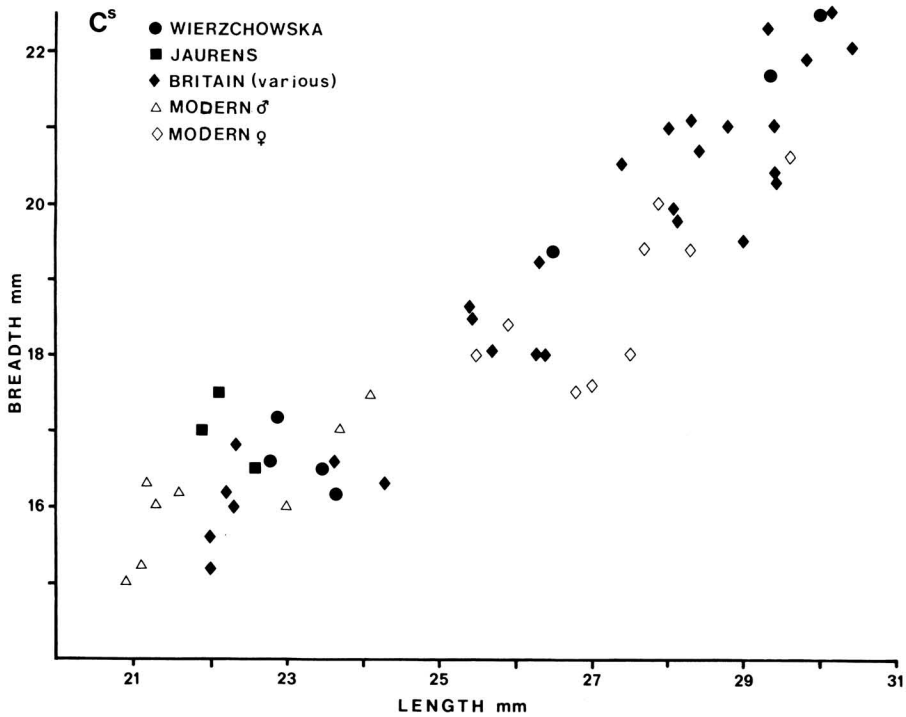
forming a small sample, clearly sit well-within the dispersals of modern males and females and the inference of sexual dimorphism is now quite strongly reinforced. Although a smaller sample than in the case of the lower molars, the Polish lower canines from Wierzchowska Górna also separate into two clear size groups.

In Fig. 3 the exercise of Figs 1 and 2 is repeated using the dispersal of upper canine lengths and breadths. The separation of modern males and females in now very clear. However, the British material falls less clearly into two groups in view of the gaps which produce an intermediate group between about 25 and 27 mm in the length measurement. But each of the dispersals of the modern lions shown on Fig. 3 is also patchy, and the interrupted nature of the dispersal in the British sample is therefore neither unusual nor excessive.

The Jaurens sample in the case of the upper canine consists solely of specimens falling within Ballesio's smaller size group. The three teeth clearly align with the modern female sample, and would be most reasonably interpreted as female. Sexual dimorphism as an explanation for the pattern is further underlined by the distribution of

specimens from the Wierzchowska Górna site.

Table 1 gives the means and observed ranges for the male and female mesio-distal canine root measurements of modern lions published by Smuts et al. (1978: table VII). Because of the shape of a lion canine, this measurement is always likely to be slightly larger than one taken at the base of the enamel. Furthermore, as Smuts et al. (1978: 139) point out, cementum deposition is likely to increase the measurement in older-age specimens. Nevertheless their data show considerable consistency with the distributions of crown-base measurements for modern lion canines in Figs 2 and 3. Such reinforcement of the

Table 1. Mesio-distal root measurement (mm) in upper and lower canines of modern lions. Data from Smuts et al. (1978: Table VII).

	Mean ± *SD*	Range	*N*
Upper canines			
Males	28.3±1.3	25–31	67
Females	23.5±1.3	21–27	96
Lower canines			
Males	25.7±1.0	24–28	65
Females	22.1±1.0	20–24	94

Table 2. PM3-M1 measurement (mm) in modern and fossil lion mandibles. V = coefficient of variation.

	N	Mean±SE	SD	V	Range	Source
Modern Transvaal Museum						Present study
Males	9	75.96±0.91	2.74	3.6	72.7–79.7	
Females	8	67.99±0.98	2.76	4.1	63.5–72.9	
Pooled	17	72.21±1.19	4.89	6.8	63.5–79.7	
Ballesio	55	68.3 ±0.63	4.69	6.9	60.0–78.0	Ballesio 1980: table 2
Fossil Gailenreuth	14	77.9 ±0.86	3.21	4.12	72.3–82.0	Dietrich 1968: table 3
Jaurens	1	80.0				Ballesio 1980: table 2
Wierzchowska	7	78.1 ±2.1	5.6	7.2	70.0–87.0	Wojtusiak 1953: table 3

bimodal nature of modern lion crown dimensions, and of their correlation with sex, offers strong support for sexual variation as the reason for size grouping in Upper Pleistocene lions from Jaurens and other sites. This evidence would appear to refute Ballesio's claim that the bimodality observable in Upper Pleistocene lion dimensions is excessive for sexually-based dimorphism.

Turning to Ballesio's claim that presence of a single size group at a site argues against sexual dimorphism as an explanation for the bimodal size groupings, we may examine this viewpoint using the material from Gailenreuth and Wierzchowska Górna. In his table 2, Ballesio (1980: 67) gives a number of mandibular measurements for samples of modern and fossil lions which include the distance between the anterior (mesial) face of lower premolar 3 and the posterior (distal) face of lower molar 1 (PM3-M1). Table 2 of this paper summarises the results of investigating distributions in PM3-M1 measurements. The modern sample from the Transvaal Museum is displayed in two ways, as single sex groups and as a pooled group. It will be seen that the width of the observed range of each of the Transvaal Museum single-sex samples is very similar to that of the Gailenreuth sample, and that the mean of the modern male sample lies close to that for Gailenreuth. The separation between the known male and female samples, with virtually no overlap and clear distinction between the means, should also be noted. It may also be seen that the observed range of the modern sample quoted by Ballesio (1980: table 2) is very much larger than than given for either of my modern single-sex samples, but very similar to that of my pooled sample. Furthermore, both the standard deviation given by Ballesio for his modern sample, and the coefficient of variation which I have calculated from his data, match the statistics of my pooled sample and disagree with those of my single-sex samples. In short, on the basis of these comparisons there is every indication that the Gailenreuth sample quoted by Ballesio is composed of one sex. Together with the large specimen from Jaurens (incorrectly given by

Ballesio as 82 mm for the PM3-M1 measurement in his table 2), these large specimens would appear to be of males. Ballesio's modern sample clearly consists of both males and females, and does not therefore form an appropriate basis for comparison with groups *within* bimodaly dispersed fossil data. The material from Wierzchowska Górna, on the other hand, which the bivariate scatter plots of tooth measurements in Figs 1–3 suggest consists of both males and females, has this interpretation of sexual dimorphism underlined in Table 2. The standard deviation, coefficient of variation and observed range of the Polish specimens agree with those statistics in my pooled modern sample, and stand in contrast to those of my single-sex samples and the material from Gailenreuth. And finally, we may note that the modern Transvaal Museum sample appears to be composed of slightly larger lions than that available to Ballesio, on the evidence of the mean sizes shown here in Table 2.

This exercise may be repeated for a second mandibular dimension given by Ballesio (1980: table 2), the distance between the anterior face of the lower canine and the posterior face of the lower molar 1 (C-M1). Precisely the same narrow distribution is observed in the case of the Gailenreuth sample by comparison with Ballesio's modern material, offering further support for the view that the fossil specimens from that site represent a single sex which is probably male.

3. Postcranial size variation in lions

In addition to the evidence afforded by dental remains, Ballesio also employs size distributions in postcranial specimens in his argument for two lion sub-species. In his figures 7–10 he shows bivariate scatter diagrams for measurements on second and fifth metacarpals, tibiae and calcanea respectively. All show a separation of fossil material into a larger and a smaller size group, and the fossil specimens exceed in size those in each modern comparative sample on each diagram. Further, the separation between the two fossil size groups of

each element is complete and exceeds that observed in the respective modern sample where the size ranges of the sexes overlap.

Clearly, the fossil lions were bigger than those in Ballesio's modern comparative sample. This is not surprising, since we saw in the discussion of PM3-M1 measurements above that the modern sample used by Ballesio contained relatively small lions. But the size increase in the fossil material is most marked in Ballesio's scatter diagrams of metacarpal two and five measurements, and less evident in the tibial and calcaneal distributions. It is also in the metacarpal dispersals that the difference between the two fossil size groups is most marked. Differences in bodily proportions in fossil populations by comparison with modern specimens are well known in the case of the spotted hyaena, *Crocuta crocuta* (Erxleben 1777), now confined to Africa but an extremely common fossil of the European Upper Pleistocene (Kurtén 1956, 1963, 1968, 1969; Turner 1981). A similar phenomenon may be observable in the relative proportions of the lions depicted by Ballesio, possibly the result of simple allometry.

The teeth and jaw fragments in the fossil samples from Gailenreuth and other sites may not come from precisely the same animals as the postcranial specimens in each case, but it is extremely unlikely that the two sets of material come from totally different populations of lions. Since we are not for the moment concerned with quantifying the relative abundances of the two sexes, but merely with establishing their presence, it would be reasonable to suppose that both dental and postcranial remains offer an adequate reflection of size and sex variation in the fossil samples. If the dental evidence in a sample clearly points to sexual dimorphism, then I can see no reason to suggest that bimodality in the postcranial remains from the same site reflects sub-specific variation.

4. Discussion

Correct interpretation of size variation in fossil lions is important. Like other large predators, these animals may have contributed not only their own bones to a fossil deposit but also those of the other members of the large-mammal fauna which they killed or from whose remains they scavenged. The resultant assemblage can therefore serve as a record of both palaeoethology and palaeoecology as well as of species presence and absence. But if we misread interspecific variation in an assemblage as sub-speciation, or worse still as speciation, then our analysis of such a record will be fatally flawed from the start. This discussion therefore examines a number of instances where analysis can only

proceed from a correct interpretation of size variation. The aim is to show the potential insight to be gained from an understanding of sex ratios in fossil lions.

1. Ballesio (1980: 78–9), on the basis of his interpretation of lion dimorphism, argues for two biogeographic areas in the region of the Jaurens cave, each exploited by one of his lion sub-species. Since, as Ballesio acknowledges, many sites tend to have both lion size groups, the implication would be that these sites all lie conveniently on the boundary between two sub-species of lion.

The analysis of size variation presented above offers strong evidence that Ballesio's interpretation is incorrect. But rejection of that interpretation leaves unanswered the interesting point raised by Ballesio in defense of his argument. Why, if the dimorphism in lions is sex-based, should only the large, presumably male, size group be represented at sites such as Gailenreuth and L'Herm? The quantity of specimens in each case dispels doubts that such distributions result from small-sample biases.

The first answer to the point is necessarily a cautious one: size distributions do not always point to sex unambiguously. If only the larger size group appears at a site, it remains possible that some of the smaller members of that group represent females. In many instances fossil assemblages probably represent accumulations over some time period, and the effect may be rather similar to that produced by sampling along a spatial cline where size groups are blurred. This effect was pointed out by Kurtén (1973) in his discussion of size variation in the extant American puma, *Felis concolor* (Linnaeus 1758). In the case of a site like Jaurens, where material comes from one stratum of a modern, controlled excavation, one would expect clear separation into two size groups if both sexes are present, as Kurtén (in lit.) has stressed. Careful analysis of the size distributions is therefore required, following which, in the case of the puma, Kurtén (1973: 8) was confident that "In practice the number of unsexable specimens will be negligible." Certainly the distributions shown here in Figs 2 and 3 in particular would support that optimism.

If we therefore accept that some sites demonstrably contain male lions, the answer to why this should be can be readily obtained from reports of modern lion behaviour. In particular, the work of Schaller (1972), who presents one of the most detailed studies of lion ethology based on observations made in the Serengeti, shows that the composition of adult lion groups may vary along a virtual continuum between all female and all male, depending very much on circumstances. If we can accept a reasonable congruence in

behavioural repertoire, then it should come as no surprise to find equal variety in the proportions of the two sexes in fossil material. Groups consisting of nomadic males may occur today in areas where prides of mixed sex are also living, and such males would then be prime contenders for the rôle of sole sex represented at a site.

2. Depending upon our ability to determine the circumstances of deposition, it is clear that sex ratios in fossil lion samples may provide precisely the kind of of palaeoethological and palaeoecological information which the palaeontologist seeks. Schaller (1972: 46) shows that, in Serengeti, subadult males tend to leave the pride in which they were born at the age of $2\frac{1}{2}$–$3\frac{1}{2}$ years, but if we confine our analysis to fully adult individuals we would generally expect to see some adult males present, as consorts of the adult females, in most lion groups, modern and fossil. Schaller (1972: 374) also suggests that, in suitable terrain, nomad male groups cannot survive for long without taking over an existing pride and ousting the incumbent males, a finding which appears to be confirmed by the work of Smuts (1976) on lions of the Kruger Park.

Thus if in a given area most fossil sites with contemporaneous deposits contain adult male and female lion remains then such assemblages probably represent stable female prides with a succession of male comings and goings. Evidence of this sort would indicate that the prides in the area were exploiting an abundant food supply to the maximum, leaving little room in which nomad male groups could survive for long. Such assemblages of males and females could be predicted to contain male specimens with relatively high frequencies of skeletal lesions, evidence of the successive oustings, and perhaps attempted oustings, of pride males by new and younger lions.

In contrast, sites with all-male assemblages, if more frequent in an area, might suggest less complete territorial tenure by resident prides. In that case, incidences of skeletal lesion might be expected to be relatively low in the all-male groups, reflecting less frequent attempts at pride seizure, and similarly low in male specimens from pride areas. Differences in age structure among dead males might also vary between the two extreme circumstances, since it is apparent that males able to retain control of a pride with little competition could have an extended life expectancy. Overall, then, we might expect to see a number of correlations between proportion of male versus male-female groups and incidences of injury to, and age at death of, male specimens.

It should be stressed that the emphasis in this discussion is upon the presence of both sexes or the preponderance of one. Attempts to discern the precise sex ratio at a site, as opposed to simply recognising the presence of both males and females, will involve the quantification of assemblage components. Quantification of vertebrate samples is a very large problem in its own right, and is dealt with in detail elsewhere (Fieller and Turner 1982; Turner 1983). The essential problem can be simply stated, however. It concerns the relationships between the recovered bone assemblage, the killed (or naturally dying) population which gave rise to that assemblage and the original living populations of animals which gave rise to the death population. In other words, relative abundances in the excavated sample may not reflect those of either the death or the living populations in any direct manner, and that applies whether one is dealing with classes within or between species. For instance, Smuts (1976) argued that sex ratios in adult pride lions are distorted, in favour of females, in relation to population density. This distortion appears to reflect the competition between males in areas where pride territories are numerous. Clearly distortion levels should in turn relate to the frequency of male-female versus all-male groups and the frequency of injuries and age at death of males discussed above. The problem for the palaeontologist who tries to integrate more detailed male-female ratio data of this kind with the analysis of fossil assemblages, however, is that these figures refer to the living population. We have no idea how a given sex ratio in an area might translate into a death assemblage in lions, or, more importantly, how it is then likely to translate into a fossil assemblage. Working on the basis of groups with all males versus groups with both sexes (albeit in the latter case with a preponderance of females) is perhaps the best we can presently aim for in the absence of clear criteria for distinguishing circumstances likely to produce x% of females in an excavated assemblage. Naturally, problems of quantification also apply to the assessment of male lion age structure in an assemblage, but in this case a broader approach, categorising a sample as simply "younger" or "older" may prove adequate.

3. Palaeoecological information may often be sought in temporal or geographic changes in the average size of a fossil species. In the case of an animal which is known to exhibit considerable sexual dimorphism, the necessity for comparing equivalent portions of the total size range is clear. Analyses based on unwitting comparisons of female lions from one site with males from another would produce a totally false result. Only a proper examination of the size distributions within a sample, of the kind presented here, will show

whether valid comparisons are being made. This point has been stressed by Kurtén (1968: 242), but the kind of problem which can arise is well-illustrated in Fig. 3 and may be reiterated. Only three lion upper canines, all falling within the smaller size group, are known from Jaurens. The contrast between these specimens and those in the larger size group from Britain and from Wierzchowska Górna is considerable. If only those three canines were available to represent lions at Jaurens, a not impossible result on the evidence of many Pleistocene sites, one would not lean heavily on such material for the palae-oecological interpretation of sex ratios in the manner discussed above. Yet unless the probability of the teeth being female is acknowledged, attempts to employ the Jaurens upper canine sample as an indicator of size changes in lions would be doomed to failure.

4. A final point to consider concerns the worst possible misreading of bimodal size distributions, the interpretation of two distinct species instead of two sexes. Such an error would not only do violence to palaeoecological and palaeoethological interpretations but also to the results of a wider field of enquiry. Increasing attention is being given to the fossil record as a source of information about macroevolutionary processes and events, rather than as a fairly patchy repetition of microevolution scaled up (Gould 1980). Numbers of species in lineages, and the rates of speciation, are an important aspect of such investigations, and a careful evaluation of the numbers of taxa proposed is therefore necessary. "Lumping" versus "splitting" in this context becomes an issue of major concern outside the field of the group of organisms studied.

5. Conclusion

Upper Pleistocene lions of Europe are seen to have been at least as sexually dimorphic as modern representatives of the species. Variation in the proportion of large and small size groups at Pleistocene sites therefore reflects the presence of male and female lions, and not sub-speciation.

The presence of males alone at certain sites is shown to be fully compatible with behavioural patterns recorded for modern lions. Consideration of recent ethological data suggests that broad patterning of male versus male and female presence at sites, considered in conjunction with the frequencies of lesions in male skeletons and the structure of the male death assemblage, may be used for palaeoethological and palaeoecological reconstructions.

Efforts to employ size variation in a sexually dimorphic species as a guide to palaeoecology must consider the sex of specimens. Moreover, attempts use the fossil record as a guide to tempo and mode in evolution risk considerable error if taxa have been proposed without regard to sexual variation. If there is to be confidence in the outcome of searches for general patterns in the fossil record then the analysis undertaken by the specialist must be reliable.

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