Pride Diaries: Sex, Brain Size and Sociality in the African Lion (*Panthera leo*) and Cougar (*Puma concolor*)

Bradley M. Arsznov^a Sharleen T. Sakai^{a, b}

^aDepartment of Psychology, and ^bNeuroscience Program, Michigan State University, East Lansing, Mich., USA

Key Words

Endocast • African lion • Mountain lion • Computed tomography

Abstract

The purpose of this study was to examine if differences in social life histories correspond to intraspecific variation in total or regional brain volumes in the African lion (*Panthera leo*) and cougar (*Puma concolor*). African lions live in gregarious prides usually consisting of related adult females, their dependent offspring, and a coalition of immigrant males. Upon reaching maturity, male lions enter a nomadic and often, solitary phase in their lives, whereas females are mainly philopatric and highly social throughout their lives. In contrast, the social life history does not differ between male and female cougars; both are solitary. Three-dimensional virtual endocasts were created using computed tomography from the skulls of 14 adult African lions (8 male, 6 female) and 14 cougars (7 male, 7 female). Endocranial volume and basal skull length were highly correlated in African lions ($r = 0.59$, $p < 0.05$) and in cougars ($r = 0.67$, $p < 0.01$). Analyses of total endocranial volume relative to skull length revealed no sex differences in either African lions or cougars. However, relative anterior cerebrum volume comprised primarily of frontal cortex and surface area was significantly greater in female African lions than males, while relative posterior cerebrum

volume and surface area was greater in males than females. These differences were specific to the neocortex and were not found in the solitary cougar, suggesting that social life history is linked to sex-specific neocortical patterns in these species. We further hypothesize that increased frontal cortical volume in female lions is related to the need for greater inhibitory control in the presence of a dominant male aggressor.

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Introduction

The social brain hypothesis advocates that sociality is the primary selection pressure responsible for the relative increase in brain size [Byrne and Whiten, 1988; Dunbar, 1992; Dunbar, 1998]. In primates, increased sociality is related to an increase in brain size; including expansion of frontal cortex. Frontal cortex is involved in executive control of cognition and regulation of social behaviors in humans and other mammals [Adolphs, 2001; Amodio and Frith, 2006], and its relative enlargement may reflect enhanced processing of social information. Analysis of relative brain size in other mammalian taxa including artiodactyls, ungulates, carnivores and bats [Shultz and Dunbar, 2007] has revealed a relationship between sociality and increased brain size.

Despite the support for the social brain hypothesis in comparative studies, few studies have examined if differences in social life history experienced by males and females is associated with differences in brain size. In humans, a portion of the ventral frontal cortex associated with social perception is larger in females than males [Wood et al., 2008]. In contrast, we recently found that males possess proportionately more frontal cortex than females in spotted hyenas [Arsznov et al., 2010]. This frontal cortical difference is attributed to the differential social life history experienced by male and female spotted hyenas. Spotted hyenas are highly gregarious living in clans of up to 90 individuals [Kruuk, 1972; Holekamp et al., 2007]. Female spotted hyenas are usually philopatric [Henschel and Skinner, 1987; Mills, 1990; Smale et al., 1997; Boydston et al., 2007], while most postpubertal male hyenas emigrate from their natal clans. Male spotted hyenas join neighboring clans at the bottom of the dominance hierarchy [East and Hofer, 2001] and behave submissively to all hyenas encountered in the new clan [Holekamp et al., 2007]. Thus, the increased frontal cortex possessed by male spotted hyenas may correspond either to the enhanced experience associated with frontal cortical processing or a sex-specific effect. The experience effect may be in response to the greater inhibitory control required of male spotted hyenas in the presence of larger, more aggressive females. Immigrant males may require enhanced inhibitory control over inappropriate behaviors, such as aggression, in order to negotiate the social system in the new clan. Alternatively, relative enlargement of frontal cortex may reflect enhanced processing of social information required of males as they immigrate from the natal clan to a new clan. Since spotted hyenas remember the identities and ranks of their clan mates throughout their lives [Holekamp et al., 2007], immigrant males would typically have a greater social memory requirement than natal females. Finally, the sex difference in frontal cortex volumes may be the result of sex-specific genes including hormonal effects [Luders et al., 2009]. The present study sought to assess each of these questions by examining regional brain volumes in two species: the African lion (*Panthera leo*) and the cougar (*Puma concolor*), members of two separate felid clades [Johnson et al., 2006].

Among the extant felids, only the African lion is consistently gregarious [Packer and Pusey, 1987]. African lions live in complex fission-fusion social groups called prides [Packer and Pusey, 1987]. Social life history patterns in the pride vary between the sexes in both immigration and dominance behavior. Male offspring emi-

grate from the natal pride upon sexual maturity where they enter a solitary nomadic phase or form a coalition with other male kin mates, whereas female offspring typically remain in the maternal pride [Packer and Pusey, 1987]. Female lions live in prides of up to 21 lions and are subordinate to males. Male lions are highly aggressive towards female lions [Mosser and Packer, 2009]. In contrast to the social organization exhibited in the African lion, most other felid species including cougars [Sunquist and Sunquist, 2002] are primarily solitary and only interact with conspecifics during the breeding season when they form pairs that last for a few weeks [Nowak and Paradiso, 1983]. Here, we compared total and regional brain volumes in male and female lions and cougars in order to determine if intraspecific variation in social life history correspond to brain volume differences. Three predictions regarding sex differences in frontal cortex were examined. (1) If the demands for inhibitory control in the presence of dominant aggressor underlie sex differences in frontal cortex, we predicted that female lions would be faced with greater demands for inhibitory control and would possess proportionately more frontal cortex than male lions. (2) If increased frontal cortical volume is related to increased social information processing, the cognitive demands resulting from emigrating to a new social group should correspond to an increase in frontal cortical volume in male lions compared to female lions, similar to our findings in male spotted hyenas. Like male spotted hyenas, male African lions also disperse from their natal pride and learn the identities of new pride members. (3) Finally, if sex-specific effects determine the difference in frontal cortex, intraspecific variation should reveal an absence of frontal cortical sex differences in the cougar, a species in which both males and females maintain a solitary life style. Here we used computed tomography (CT) to create virtual endocasts from lion and cougar skulls. The virtual endocasts are based on serial analysis of coronal images and yield quantitative regional and total brain volume data that were used to examine intraspecific variations.

Methods

Specimens

Skulls of 14 adult African lions (8 male, 6 female) and 14 cougars (7 male, 7 female) were obtained from the collections of the Michigan State University Museum, Field Museum of Natural History and University of Michigan Museum of Zoology (see Appendix).

Digital Measurements

Each skull was aligned along an anterior-posterior axis and scanned using either a General Electric Lightspeed 4 slice scanner or a General Electric Discovery ST 16 slice scanner at the Department of Radiology at Michigan State University (see Appendix). The following scanning parameters were used: a slice thickness of 0.625 mm, a table speed of 5.62 mm/rotation, a pitch of 0.562:1 and a 30-cm field of view. The CT data were saved in the Digital Imaging and Communications in Medicine (DICOM) Centricity Version 2.2 format and the virtual endocasts were created using MIMICS 13.1 software (Materialise, Inc., Ann Arbor, Mich., USA). Virtual endocasts were created for each scanned skull using the procedures described in Sakai et al. [2011b]. Briefly, the skull was isolated from the surrounding air space, defined as a pixel value of -1024 Hounsfield units (HU). Next, the endocranial air space was filled for each slice in the coronal plane starting where the cribriform plate forms the floor of the endocranial cavity and extending caudally through the foramen magnum. The filled coronal sections were then stacked to create a three-dimensional reconstruction of the endocranial cavity (virtual endocast) using the MIMICS 3D object operation. Detailed external brain morphology, including gyral and sulcal patterns, can be seen in the virtual endocasts.

Skull basal length, defined as the distance from the anterior border of the median incisive alveolus to the mid-ventral border of the foramen magnum, was collected from each specimen as a measure of body size (fig. 1). Since skull basal length is highly correlated with body weight, the former is a reasonable proxy for body size when other measures (e.g., individual body weight, postcranial dimensions) are not available [Janis, 1990; Van Valkenburgh, 1990]. A single observer (B.M.A.) collected all linear skull measurements from the CT images.

Validation of Virtual Endocasts

Whole Endocasts

In order to confirm the general brain morphology obtained from the endocast, the gyral and sulcal patterns seen in the virtual endocasts were directly compared to the external morphological features on whole brain photographs of standard anatomical orientations, including dorsal, ventral, left lateral, and right lateral views, of a formalin-fixed African lion brain (specimen No. 62-79) and cougar (specimen No. 60-206) from the Comparative Mammalian Brain Collection (www.brainmuseum.org) (fig. 2). All volumetric data were made by a single observer (B.M.A.) and were obtained using the MIMICS 3D volume measurement operation. These measurements were assessed for reliability by comparing whole endocast volumes from a subset of 11 specimens obtained from 2 separate raters. An inter-rater reliability analysis revealed no significant difference in volumetric assessment from the endocasts created from each individual ($t(20) = 0.07$, $p = 0.95$). CT files were coded by animal number only, and the analysis and demarcation of brain regions was conducted blind with regard to the sex of the specimen.

Magnetic Resonance Imaging (MRI) and Volume Analysis

In order to assess the difference between endocranial volume and brain volume, we analyzed archived MR images of a 10-year-old captive male African lion (John Ball Zoo, Grand Rapids, Mich., USA).

Magnetic Resonance Data Acquisitions

The lion was imaged at the Veterinary Medical Center, College of Veterinary Medicine, Michigan State University. The lion was darted to induce anesthesia and maintained using sevoflurane. The brain was imaged in a 1.5-T Siemens Espree (Siemens, Munich, Germany). T_1 - and T_2 -weighted images in the transverse and sagittal planes were acquired with pre- and post-contrast medium T_1 sequences obtained in axial (transverse), sagittal and coronal (dorsal) planes. The image sequences were obtained using the following parameters: T_1 sequence: TR = 615 ms, TE = 15 ms, FOV = 24 cm, slice thickness = 5 mm, resolution: $256 \times 256 \times 16$, flip angle of 150 degrees and interslice gap = 1.5 mm. T_2 sequence: TR = 6,920 ms, TE = 79 ms, FOV = 24 cm, slice thickness = 5 mm, resolution: $320 \times 320 \times 16$, flip angle of 150 degrees and interslice gap = 1.5 mm. The animal used in this study was treated as a hospital patient according to guidelines set by the American Veterinary Medical Association.

Post-processing, reconstruction of the whole brain and endocranium and volume acquisition were performed using MIMICS 13.1 software (Materialise, Inc., Ann Arbor, Mich., USA). Volumetric measurements were made in three separate anatomical orientations: coronal, sagittal and axial. In each of these orientations, masks for total brain volume and endocranial volume were created by tracing the region of interest each serial section. This masking process was similar to the selection process of total endocranial volume for the CT data starting where the cribriform plate forms the floor of the endocranial cavity and extending caudally through the foramen magnum.

Delineation of Brain Regions in Virtual Endocasts

The gyral and sulcal pattern as well as bony landmarks were used as a guide to further subdivide the endocranium into 3 regions: anterior cerebrum, posterior cerebrum, and cerebellum/brain stem using the procedures described in Arsznov et al. [2010] (fig. 3). A brief description of the criteria employed follows.

Anterior Cerebrum Volume (AC)

To our knowledge, no cortical map is available for the African lion or cougar. Therefore, we relied on the identification of anterior cortical areas reported in other carnivores and applied these criteria to the African lion and cougar. Anterior cortex, specifically, the frontal cortex is defined in primates as cortex rostral to the central sulcus. However, the central sulcus is absent in carnivores and its putative homologue, the postcruciate dimple or sulcus, which delimits the boundary between motor and somatosensory cortex in some carnivores [Hardin et al., 1968; Gorska, 1974], is not present in all carnivore species and, where present, can be highly variable between hemispheres, even within the same individual [Hassler and Muhs-Clement, 1964; Kawamura, 1971]. Here, we use the cruciate sulcus as a landmark for demarcating anterior from posterior cerebrum, as it is a prominent feature that demonstrates less intra- and interspecific variation than the postcruciate dimple [Radinsky, 1969; Myasnikov et al., 1997]. The cruciate sulcus is coincident with the rostral-most portion of the motor cortex (cytoarchitectonic areas 4 and 6) in the cat [Hassler and Muhs-Clement, 1964], dog [Gorska, 1974; Stanton et al., 1986; Tanaka, 1987; Sakai et al., 1993], raccoon [Sakai, 1982; Sakai, 1990], and spotted hyena [Arsznov et al., 2010].

A histological series of sections through the pericruciate region of the African lion (62-79) was examined to determine if the

Fig. 1. **A, C** Lateral and ventral views of a CT-scanned skull of an adult male African lion (**A**) and cougar (**C**). Arrow indicates the linear measurement of skull basal length (SBL), defined as the distance from the anterior border of the median incisor alveolus to the mid-ventral border of the foramen magnum. SBL is used

here as a proxy for body size. **B, D** Log cube root of endocranial volume regressed against log skull basal length for African lion (**B**) males (solid circles) and females (open circles) and cougar (**D**) males (solid triangles) females (open triangles). African lion: Pearson's $r = 0.59$, $p < 0.05$ and cougar: Pearson's $r = 0.67$, $p < 0.01$.

Fig. 2. **A** Photograph of a whole brain of an African lion (*P. leo*) from the Comparative Mammalian Brain Collection (No. 64352) and three-dimensional virtual endocast reconstructed from a African lion skull (Michigan State University specimen No. 11242). **B** Photograph of a whole brain of a cougar (*P. concolor*) from the Comparative Mammalian Brain Collection (No. 60206) and

three-dimensional virtual endocast reconstructed from a cougar skull (Michigan State University specimen No. 12240). Major sulci and other anatomical features in both the whole brain and virtual endocast are shown. an = Ansate sulcus; cs = cruciate sulcus; la = lateral sulcus; pl = postlateral sulcus; pr = prorreal sulcus; ss = suprasylvian sulcus.

cruciate sulcus displays the characteristic cytoarchitectonic features as those described in other carnivore species. A similar histological series in the cougar brain was not available. Analysis of the Nissl-stained lion brain sections revealed that the fundus of the postcruciate dimple delimits the boundary between cytoarchitectonic area 4 and area 3a. Area 4 is primarily defined by the absence of a granular cell layer IV and the presence of giant and large pyramidal cells in layer V. In the somatosensory cortex, area 3a is characterized by the presence of a granular cell layer IV and small pyramidal cells located in layer V [Hassler and Muhs-Clement, 1964]. The dorsal bank of the cruciate sulcus contains large and giant pyramidal cells in layer V consistent with cytoarchitectonic area 4 and the primary motor cortex as mapped in other carnivores [Hardin et al., 1968; Gorska, 1974; Nieoullon and Rispal-Padel, 1976] (fig. 4).

Anterior cerebral volume was calculated from the endocranial slices and was defined as the region rostral to the junction of the cruciate sulcus and midline, but caudal to the olfactory bulbs. The anterior cerebrum volume here is thus comprised of the frontal cortex and subcortical structures, including a small portion of the rostral-most head of the caudate nucleus, ventral pallidum, olfactory tubercle and prepiriform cortex (fig. 3, 4).

Posterior Cerebrum Volume (PC)

The endocranial volume posterior to the cruciate sulcus, but anterior to the tentorium cerebelli, is here referred to as the pos-

terior cerebrum (fig. 3). This region included all cortex posterior to the cruciate sulcus as well as underlying diencephalic and rostral mesencephalic structures.

Cerebellum plus Brain Stem Volume (CB+BS)

The cerebellum and brain stem are housed within the posterior cranial fossa (fig. 4). This region was defined on the CT images of the skull as the area between the foramen magnum and the tentorium cerebelli, which covers the superior surface of the cerebellum. Thus, the volume measurement for cerebellum/brain stem included cerebellum, medulla, pons, and brain stem as far caudal as its junction with the spinal cord.

Whole and Regional Surface Areas

Since the endocast is based on the surface impression of the endocranium, it is limited in providing information regarding detailed brain structure. However, one measure, endocranial surface area dorsal to the rhinal fissure, has been used as an indicator of neocortical area [Jerison, 2007]. Here, neocortical surface area was measured from a 1-pixel deep outer mask of the endocast. Surface area located ventral to the rhinal fissure was excluded from this measure. Regional neocortical surface areas were obtained by segmenting the whole surface area mask at the same coordinates used for the regional endocranial volume masks for anterior cerebrum and posterior cerebrum.

Fig. 3. **A** Dorsolateral view of the virtual endocast reconstructed from an African lion. Outlines indicate boundaries of the anterior cerebrum (AC), posterior cerebrum (PC), and cerebellum brain stem (CB+BS). Arrows denote the location of proreal gyrus (pg), anterior sigmoid gyrus (asg), and posterior sigmoid gyrus (psg). **B** Dorsolateral view of the virtual endocast showing neocortical surface area (shaded) and subcortical volume (solid). Neocortical surface area was measured as a 1-pixel deep outer mask of the endocranium dorsal to the rhinal fissure. Regional neocortical surface area measures, AC and PC, were defined using the same landmarks used for regional endocranial AC and PC volumes. Subcortical volumes were measured by subtracting the regional neocortical volume from the corresponding regional brain volume.

Subcortical Regional Volumes

In order to determine if differences in either total or regional brain volume might be due to relative enlargement of the subcortical areas, we estimated subcortical volumes in the endocast by subtracting from the total volume the outermost 3 mm of the endocast. Neocortical depth was measured in cortex dorsal to the rhinal fissure in Nissl-stained coronal sections of the African lion (62–79) (fig. 4). The average depth of cortex was 2.5 mm. This measure was combined with an approximation of the dura mater thickness ranging from 0.2 mm in the cat to 0.25 mm in the dog [McComb et al., 1981]. Then, a measure for cortical volume was

calculated using the MIMICS morphology operation to dilate the 1-pixel neocortex surface area mask to a depth of 8 pixels or approximately 3 mm. Subcortical volumes were calculated by subtracting the regional neocortical volume from the corresponding regional brain volume.

Statistical Analyses

Statistical analyses were based on the endocasts of 8 male and 6 female African lions and 7 male and 7 female cougars. Prior to statistical analyses, skull basal length and endocranial volumes were log-transformed in order to improve graphical representation of the data. The allometric relationship between total endocranial volume and skull basal length was assessed using a bivariate correlation coefficient, Pearson's r for each species. Two sets of statistical analyses were employed to determine sex differences in endocranial or regional brain volumes. First, mean residual values obtained from linear regressions of log cube root of total endocranial volume plotted against log skull basal length, regional brain volume plotted against endocranial volume, regional surface area plotted against total neocortical surface area and regional subcortical volume plotted against regional volume were compared using independent t tests. Second, an analysis of variance (ANOVA) was employed comparing the mean residual values obtained from a linear regression of log cube root of total endocranial volume plotted against log skull basal length, and the following proportions: regional brain volume relative to total endocranial volume, regional neocortical surface area relative to total neocortical surface area and regional subcortical volume relative to regional volume. All statistical analyses were performed using the statistical software package PASW Statistics 18 (SPSS Inc., Chicago, Ill., USA).

Lastly, based on lion MRI analysis, the percentage difference between total endocranial and brain volume was calculated for each orientation plane (axial, sagittal, and coronal), and these measurements were averaged.

Results

Whole Endocasts

The virtual endocast and surface brain morphology is compared in the African lion and cougar in figure 2. Major morphological features are visible in both whole brain photographs and virtual endocasts. These include proreal gyrus, cruciate sulcus, ansate sulcus, lateral sulcus and suprasylvian sulcus (fig. 2, 5).

Virtual endocasts of both the African lions and cougars share similar external morphology, with all of the major sulci present in both species (fig. 2). Despite the similarities in overall sulcal pattern, morphological differences are notable between the species. The shape of the rostral brain including the pericruciate region and proreal gyrus appears larger both mediolaterally and rostrocaudally in the African lion compared to the cougar. This is most apparent by comparing the dorsal views of the

Fig. 4. **A** Low-power photomicrograph of a Nissl-stained coronal section through the posterior sigmoid gyrus (No. 630) of the African lion from the Comparative Mammalian Brain Collection (No. 62-79). The arrows show the location of cruciate sulcus (cs), coronal sulcus (co), presylvian sulcus (ps) and rhinal sulcus (rh). **B** Higher magnification photomicrograph showing the cytoarchitectonic features of the dorsal bank of cruciate sulcus, including primarily large layer V pyramidal cells (No. 622). Boxed area in **A** shows the relative location within the pericruciate cortex. **A** Scale bar = 1 cm. **B** Scale bar = 25 μ m.

Fig. 5. **A, B** Line drawings of a dorsolateral view of the virtual endocast representing the African lion (**A**) and cougar (**B**), showing the location and relative position of prominent sulci. ae = Anterior ectosylvian sulcus; an = ansate sulcus; co = coronal sulcus;

cs = cruciate sulcus; io = intraorbital sulcus; la = lateral sulcus; pc = post cruciate sulcus; pe = posterior ectosylvian; pl = postlateral sulcus; pr = prereal sulcus; ss = suprasylvian sulcus.

Table 1. African lion (female and male) and cougar (female and male) averages $\pm$ standard deviations on measures for skull basal length (SBL), endocranial volume (Endo), anterior cerebrum volume (AC), posterior cerebrum volume (PC), cerebellum plus brain stem (CB+BS), anterior cerebrum neocortex surface area (AC neo.ctx), posterior cerebrum neocortex surface area (PC neo.ctx), anterior subcortical volume (AC sub.ctx), and posterior cerebrum subcortical volume (PC sub.ctx)

Species	<i>P. leo</i>		<i>P. concolor</i>	
Sex	♀	♂	♀	♂
SBL, mm	251.81 $\pm$ 13.75	289.31 $\pm$ 23.90	148.67 $\pm$ 15.25	158.10 $\pm$ 6.53
Endo, mm ³	232,257.54 $\pm$ 10,538.41	252,464.38 $\pm$ 22,155.70	128,465.46 $\pm$ 11,015.45	133,359.40 $\pm$ 6,159.23
AC, mm ³	36,173.40 $\pm$ 5,924.53	26,511.25 $\pm$ 6,619.60	9,480.45 $\pm$ 2,077.50	10,727.17 $\pm$ 1,096.37
PC, mm ³	136,756.60 $\pm$ 15,101.13	165,082.30 $\pm$ 12,421.10	91,570.95 $\pm$ 7,405.97	92,372.98 $\pm$ 5,630.02
CB+BS, mm ³	46,767.36 $\pm$ 2,628.64	52,059.72 $\pm$ 5,298.10	23,692.99 $\pm$ 3,660.59	27,007.52 $\pm$ 1,586.12
AC neo.ctx, mm ²	5,068.30 $\pm$ 1,566.17	4,030.60 $\pm$ 1,328.99	998.98 $\pm$ 542.70	1,028.46 $\pm$ 309.25
PC neo.ctx, mm ²	17,060.52 $\pm$ 2,411.01	20,358.11 $\pm$ 1,531.65	10,733.44 $\pm$ 2,504.51	10,857.83 $\pm$ 822.05
AC sub.ctx, mm ³	24,347.02 $\pm$ 4,486.73	16,632.30 $\pm$ 5,832.82	6,230.71 $\pm$ 1,384.98	6,971.40 $\pm$ 706.95
PC sub.ctx, mm ³	98,152.31 $\pm$ 12,807.58	117,347.77 $\pm$ 13,443.04	69,384.45 $\pm$ 7,549.77	68,682.95 $\pm$ 4,174.90

endocast and whole brain in the two species. The anterior sigmoid gyrus and preoreal gyrus in the lion is clearly visible from this view but the same region is quite limited in the cougar (fig. 2, 3, 5). Additionally, the postcruciate sulcus is elongated in the African lion and extends parallel to the ansate sulcus, whereas in comparison the postcruciate sulcus is inconsistent in its length and extent varying both between individuals and between hemispheres in the same cougar. Finally, the extent to which the posterior cerebrum overlies the cerebellum differs in the two species. As seen from a dorsal view, the cerebellum is clearly visible in the cougar, but the posterior cerebrum largely overlies the cerebellum in the African lion (fig. 2).

MRI Data

Analysis of the MRI data of an African lion revealed the following percent differences between brain volume and total endocranial volume in each of 3 planes: axial – 5.60%; sagittal – 3.19%; coronal – 2.25%. On average, total endocranial volume was 3.65% greater than brain volume. An image of a sagittal section through the lion skull is shown in the online supplementary figure (www.karger.com/doi/10.1159/000338670).

Sex Differences

Endocranial volume and skull basal length are highly correlated in African lions and cougars (Pearson's $r = 0.59$, $p < 0.05$ and Pearson's $r = 0.67$, $p < 0.01$, respectively). In lions, total endocranial volume was on average 252,464 mm³ (SD 22,155) in males and 232,257 mm³

(SD 10,538) in females. In cougars, total endocranial volume was on average 133,359 mm³ (SD 6,159) in males and 128,465 mm³ (SD 11,015) in females. However, these sex differences in endocranial volume were not significant in either African lions ($t(12) = 2.05$, $p = 0.063$) or cougars ($t(12) = 1.03$, $p = 0.325$). Endocranial volume, skull basal length and regional brain volumes are presented in table 1. Residual analysis from separate linear regressions for each species of the influence of sex on endocranial volume as a function of skull basal length revealed no significant difference between the sexes in either the African lion or cougar ($t(12) = 0.40$, $p = 0.69$ and $t(12) = 0.080$, $p = 0.94$, respectively) (fig. 1). Additionally, an ANOVA comparing sex differences in endocranial volume relative to skull basal length revealed no significant differences in either African lions or cougars ($F(1,13) = 0.162$, $p = 0.69$ and $F(1,13) = 0.006$, $p = 0.94$, respectively).

Regional Brain Volume Differences

Sex differences in regional brain volumes were examined in two ways: proportional brain volume differences were analyzed using ANOVA and by using t tests on residual values obtained by regressing regional brain volumes as a function of total endocranial volume, regional neocortical surface area as a function of total neocortical surface area, and regional subcortical volumes as a function of regional volume. Analysis of the proportional regional brain volumes revealed significant differences between male and female African lions in AC ($F(1,13) = 16.39$, $p = 0.002$) and PC ($F(1,13) = 8.83$, $p = 0.012$), such

Fig. 6. A, B Proportional regional brain volumes: (AC, PC, and CB+BS, all relative to total endocranial volume, regional surface areas: AC and PC, all relative to total surface area dorsal to rhinal fissure, and regional subcortical volumes, AC and PC, all relative to regional total volume for African lion (**A**) males (solid bars) and females (open bars) and cougar (**B**) males (solid bars) and

females (open bars). Error bars indicate ± 1 SEM. AC volume and AC surface area are significantly larger in female than male African lions ($p = 0.002$ and $p = 0.008$, respectively). PC volume and PC surface area are significantly larger in male than female African lions ($p = 0.012$ and $p = 0.007$, respectively). * $p < 0.05$, ** $p < 0.01$.

that females have a greater amount of AC and males have a greater amount of PC (fig. 6). No significant difference was present for the relative amount of CB+BS ($F(1,13) = 0.35$, $p = 0.56$). In contrast, no significant differences in either AC or PC were found between female and male cougars ($F(1,13) = 0.90$, $p = 0.36$ and $F(1,13) = 3.75$, $p = 0.08$, respectively). However, CB+BS volumes significantly differed such that male cougars had a greater relative amount of CB+BS than female cougars ($F(1,13) = 8.85$, $p = 0.012$) (fig. 6).

Analysis of residuals of regional brain volumes as a function of total endocranial volume revealed results similar to those reported above. Significant differences between male and female African lions in AC ($t(12) = 2.94$, $p = 0.012$) and PC ($t(12) = 2.31$, $p = 0.03$) volumes were found, but the relative amount of CB+BS volumes did not significantly differ between the sexes ($t(12) = 0.81$, $p = 0.44$). In cougars, there were no significant differences in AC or PC relative volumes between females and males ($t(12) = 1.14$, $p = 0.28$ and $t(12) = 1.63$, $p = 0.13$, respectively). However, male cougars have significantly more relative CB+BS volume than female cougars ($t(12) = 2.47$, $p = 0.03$).

Surface Area and Subcortical Volume Differences

Analysis of regional neocortical surface areas as a proportion of total neocortical surface area revealed that female African lions have a greater amount of AC neocortical surface area compared to males, while males have a greater amount of neocortical surface area devoted to PC ($F(1,13) = 10.02$, $p = 0.008$ and $F(1,13) = 10.32$, $p = 0.007$, respectively) (fig. 6). No significant differences were detected in regional neocortical surface areas in male compared to female cougars.

Interestingly, no sex differences were present in either the African lions or cougars when comparing the regional AC subcortical volumes as relative to total regional AC volume ($F(1,13) = 2.40$, $p = 0.15$ and $F(1,13) = 0.096$, $p = 0.76$, respectively) (fig. 6). Similarly, no sex differences were present in either species when comparing the regional PC subcortical volume relative to total PC volume ($F(1,13) = 0.16$, $p = 0.70$ and $F(1,13) = 0.39$, $p = 0.56$, respectively). These findings suggest that the difference in regional volumes for AC and PC is not due to differences in subcortical volumes.

Additionally, independent t tests comparing residual differences between the sexes in regional neocortical sur-

face area as a function of total neocortical surface area and regional subcortical volumes as a function of total regional volume produced similar results to those reported above using ANOVA. Among lions, females possess greater AC neocortical surface area than that found in males, while males have a greater PC neocortical surface area than that found in females ($t(12) = 4.06$, $p = 0.002$ and $t(12) = 3.78$, $p = 0.003$, respectively). No significant differences were detected in regional surface areas in the cougars. Finally, comparison of the residual differences of AC subcortical volumes as a function of total AC volume ($t(12) = 0.26$, $p = 0.80$ and $t(12) = 0.08$, $p = 0.94$, respectively) or of PC subcortical volumes as a function of total PC volumes ($t(12) = 1.05$, $p = 0.31$ and $t(12) = 0.66$, $p = 0.52$, respectively) did not result in a sex difference among either lions or cougars.

Discussion

The present study utilized CT imaging techniques to create virtual 3-dimensional brain endocasts in two extant species from the family Felidae, the African lion and cougar. Previously, this nondestructive imaging technique has been shown to be useful in creating virtual endocasts in species where preservation of the brain is difficult or impossible, but skull specimens are readily available [Arsznov et al., 2010; Sakai et al., 2011a; Sakai et al., 2011b]. The virtual endocasts show the external morphology of the African lion and cougar brain (fig. 2). We found no sex difference in brain size relative to skull basal length in either African lions or cougars. No sex differences in the relative amounts of anterior cerebrum volume, anterior cerebrum surface area, or anterior subcortical volume were found in cougars where both males and females are primarily solitary. However, we found female African lions possess significantly greater anterior cerebrum volume, including anterior cerebrum surface area, than that found in male African lions. Interestingly, no sex difference was found in the relative amount of anterior cerebrum subcortical volume in lions. Collectively, these findings suggest that the observed sex differences may be due to differences in frontal cortex and thus may be concomitant with differences in the social life histories of African lions. These findings lend support to previous findings that differences in social behaviors may correlate to dimorphisms in the amount of neural tissue devoted to the mediation of social behaviors [Arsznov et al., 2010; Sakai et al., 2011a].

Endocranial Measurements

Virtual endocasts have previously been used to examine sex differences in overall and regional brain volumes in carnivores [Arsznov et al., 2010]. These analyses are greatly informative regarding both encephalization, the relative increase in brain size as a whole, and the 'principle of proper mass': the relative importance of a function to a species is related to the amount of neural tissue devoted to that function [Jerison, 1973]. However, in many mammalian species, encephalization is accompanied by an increase in the relative amount of neocortex, known as neocorticalization [Jerison, 2007]. Furthermore, in mammals, as brain size increases, the neocortex increases in surface area and displays a greater degree of neocortical gyrification, a marked increase in gyral and sulcal convolutions [Welker, 1990]. Although our methodology using CT analysis of skulls prevents detailed analysis of brain structures, we address the question of whether differences may be attributed to neocorticalization by including two additional measures: relative neocortical surface area and relative subcortical volume. Here, neocortical surface area was an indicator of neocorticalization based on surface area measures dorsal to the rhinal fissure, a landmark readily identifiable on the virtual endocasts. These measurements allow us to assess whether observed sex differences in the regional brain endocasts are differentially related to neocortex or subcortical structures.

As with any derived measures, these additional measurements are not without their caveats. First, sulci as seen on the virtual endocast do not extend to the full cortical depth as observed in whole brain specimens. Thus, it does not reflect the total neocortical folding that is present in a whole brain specimen. Nevertheless, this measure provides an approximation of neocortical surface area from a virtual endocast when a whole brain specimen is difficult to obtain. Finally, our measure of subcortical volume does not provide information regarding the volume of particular subcortical structures. Instead, it is an approximation of the cerebral hemispheric volume excluding the outer 3 mm dorsal to the rhinal fissure. Despite these drawbacks, these indirect estimates of neocortical surface area and subcortical volume provide important information in making intra- and interspecies brain comparisons using the CT endocast methodology.

Endocranial volumes obtained from our analyses of the CT data provide estimates of brain volume. Since endocranial volume includes meninges, vasculature, cerebrospinal fluid and cranial nerves as well as the brain, this volume overestimates total brain volume. Compari-

sons of endocranial and brain volumes in humans using CT have reported an average difference of 0.87% with increasing differences as a function of age [Ricard et al., 2010]. In an analysis of 82 bird species, brain mass and endocranial volume did not significantly differ [Iwaniuk and Nelson, 2002]. However, similar studies in carnivores are lacking. Here, MRI analysis revealed endocranial volume exceeds brain volume by 3.65% in a live African lion. While this difference is relatively small in view of the estimated brain shrinkage of 32–58% based on histological tissue section analysis [Stephan et al., 1981; Bush and Allman, 2004], this difference suggests caution in interpreting these volumes as brain measures. At the same time, we suggest that endocranial volume serves as useful and robust estimate of brain volume in comparative analyses.

Comparison of Endocranial Volumes in Males and Females

Cougars

The cougar is primarily solitary, with the exception of mating and periods of juvenile dependence as typical of members of Felidae [Kleiman and Eisenberg, 1973; Ewer, 1976; Sunquist and Sunquist, 2002]. The absence of major differences in the social behavioral repertoires of male and female cougars may suggest that the cognitive demands also do not differ between the sexes. Indeed, the present study found no sex difference in overall endocranial volume relative to skull length in cougars. Furthermore, no sex differences were present in relative anterior cerebrum volume, relative posterior cerebrum volume, relative anterior cerebrum surface area, relative posterior cerebrum surface area, relative anterior subcortical volume, or relative posterior subcortical volume. However, the relative cerebellum plus brain stem volume was significantly greater in male than female cougars. The cerebellum plays an important role in voluntary movement, gait, posture, and motor functions [Ghez and Fahn, 1985]. Cougars display incredible balance and agility, enabling them to effortlessly navigate a variety of difficult mountainous terrains [Busch, 1996]. Since the size of the cerebellum is typically conserved [Finlay and Darlington, 1995], our finding that male cougars possess a greater proportion of cerebellum plus brain stem even after controlling for skull basal length than female cougars is surprising. In primates, cerebellum size has been shown to vary independent of brain size, and species differences in relative cerebellum volume have been correlated with locomotion versatility [Rilling and Insel, 1998]. On average, an adult male cougar is 1.4 times larger in body mass than an adult female. The larger stature and more mus-

cular build of males might require a greater degree of motor coordination than females, particularly in negotiating challenging physical environments. Additionally, male cougars occupy territories up to three times that of females [Logan and Sweanor, 2001]. Thus, it might be that male cougars require greater motor coordination and agility due to difficult physical environments such as mountainous terrain while navigating a larger home range than their smaller female counterpart.

African Lions

Comparison of total endocranial volumes relative to skull basal length in female and male African lions also revealed no significant differences. These findings are similar to our previous ones in the spotted hyena (*Crocuta crocuta*); total endocranial volume relative to body size did not differ between the sexes [Arsznov et al., 2010]. In humans, males are reported to have a larger brain size compared with females [Rodrigues, 1991; Pakkenberg and Gundersen, 1997; Nopoulos et al., 2000; Allen et al., 2002; Leonard et al., 2008]. However, this sex difference in brain size is small when body size is controlled [Breedlove, 1994; Ellis et al., 2008]. At the same time, sex differences in human social cognitive skills have been linked to observed sexual dimorphisms in brain regions known to mediate social behavior. Females possess proportionately greater orbital frontal cortex [Gur et al., 2002] and ventral frontal cortex [Wood et al., 2008] than males. These results are equivocal since other studies conclude that the ratio of frontal lobe volume to total intracranial volume in humans does not differ between the sexes [Allen et al., 2002; DeCarli et al., 2005; Ellis et al., 2008].

Notably, the present study found that the relative volume and surface area of anterior cerebrum are significantly larger in female than male African lions. Moreover, there was no sex difference in the amount of relative anterior subcortical volume. Thus, our data suggest that frontal cortex may be significantly greater in female than male African lions. A potential explanation for this finding is that sexual differences exist in the neural processing associated with different underlying cognitive demands. This explanation supports the 'principle of proper mass': the amount of neural tissue devoted to a function is related to the relative importance of that function [Jerison, 1973]. Therefore, an expansion in a particular brain is indicative of greater behavioral capacity associated with that brain region. The frontal cortex is associated with the mediation of complex social behaviors in humans and other mammals [Adolphs,

2001; Amodio and Frith, 2006], and its relative enlargement may be related to an increase in the cognitive demands of social information processing that differ between the sexes.

Additionally, frontal cortex is related to the inhibition of inappropriate behavior in monkeys [Mishkin, 1964; Iversen and Mishkin, 1970; Fuster, 2002]. Moreover, in humans, impulsive aggression, as evidenced by acts of violence, is associated with reduced frontal lobe functioning [Bufkin and Luttrell, 2005]. Patients suffering damage to the ventral prefrontal cortex show inappropriate social responses and disinhibition in addition to other deficits [Adolphs, 2001]. It is intriguing to speculate that the frontal cortex in the African lion may play a role in the mediation of appropriate social behavior. Indeed, male African lions are not only dominant to females, but are also much more aggressive than females. During the inception of a coalition's reign, subadult males and those females that have not yet reached sexual maturity will disperse or be killed by the immigrant males [Hanby and Bygott, 1987]. In addition to aggression towards subadult males and females, male lions are highly aggressive and have been observed using lethal aggression towards adult females [Mosser and Packer, 2009]. Conversely, females are philopatric and are typically recruited into the maternal pride [Pusey and Packer, 1987]. Female lions achieve many benefits from group living; they are an interesting example of social structure in carnivores, in that they are egalitarian and lack a formal dominance hierarchy [Packer et al., 2001]. Female lions form symmetrical relationships and have a communal cub rearing system with multiple reproducing females [Packer et al., 2001]. This relationship provides protection for their young against attacks from outside males [Packer et al., 1990]. Thus, it seems plausible that the greater expanse of frontal cortex in female lions may be related to the mediation of appropriate social behaviors in the presence of a dominant male aggressor and not due to social information processing related to immigrating behaviors or navigation of a social hierarchy. While the precise roles of the frontal cortex in the mediation of African lion behavior are, of course, unknown, behavioral studies report previously learned inhibitory responses are disinhibited following lesions of the prefrontal cortex in dogs [Brutkowski and Davrowska, 1963; Brutkowski, 1965] and cats [Warren et al., 1969]. Thus, it is tempting to hypothesize that the larger anterior cerebrum volume and surface area found in female lions reflect their unique social conditions, and resulting need for greater inhibitory control, as they cope with selection

pressures imposed by the socially dominant and more aggressive males.

We found that the relative volume of the posterior cerebrum is significantly greater in male than female African lions. The posterior cerebrum volume was delineated in such a manner to include the cortex posterior to the cruciate sulcus and the underlying subcortical regions. However, we also found that the relative amount of posterior neocortical surface area is larger in male than female African lions, while there is no sex difference in the relative amount of posterior subcortical volume. These findings suggest that the observed sex difference in posterior cerebrum in African lions is due to greater posterior neocortex in males than females. Posterior cortex including the posterior parietal area has been implicated in visuospatial processing [Lomber et al., 1996]. It is intriguing to speculate that since male lions occupy and defend larger home range and territory than female lions [Pusey and Packer, 1987], visuospatial demands may be greater in males than female lions. At the same time, the larger posterior cortex may simply be a consequence of smaller frontal cortex found in males.

The African lion provides a unique model where the cognitive demands of life in the social pride appear to differ between the sexes. The sex difference in anterior cerebrum found in the African lion lends support to our previous finding in the spotted hyena [Arsznov et al., 2010]. The data suggests that sex differences in social cognitive demands, marked by the presence of a dominant aggressor, seem to be related to differences in brain morphology, specifically frontal cortex. Additionally, the absence of a sex difference in anterior cerebrum volumes in the cougar, where both males and females are solitary, suggests that this volume difference is related to the degree of sociality and not the sex of the animal. These data provide support for the comparative neurological principle that behavioral specializations, e.g. inhibitory control in the presence of a dominant aggressor, correspond to an expansion of the neural tissue mediating that function, e.g. frontal cortex. Whether other carnivore species in which sex differences in social behavior exist also possess similar sexual dimorphisms in brain morphology awaits further study.

Appendix 1

Field Museum (FMNH); Michigan State University Museum (MSUM); University of Michigan Museum of Zoology (UMMZ)

Location	Catalog No.	Genus and species	Sex	Scanner
MSUM	14954	<i>Panthera leo</i>	female	16
MSUM	8046	<i>Panthera leo</i>	female	16
MSUM	36073	<i>Panthera leo</i>	female	4
FMNH	20756	<i>Panthera leo</i>	female	16
FMNH	20758	<i>Panthera leo</i>	female	16
UMMZ	114803	<i>Panthera leo</i>	female	16
MSUM	24411	<i>Panthera leo</i>	male	16
MSUM	11241	<i>Panthera leo</i>	male	16
MSUM	11242	<i>Panthera leo</i>	male	16
MSUM	11675	<i>Panthera leo</i>	male	16
MSUM	3949	<i>Panthera leo</i>	male	16
MSUM	29988	<i>Panthera leo</i>	male	16
FMNH	20762	<i>Panthera leo</i>	male	16
MSUM	21884	<i>Panthera leo</i>	male	16
MSUM	10658	<i>Puma concolor</i>	female	4
MSUM	3810	<i>Puma concolor</i>	female	16
MSUM	3811	<i>Puma concolor</i>	female	16
MSUM	6321	<i>Puma concolor</i>	female	16
MSUM	6322	<i>Puma concolor</i>	female	16
MSUM	6325	<i>Puma concolor</i>	female	16
MSUM	12387	<i>Puma concolor</i>	female	16
MSUM	10659	<i>Puma concolor</i>	male	16
MSUM	12240	<i>Puma concolor</i>	male	16
MSUM	13071	<i>Puma concolor</i>	male	16
MSUM	14361	<i>Puma concolor</i>	male	16
MSUM	14363	<i>Puma concolor</i>	male	16
MSUM	14365	<i>Puma concolor</i>	male	16
MSUM	35996	<i>Puma concolor</i>	male	16

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