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Source: *Bios*, Vol. 75, No. 4 (Dec., 2004), pp. 131-138
Published by: Beta Beta Beta Biological Society
Stable URL: http://www.jstor.org/stable/4608712
Accessed: 15/09/2009 17:00

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Research Article

Comparative morphometric analysis of captive vs. wild African lion (*Panthera leo*) skulls

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Abstract. Panthera leo are a carnivorous species with significant bone growth occurring from gestation to 3–4 yrs. In captivity, species are not necessarily subject to all stresses influencing bone development that would otherwise result in the wild. The factors fully influencing bone development in the wild are unknown. The purpose of this study was to determine if differences in morphometric measurements are present between wild and captive populations of lions, specifically in the regions of mastication. Twenty-one different measurements were taken on fifty-seven skulls. Morphometric measurements of museum specimens from the wild were compared with specimens obtained from zoos and other captive environments. Results from analysis indicate significant differences between captive and wild specimens. The majority of these variances were in the regions of mastication; areas influenced by external stress. Wild specimens possess greater morphometric dimensions in regions of stress.

Introduction

Panthera leo africana are large, carnivorous felines ranging south of the Sahara Desert to Botswana. They are found in captivity at wildlife preserves, zoos, and nature centers across the world. In the wild, the bulk of their diet consists of large to medium-sized prey including but not limited to ungulates such as buffalo, zebra, wildebeest, roan, sable, springbok, gemsbok, kob, impala, warthog, waterbuck and hartebeest (Mitchell, 1965; Makacha and Schaller, 1969; de Pienaar, 1969; Rodgers, 1974; Rudnai, 1974, van Orsdol, 1982; 1984; Prins and Iason, 1989; Ruggiero, 1991; Scheel, 1993). However, as generalist hunters, they will take a wide range of prey, from small rodents to young rhinos, hippos and elephants (Ruggiero, 1991). Prey is usually killed with a throttling throat bite or a powerful bite to the neck (Radinsky, 1982). In contrast, the diet of *P. leo* in captivity consists primarily of prepackaged feline feed developed to simulate the nutritional needs of large cats (e.g. Mazuri Exotic Feline Diet, ZuPreem Exotic Feline Diet, and Central Nebraska Packing, Inc.). According to *Zoo Guidelines for Keeping Large Felids in Captivity* (Shoemaker et al., 1985; 1997) large felids are easily maintained when fed prepared diets made from beef or horse products.

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The morphology of the skull of *P. leo* is relatively short and designed to exert powerful forces at the level of the canines when closing its jaws (Buckland-Wright, 1978; Radinsky, 1982). The primary jaw muscles involved in this action are the temporalis and masseter (Cockrum, 1962; Milton, 1974). Ptergoid muscles are also involved although to a much lesser extent. These primary muscles are responsible for the movements of the jaw: the hinge movement by which the jaw is raised and lowered, the gliding movement by which the jaw is protruded and retracted, and the rotary movement by which the jaw is moved from side to side (Frank, 1950). The mandible hangs in a muscular sling composed of the masseter and the internal pterygoid muscles, with the external pterygoid muscle attached to the mandibular condyle (Frank, 1950). *P. leo* relies heavily on its massive canines and carnassials when feeding in the wild and to a far less extent in captivity.

P. leo achieves full skeletal growth around 3–4 years of age (Smuts et al., 1978). Certain stresses such as diet may impact the development of skulls up to full maturity and the results of these stresses are often visible when subject to morphometric analysis. Captivity has been shown to indirectly impact skull development of small mammals such as chinchillas (Crossley and Miguelez, 2001). Diet is known to be one of the greatest influences upon skull morphology of vertebrates (Smuts et al., 1978). The requirements upon maxillary and mandibular regions, as the regions of mastication, are illustrated by the size of their bones. A diet other than that available in the wild incurs certain morphometric differences in the cranium (Crossley and Miguelez, 2001). A diet consisting of high bone and connective tissue content requires greater bone mass and muscle strength to compensate for increased stress placed upon the cranial region. This may result in differences in cranial dimensions between wild and captive *P. leo*. In a study of force transmission by Buckland-Wright (1978) on the skull of *Felis catus*, the major areas of stress caused by biting against a resistant force were in the alveolar processes; the sites of attachment of the muscles of mastication and the region of the glenoid fossa at its point of articulation with the mandible.

It is not known whether differences in diet have a direct impact upon *P. leo* skull morphology. In particular, the diet of captive lions may result in smaller size of mandibular and maxillary bones. My objective was to test this hypothesis by comparing morphometric data gathered from skulls of wild-caught and captive-bred *P. leo*.

Material and Methods

Forty-five *P. leo* skulls originating from southern Africa, along with twelve originating from various zoos were available for examination by permission of the James Ford Bell Museum of Natural History (St. Paul, MN), the Field Museum of Natural History (Chicago, IL), and the Milwaukee Public Museum (Milwaukee, WI). See Figure 1 for visual of captive male *P. leo* skull. The wild specimens had been collected during the late 19th to late 20th century either by research expeditions in Africa or donated upon discovery by African park rangers. Captive specimens originated from Como Zoo, St. Paul, Lincoln Park Zoo, Chicago, and Milwaukee County Zoo, Milwaukee. Captive specimens had been collected throughout the 20th century. The cause of death was unavailable for the majority of the wild and captive specimens. All specimens examined possessed permanent canines, thus aging them at two years and older. Juveniles (those lacking permanent canines) were excluded from

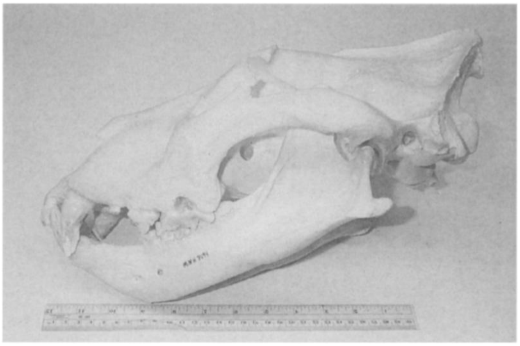

Figure 1. Right side view of skull and regions of mastication from a captive, large male *P. leo*.

the study, as environmental influence upon skull morphology would have been less evident. When taking measurements of specimens with parts of skull missing estimates of prior dimensions were made. Estimates were confirmed through bilateral symmetry. In a study on fluctuating asymmetry in sea otters (*Enhydra lutris*) conducted by the U.S.G.S. Biological Research Division, measurements were taken of skull symmetry on complete skulls with very little to no variance in measurement (Bodkin et al., 1999). Estimates taken from severely damaged skulls were excluded from study.

Twenty-one different measurements were recorded from the maxillary and mandibular regions of the skull. Several adjoining regions were also taken into consideration by the study. Table 1 contains a listing and description of the measurements taken. Straight-line measurements were recorded of maximum skull width and length for standardization among populations (Radinsky, 1982). Dial calipers with an accuracy of 0.1 mm were used for direct measurement. Each specimen was measured twice. To standardize data with the overall dimension of the skull, measurements were divided by maximum width of skull. This division was found to provide the best standardization by least significant of measurements taken (P=0.61). One-Way-ANOVA, T-tests, and Logistic Fit were performed with statistical software (JMP IN, Version 4.0.4). Data were considered statisti-

Table 1. Description of measurements taken.

Description of Measurements	
Measurement	**Description**
Overall length:	Maximum dimension of skull when laid on level surface
Overall width:	Maximum width of skull when laid on level surface
Overall height:	Maximum height of skull when laid on level surface
Mastoid breadth:	Maximum width of skull across mastoid
Jaw height:	Maximum height from coronoid process to angular process
Jaw width:	Maximum width of jaw measured at the dentary (dorsal to last molar)
Mandible length:	Maximum length of the lower jaw from front tip of the dentary bone to the angle
Mandible width:	Maximum width of mandibles measured from right coronoid process to left coronoid process
Maximum palate width:	Maximum width across the alveoli of the cheek teeth
Minimum palate width:	Minimum width across the palate measured behind the canines
Maximum palate length:	From the front of the alveolus of a first incisor, to anterior most point on the posterior edge of palate
Incisive foramina length:	Maximum length of the anterior palatal foramina
Alveolar length of maxillary toothrow:	Length of upper toothrow from the anterior surface of the canine near its junction with the jawbone to the posterior surface of the last molar near its junction with the jawbone
Alveolar length of mandibular molar toothrow:	Length from anterior edge of first premolar to posterior edge of last molar
Alveolar length of mandibular toothrow:	Length of lower toothrow from the anterior surface of the canine near its junction with the jawbone to the posterior surface of the last molar near its junction with the jawbone
Bicanine breadth maxillary:	Maximum breadth of maxilla from upper canine to upper canine
Bicanine breadth mandibular:	Maximum breadth of mandible from lower canine to lower canine
Condylo-canine length:	Length from anterior edges of alveoli of the upper canines to the posterior edge of the occipital condyles
Condyle width:	Maximum width from right to left extension of condyle
Condyle height:	Most superior to most inferior portion of condyle
Jaw height posterior to last molar:	Height of jaw measured posterior to last molar from dorsal to ventral side of jaw directly inferior

cally significant at a probability of 0.1 due to small sample size.

Results

Significant differences were detected between wild and captive-bred *P. leo* skulls, especially in the maxillary and mandibular regions (Table 2). No significant difference was detected in overall skull length between wild and captive specimens (312.7 mm vs. 303.5 mm; P=0.5634). Differences in overall height of skulls between wild and captive *P. leo* were found to be significant with wild specimens possessing greater height (128.2 mm vs. 119.5 mm; P=0.0565). Differences in mastoid breadth between wild and captive specimens were not significant (122.6 mm vs. 111.6mm; P=0.1925); however, in all samples measured wild specimens tended to posses greater breadth. A significant difference was detected in jaw height between wild and captive specimens with wild possessing greater height (97.9 mm vs. 87.8; P=0.0394). Although no significant difference in jaw width was detected (19.8 mm vs. 24.2 mm; P=0.1322), captive specimens tended to be wider. Wild specimens were found to possess a significantly greater mandible length than captive specimens (210.2 mm vs. 198.1 mm; P=0.0117). Differences in mandible width between wild and captive were not found to be significant, although captive tended to possess greater width (129.6 mm vs.

Table 2. Analyzed data comparing wild and captive specimens. Sample size n = 57 (captive n = 12, wild n = 45). P values considered statistically significant at ≤0.10.

	Mean (mm)		
Measurement	**Wild n=45**	**Captive n=12**	**P value**
Overall width	204.6	205.2	0.61
Overall length	312.7	303.5	0.56
Overall height	**128.2**	**119.5**	**0.06**
Mastoid breath	122.6	111.6	0.19
Jaw height	**97.9**	**87.8**	**0.04**
Jaw width	19.8	24.2	0.13
Mandible length	**210.2**	**198.1**	**0.01**
Mandible width	129.6	130.1	0.24
Maximum palate width	108.9	109.6	0.10
Minimum palate width	63.7	64.2	0.15
Maximum palate length	**142.3**	**135.9**	**0.067**
Incisive foramina length	7.0	7.6	0.26
Alveolar length of maxillary toothrow	98.2	97.2	0.89
Alveolar length of mandibular toothrow	115.7	112.1	0.58
Alveolar length of mandibular molar toothrow	68.0	63.8	0.19
Bicanine breadth (maxillary)	**48.0**	**50.2**	**0.002**
Bicanine breadth (mandible)	26.0	26.6	0.15
Condylo-canine length	266.7	257.0	0.24
Condyle width	**50.6**	**47.5**	**0.06**
Condyle height	17.9	16.3	0.57
Jaw height posterior to last molar	61.9	36.6	0.49

130.1 mm; P=0.2350). Difference in maximum palate width was highly visible, with captive tending to possess greater width than wild (108.9 mm vs. 109.6 mm; P=0.1010). Minimum palate width was less obvious in the difference between wild and captive specimens, although captive tended to demonstrate greater width (63.7 mm vs. 64.2 mm; P=0.1488). Significant differences were determined between wild and captive specimens in maximum palate length, with wild having greater length (142.3 mm vs. 135.9 mm; P=0.0699). Although not significant, differences were determined in incisive foramina length with captive tending to possess greater length (7.0 mm vs. 7.6 mm; P=0.2553). Data recorded on alveolar length of mandibular and maxillary toothrows showed no significant difference between wild and captive specimens (mandibular: 115.7 mm vs. 112.1 mm; P=0.5760; and maxillary: 98.2 mm vs. 97.2 mm; P=0.8899). Although not significant, alveolar length of mandibular molar toothrow tended to be greater for wild than captive specimens (68.0 mm vs. 63.8 mm; P=0.1939). Differences in maxillary bicanine breadth were strongly significant between wild and captive specimens, with captive possessing greater breadth (48.0 mm vs. 50.2 mm; P=0.0020). Mandibular bicanine breadth was less clearly defined, although captive specimens tended to possess greater breadth than wild (26 mm vs. 26.6 mm; P=0.1511). Differences in condylo-canine length were not found to be significant between wild and captive specimens although wild tended to possess greater length (266.7 mm vs. 257.0 mm; P=0.2416). Significant difference was determined in condyle width with wild specimens possessing greater width than captive (50.6 mm vs. 47.5 mm; P=0.0616). Data from condyle height showed no significant difference between wild and captive specimens (17.9 mm vs. 16.3 mm; P=0.5723). No significant differences were found of jaw height posterior to last molar between wild and captive specimens (61.9 mm vs. 36.6 mm; P=0.4929).

Using a nominal logistic fit function; models were created to determine if origin of skulls could be determined based upon dimensions. The nominal logistic fit platform fits a linear model to a multi-level logistic response function using maximum likelihood. Likelihood ratio test statistics are computed for the whole model. The models were based on three measurements taken from each of the 57 specimens. Models were then selected by statistical significance of the three measurements. Three of the models tested, using measurements from the condyle and jaw region, showed good fit (P<0.0015). See Table 3 for measurements and significance of models.

Discussion

The mandibular, maxillary, and directly adjoining regions are morphometrically different between wild and captive *P. leo* skulls. Significant differences in width, height, and length of bones in the mandibular and maxillary regions are likely the result of stress upon those regions. The motion of biting down on resistant structures such as bone and cartilage places stress upon these regions of the skull as well as directly on adjoining bones. As a result, adaptation occurs, increasing the bones width, length, and height based upon the direction of stress. According to Greaves (1983, 1985), adaptation can occur in two ways: (1) through an increase in bone dimensions and therefore an increase in musculature and/or (2) addition of musculature alone. By providing an increased base for muscle attachment and therefore a potential increase in muscle mass, an increase in biting force would be gained (DeMar and Barghusen, 1972; Greaves, 1985).

According to Barghusen (1972), the increase in muscular force suggests a greater capacity of predators to overcome weight and struggles of prey during jaw adduction. In the wild, requirements upon mandibular and maxillary regions are far greater than in captivity as a result of diet. Wild specimens showed significantly greater skull height over captive specimens (P= 0.0565). Increased pressure on jaws requires a larger base for attachment of muscles, resulting in increased skull height and thickness. In the same way, jaw height was greater in wild specimens (P=0.0394). The muscles primarily responsible for jaw movement and force are the temporalis and masseter muscles. The temporalis mass is connected at the medial and dorsal surface of the ascending ramus of the dentary and arises from the dorsal region of the temporal fossa. The masseteric muscle mass is connected to the zygomatic arch and inserts on the external and ventral surface of the mandible (de Beer, 1985; Hiiemae and Crompton, 1985). The connection of the muscles to the jaw is designed to produce the largest average bite force. In carnivores this takes place at the posterior third of the jaw (Greaves, 1988). The midpoint of the jaw where the carnassial is located produces the greatest output force (Greaves, 1982; 1983). Muscle influence upon the condyle region has been studied by x-ray by Frank (1950). As stress is placed upon the jaws the condyle region experiences perhaps the greatest stress acting as the jaw's hinge. This stress would result in an increase in condyle width as was observed in the wild specimens measured (P=0.0616). Studies performed by Buckland-Wright (1978) found that the biting action of cats against a resistance results in stress in three major areas: (1) the alveolar process, (2) the sites of attachment of the muscles of mastication, and (3) the region of the glenoid fossa at the point of articulation to mandible. The masseter muscles are responsible for generating the highest degree of strain upon these areas (Buckland-Wright, 1978). Studies in bite force by Greaves (1988) demonstrated similar results with the greatest degree of tooth force being located at the rear of the jaws and decreasing anteriorly. To compensate for the higher degree of strain placed upon regions of the skull, wild specimens showed an increase in skull surface area, which permits greater distribution of strain as well as increased area for muscle attachment. While maximum skull width was not found to be greater in wild than in captive specimens, mandible length as well as palate length, were found to be significantly greater (P=0.0117, P=0.0699). This indicates that wild specimens may possess a morphology permitting greater distribution of strain upon skull and an increased base for

Table 3. Models created using nominal logistic fit function for skull identification.

Model #	Measurements	P value
1	Condyle width	0.0015
	Condyle height	
	Jaw height	
2	Condyle width	0.0001
	Condyle height	
	Jaw width	
3	Condyle width	0.0001
	Jaw width	
	Jaw height posterior to last molar	
4	Condyle width	0.007
	Mandible length	
	Overall height	
5	Condyle width	0.0018
	Condyle height	
	Maximum palate width	
6	Mandible width	0.0031
	Jaw length	
	Jaw height	

muscle attachment. Maxillary bicanine breadth was expected to follow the same trend, being wider in wild specimens than captive. However, analysis indicated that captive specimens possess significantly greater maxillary bicanine breadth (P=0.01529). According to Greaves (1985), the magnitude of bite force of the general carnivore jaw is mainly determined by the absolute amount of jaw musculature. The larger dimensions of the wild *P. leo* skulls indicate they may possess a greater muscle mass and therefore bite force than captive.

Skull growth and development in *P. leo* is subject to variation not only in different populations but even between individuals from neighboring prides or from the same pride (Smuts et al., 1978). Similar results are found in many mammals such as the rodentia *Oryzomys* (Weksler et al., 1997). These variations are for the most part believed to be the result of different foods available to individuals as well as prides and populations. Such evidence was seen when morphometric measurements were taken during the study of the legendary man-eating lions of Tsavo, Kenya. Three theories of why these lions became man-eaters have been proposed: (1) In the 1890s, an outbreak of rinderpest disease killed millions of zebras, gazelles and other African wildlife resulting in lions having to look elsewhere for food; (2) poor human burial practices may have also contributed to the Tsavo tragedy by providing lions with an opportunity to develop a taste for human; (3) the Tsavo region experienced a long drought (Field Museum, Department of Zoology). A drought would force most herbivores from the area in search of food. Lions, being highly territorial mammals, often refuse to leave their territory even when their prey moves on or dies off. In the first and third theories, with the departure of the herbivores, the lions would have little prey available other than man, a problem to which the third theory would only add. Measurements performed in this study, on the two Tsavo males, showed skulls of average length, below average width, and below average height for their sex. This morphometric variance between the two Tsavo lions and other wild African lions may have been the result of food availability.

While not statistically significant, several analyzed measurements were found to indicate the opposite trend of what was originally predicted. Based on the study's hypothesis, mastoid breadth, jaw width, mandible width, maximum palate width, minimum palate width, and bicanine breadth, were expected to be greater in wild specimens than captive. However, opposite trends were observed. This may have resulted from the small sample size due to low availability of captive specimens. Further investigation is required to confirm whether these measurements represent an actual pattern or if they are simply the result of small sample size.

Studies performed by Greaves (1988) on average bite force, as well as studies performed by Buckland and Wright (1978) on force transmission, have provided evidence for the advantage of larger mandibular molar toothrow. While not significant, analysis indicated that wild specimens possess a larger mandibular molar toothrow than captives (P=0.1939). Advantages of this morphology would provide individuals with greater shearing (carnassials) and grinding (molars) ability as well as increased distribution of stress. The carnassials, being the major teeth used in shearing and crushing, would especially benefit from this arrangement.

The models created using nominal logistic fit function were used to determine if a skull could be identified through morphometrics as a captive or wild specimen. The measurements used in the models to achieve the highest degree of significance were not taken from any one region of the skull. This indicates that variances in skull dimension between captive and wild specimens are not restricted to one particular region. To achieve the highest degree of significance, three specific measurements were needed for each model. The removal of one of these measurements invalidated the model. Of the measurements used in the models those of the mandible and condyle were most important. Condyle width was used in five of the six models, condyle height in two of the six, and mandible length in two of the six. The statistically significant models indicate that further differences between captive and wild specimens were present beyond what was indicated in the statistical T-tests, although to a lesser degree. These variances used collectively in conjunction with the significant differences observed in individual measurements provide further evidence of the difference in skull morphology between captive and wild specimens. However, none of the six models calculated should be used alone to identify the origin of a skull. For greatest degree of certainty, all six models should be used together and at no point is certainty of the models absolute in identification.

Acknowledgements: I wish to thank the James Ford Bell Museum of Natural History, St. Paul, the Field Museum of Natural History, Chicago, and the Milwaukee Museum of Natural History for permission to examine and assistance in examining the museum collections. I would also like to thank Dr. Anja Brunet of the Bell Museum, University of Minnesota, St. Paul, for her assistance and advice given throughout the study and my undergraduate advisor Dr. Teresa DeGolier, Bethel College, St. Paul, for reading the manuscript and her advice during this study.

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Received 13 February 2003; accepted 24 March 2004.