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# Brain and Body Size Relations among Spotted Hyenas (*Crocuta crocuta*)

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#### Keywords

Brain size  $\cdot$  Body size  $\cdot$  Spotted hyena  $\cdot$  Linear regression  $\cdot$  Negative slope

#### Abstract

The relationship between brain size and body size across species "from mouse to elephant" is described by a function of positive slope. Almost uniformly, the relationship between brain size and body size within a species has a positive slope, though this is less steep than across species. The spotted hyena, Crocuta crocuta, differs from most other mammals in a number of ways including the fact that, on average, adult females weigh more than adult males and occasionally display greater body lengths. Brains of 5 female and 4 male hyenas were weighed in the field near Moyale in Northern Kenya, and body weights and body lengths were obtained from the same animals. When our analyses of brain/ body relationships in these animals revealed an unanticipated negative relationship between brain size and body length, we extended our measurements to include intracranial volume in 19 skulls (8 females and 11 males) from the collection at the Museum of Vertebrate Zoology, University of California Berkeley; body weights and lengths were also available. A third dataset was formed by measuring intracranial volumes in 60 spotted hyena skulls (27 females and 33 males) in the Natural History Museum, London, UK; body lengths and intracranial volumes were available. Brain/body

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E-Mail karger@karger.com www.karger.com/bbe size slopes, in general, were not significantly different from zero except in 3 cases: brain weight/body length for Moyale males alone and males and females together, and cranial volume/body weight for Museum of Vertebrate Zoology males and females together. Although most of the slopes were not significantly different from zero, they were all negative, and a statistical test which combined probabilities from the 3 datasets supports the conclusion that there is a negative relationship between brain size and body size in spotted hyenas. Possible explanations for the negative slopes are discussed, including costs and benefits of large brains and large bodies and physiological mechanisms.

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#### Introduction

Whoever was the first to say that there's an exception to every rule must have had spotted hyenas in mind. They are the only extant female mammals that, lacking an external vagina, urinate, mate, and ultimately give birth through the tip of a hypertrophied penile clitoris [Matthews, 1939; Neaves et al., 1980; Frank et al., 1990; Frank and Glickman, 1994; Frank, 1997]. Females are also slightly larger than males [Matthews, 1939; Hamilton et al., 1986] and, within the multi-male, multi-female clans that characterize these carnivores, adult females (and their juvenile offspring) dominate adult males, who join

Michael D. Mann, PhD 519 rue Helene-Baillargeon Montreal, QC H2J4E8 (Canada) E-Mail mmann@unmc.edu the clan as immigrants [Kruuk, 1972; Frank, 1986b; Hole-kamp and Smale, 1991].

The relationship between brain size and body weight has been studied in a broad array of mammalian species [Jerison, 1973; Martin, 1981; Gittleman, 1986; Deacon, 1990b]. It is typically described by the standard equation:

 $Y = kX^a$ 

where Y = brain weight, X = body weight, k is a proportionality constant (the y intercept), and "a" is an exponential constant reflecting the slope of the line depicting brain/body allometry in the traditional log/log plot. In general, the slope is positive and relatively steep when the data points are drawn from taxonomically divergent groups, and shallow (but still positive) when within-species variation is portraved [Gould, 1975]. Martin and Harvey [1985] argued that the shallow intraspecific slopes, associated with exponents of 0.2-0.4, are often an artifact of including immature animals in the sample, and that, among truly adult animals, the brain/body relationship would be essentially flat. However, even in their analysis, the existence of a positive slope is acknowledged for some species, and there is no obvious explanation that would account for a negative slope when brain size is plotted against body size.

"Explanations" of the relationship between brain size and body size in mammals have diverged. Jerison [1973] divided mammalian brains into 2 components: a basic representation of the body surface, and another component containing "extra" neurons, which reflected information processing capacity. Other researchers have employed multivariate procedures to detect lifestyle correlates of brain/body relationships with diet [Mace et al., 1980; Gittleman, 1986], complexity of social systems [Harvey et al., 1986; Dunbar 2003; Holekamp et al., 2007], and/or maternal investment [Gittleman, 1994] as predictors of brain size for a given body size. Armstrong [1983] argued that mammalian brain size is limited by metabolic needs, noting that neural tissue is particularly "expensive" in metabolic terms. Deacon [1990a] presented a detailed outline of how adult brain and body sizes might be regulated by trajectories of prenatal and postnatal growth. The relative importance of each may vary across species.

We were particularly interested in the quantitative intraspecific slopes that characterized brain/body relationships in male and female spotted hyenas drawn from several different African ecosystems. Although the 2 sexes share a hunting and scavenging mode of food acquisition, their lifestyle diverges in other respects. For example, females remain in the clan of their birth, and (on average) have a smaller lifetime range than males, who disperse at puberty and wander until they locate a new clan [Frank, 1986a]. In addition, although female hyenas have priority of access to food at a kill, they also have exceptional energy burdens, resulting from a prolonged pregnancy (compared with other hyaenids), and an even longer period of lactation, typically nursing 1–2 offspring for a year or more [Holekamp and Smale, 1990]. Adult immigrant males must deal with groups of dominant females and their offspring, but they only need food for themselves, and their bodies are smaller than those of the adult females. It thus seems possible that the differing demands placed by the divergent lifestyles would result in different relationships between brain weight and body size for the 2 sexes.

With regard to the ecological correlates of brain size, it might be anticipated that spotted hyenas would have large brains relative to body size, as carnivores eating a high-calorie diet and living in complex social groups. Sakai et al. [2011], in a study that compared brain size relative to body size in all 4 species in Hyaenidae, reported that spotted hyenas have the largest brain volume relative to body size. We were consequently surprised by their relatively low encephalization in the published literature [Gittleman, 1986], and we thought that this issue should be explored more fully.

Male mammals often have larger brains than female mammals, but they also have larger bodies, and comparisons typically involve the use of an allometric equation that predicts an anticipated brain weight for a given body weight [Gould, 1975]. A set of brains from adult female and male spotted hyenas, with data on associated body weights and lengths, offered us the opportunity to reexamine sexual dimorphism in brain/body relationships in a species in which adult females are generally larger than adult males. Arzsnov et al. [2010] have already failed to demonstrate a sexual dimorphism in spotted hyenas, but we had the data, so we looked at sexual dimorphism.

## **Materials and Methods**

## Brain Weight, Cranial Volume, and Body Size

The focal data for this study were derived from 3 separate collections of brains or skulls. First, brains were acquired from 5 female and 4 male hyenas in northern Kenya, animals that had been shot during a Kenya Wildlife Service operation to reduce numbers in the town of Moyale. The brains were removed and weighed in the field (brain weight, E), and preserved in 10% formalin. Standard body measurements were made in the field, shortly after the animals had been shot. These included body weight (P) and headbody length (L), from the tip of the nose to the base of the tail. One

of the females was a juvenile that weighed 35 kg, had a body length of 107 cm, and a brain weighing 161 g; this animal was excluded from our analysis of adult brains.

Photographs of each brain were taken in the field, portraying them as standard dorsal, ventral, and lateral views (Fig. 1). A ruler was included in each photograph, facilitating later measurement. Unfortunately, the actual brains were cut into blocks in the field for studies of sexual dimorphism in the hyena hypothalamus [Fenstemaker et al., 1999]. Consequently, studies of regional allometry, based on histological sections, were rendered impossible. Data presented in this paper are limited to a description of the measurements of the dorsal and lateral surfaces of the cerebral hemispheres as well as the brainstem width (BSW) and pyramidal tract width (PTW) taken from photographs.

Our investigation of brain/body relationships in spotted hyenas was then extended by measuring the cranial volume of spotted hyena skulls maintained in 2 museum collections. Nineteen skulls, with body weights and body lengths, were available in the Museum of Vertebrate Zoology (MVZ), University of California (UC) Berkeley, originally collected by L.G.F. (and colleagues) at 2 different sites in Kenya, southern Narok County, and northern Turkana County, mostly from animals collected for epidemiological research. Cranial volume (C) was measured at UC Berkeley, by filling the cranium with 6-mm glass beads. Each cranium was measured 3 or 4 times, and the largest volume was taken as descriptive. Body weights and head-body lengths had been recorded for each carcass in the field.

Cranial volumes of an additional 60 skulls were measured in the L. Harrison Matthews collection at the British Museum of Natural History, London (BMNH), UK. These animals had originally been shot or poisoned by Matthews and his associates in northern Tanzania in the 1930s while gathering materials for his classic monograph on the urogenital anatomy of the spotted hyena [Matthews, 1939], for which he made measurements of body length, but not weight.

#### Neonatal/Fetal Material from the UC Berkeley Colony

A research colony of spotted hyenas at UC Berkeley provided a series of fetuses in which brain and body weights were recorded. Stillbirths are common at a female's first parturition, as the urogenital meatus of the mother's clitoris must tear to permit exit of the fetus [Frank et al., 1990, 1995]. This can be a time-consuming process in primiparous females, and, as the placenta has detached from the uterus earlier, the fetuses frequently die of anoxia if birth does not proceed quickly. Stillbirths resulted in brain and body weights being available for 3 male and 3 female infants that had been carried to term (as judged by tooth eruption and open eyes) but died during prolonged delivery. Brain and body weights were also available for 4 spotted hyena litters delivered by cesarian section at varying stages of fetal life, performed as part of the research into the embryology of sexual differentiation [e.g., Licht et al., 1992, 1998; Cunha et al., 2003].

#### Statistical Analyses

Standard statistical descriptions were made of all data derived from adult subjects. These included mean and median values, standard deviations, standard errors, and coefficients of variation. Correlation and linear (least-squares) regression analyses were performed on pairs of variables, and 95% confidence intervals (CIs) and the probability that the slope was zero were calculated.



**Fig. 1.** Photos of dorsal (**a**), ventral (**b**), and lateral (**c**) views of a male hyena brain illustrating how measurements of cortical length (L), width (W), height (H), pyramidal tract width (PTW), and brainstem width (BSW) were measured. Scale bar (**b**) is calibrated to represent 10 mm in each photo.

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**Fig. 2.** Statistical description of the Moyale sample. Box and whisker plots for body weight, brain weight, and body length (+ indicates mean). Using a *t* test, the probability that females and males are different are body weight p < 0.013 (significant), brain weight p < 0.47, and body length p < 0.24.

Student's *t* test was used to clarify the observed differences between pairs of variables. All probabilities were rounded to 2 decimal places, except when p < 0.10. In such cases, the probability was rounded to 3 places (a few cases yielded p < 0.0001). The pattern of p values among the pairs of variables and the pattern of similarity across different samples, carry more weight than whether a particular threshold has been crossed.

Meta-analyses of datasets from Moyale, the MVZ, and the BMNH, were conducted using the method for combining probabilities described by Rosenthal [1984; p. 94]. The method is applicable to small sets of studies essentially testing the same directional hypothesis. The formula suggested by Rosenthal is:

 $p_{\text{combined}} = (\text{sum individual } p \text{ values})^N / N!$ 

where the "sum individual *p* values" must be near unity or less, a requirement met in each application here. *N* is the number of studies being combined, and *N*! is the factorial.

Data sets are graphically summarized as box-and-whisker plots which show the minimum, first quartile, median, third quartile, and maximum of a set. The upper bound of the box is the third quartile, the lower is the first quartile, and the line through the box is the median; the top of the upper whisker is the maximum value, and the bottom of the lower whisker is the minimum value. The "+" within the box is the mean value.

## Results

## Moyale Sample

Sex Differences in Brains and Bodies

A box plot summary of the data for each sex is shown in Figure 2. Females were, on average, 29% heavier and 3% longer than males, but their brains were 7% lighter. As a result, female brains comprised only 0.29% of their body weight whereas male brains comprised 0.40% of their body weight. However, only the sex difference in body weight achieved statistical significance (p < 0.013) [Hamilton et al., 1986].

Brain Weight, Body Weight, and Body Length

The scatter plots of Figure 3 suggest that the sexes could be treated as a continuous distribution, thus increasing the sample size. Table 1 records the unexpected finding of this study: brain weight varied inversely with body weight and length. Correlation values for each sex were modest, except for the male brain weight/body length value and the female body weight/body length value, which were high. When treated as a single population, the correlation values increased and the p values decreased (or, in the case of E/L, remained unchanged) as the range was extended and the number of subjects increased. The scatter of residuals around the regression lines showed the descriptions to be adequate. The 95% CIs for these slopes were: -0.73 to -1.32 for body weight and -0.28 to -0.43 for body length. Hence, it is unlikely that these samples came from a population in which brain size was independent of body size or brain size varied positively with body size.

# UC Berkeley MVZ Sample

Fully intact skulls and complete field data were available for 8 specimens from Narok County and 11 from Turkana County. The slopes for cranial volume on body weight and body length were negative for both samples, so they were combined.



**Fig. 3.** Scatter plots of body weight against brain weight (**a**) and body length against brain weight (**b**) for the Moyale sample of hyena materials (summarized in Tables 1 and 2). Open squares, males; filled squares, females. The regression lines for combined males and females have slopes of a = -1.02 (**a**) and a = -1.54 (**b**). The slope in **b** is significantly different from zero by the usual criteria (p < 0.023).

**Table 1.** Relations between pairs of variables for the Moyale sample: correlation (r), slope of linear regression (a), and probability (p) that the slope was zero for brain weight on body weight (E/P), brain weight on body length (E/L), and body weight on body length (P/L)

Variable	Females $(n = 5)$		Males (	Males $(n = 4)$			Both $(n = 9)$		
	r	а	р	r	а	Р	r	а	P
E/P	-0.58	-1.18	< 0.30	-0.53	-1.44	< 0.47	-0.65	-1.02	< 0.057
E/L	-0.42	-0.91	< 0.49	-0.98	-1.74	< 0.019*	-0.74	-1.54	< 0.023*
P/L	0.92	1.00	<0.026*	0.37	0.24	< 0.63	0.60	0.80	< 0.085

\* Significant using the usual criteria.

## Sex Differences in Brains and Bodies

A box plot summary of the data is shown in Figure 4. Females had 11% heavier and slightly longer (3%) bodies than males, but 9% smaller cranial volumes, as in the Moyale sample. In this case, cranial volumes in males were significantly larger than in females. It should be noted that Arsznov et al. [2010] failed to find a significant difference in the size of male and female brains as measured from CT scans, an alternative measure of cranial volume. The scatter plots and regression lines in Figure 5 show that the variation in brain size was similar to the Moyale sample, and that the female and male values overlapped.

Brain Size, Body Weight, and Body Length

Table 2 shows that the overall relations were not as strong as in the Moyale sample, although the pattern of

relations was the same. Within the MVZ sample, the average Turkana female was 107% the weight and 106% the length of the average Narok female, but her cranial volume was only 96.6% that of the average Narok female, thus reinforcing the overall negative relationship (despite the fact that they were from geographically distinct populations). The corresponding values for Turkana males were 105% (weight), 101% (length), and 100% (cranial volume) that of the Narok males.

## *BMNH Sample (L.H. Matthews Collection)* Sex Differences in Brains and Bodies

As noted above, no data on body weights are available for this sample. The box plot of Figure 6 shows that females were significantly longer (2%) than males, but had slightly smaller (1%) cranial volumes, thus presenting the same pattern of relations found in both the Moyale and



**Fig. 4.** Statistical description of the MVZ sample. Box and whisker plots for body weight, cranial volume, and body length (+ indicates mean). Using a *t* test, the probability that females and males are different are body weight  $p < 0.036^*$ , cranial volume  $p < 0.008^*$ , and body length p < 0.34 (asterisks denote significance).



**Fig. 5.** Scatter plots of body weight against cranial volume (**a**) and body length against cranial volume (**b**) for the MVZ sample of hyena materials (summarized in Tables 3 and 4). Open squares, males; filled squares, females. The regression lines for combined males and females have slopes of a = -0.94 (**a**) and a = -0.52 (**b**). The slope in **a** is significantly different from zero by the usual criteria.

<b>Table 2.</b> Relations between pairs of variables for the MVZ sample: correlation $(r)$ , slope of linear regression	. (a),
and probability $(p)$ that the slope was zero for cranial volume on body weight $(C/P)$ , cranial volume on b	ody
length $(C/L)$ , and body weight on body length $(P/L)$	

Variable	Females $(n = 8)$			Males $(n = 11)$			Both ( <i>n</i> = 19)		
	r	а	P	r	а	р	r	а	P
C/P	-0.54	-1.01	<0.16	-0.08	-0.10	< 0.81	-0.55	-0.94	< 0.016*
C/L	-0.39	-0.66	< 0.35	-0.30	-0.21	< 0.37	-0.38	-0.52	< 0.11
P/L	0.36	0.40	< 0.37	0.43	0.74	< 0.19	0.45	0.35	< 0.056

\* Significant using the usual criteria.



**Fig. 6.** Statistical description of the BMNH sample. Box and whisker plots for cranial volume and body length (+ indicates mean). Using a *t* test, the probability that females and males are different are cranial volume p < 0.42 and body length p < 0.028 (significant).

**Table 3.** Relation between cranial volume and body length (C/L) for the BMNH sample: correlation (r), slope of linear regression (a), and probability (p) that the slope was zero

Variable	Females $(n = 27)$			Males ( <i>n</i> = 33)			Both sexes $(n = 60)$		
	r	а	p	r	а	р	r	а	р
C/L	0.05	0.10	<0.82	-0.31	-0.67	<0.80	-0.18	-0.40	<0.15

MVZ samples, albeit weakly and without achieving statistical significance. This may have resulted from combining animals from many different clans (social groups of related females, their cubs, and unrelated adult males), amplifying the situation in our MVZ sample from the Mara and Turkana.

## Brain Size and Body Length

The relations between cranial volume and body length for the total sample of 60 specimens are presented in Table 3. The negative correlations/slopes, observed when the entire sample was analyzed, yielded a pattern similar to that observed in the overall MVZ sample (line C/L, combined sexes in Table 2), but less robust than in the Moyale sample (Table 1). In addition, the only instance of a positive relation between brain size and body size, i.e., length, appeared in this dataset. The cranial volumes and body lengths of female hyenas drawn from the BMNH collection displayed a low positive correlation and a shallow positive slope. Both indices are far from achieving statistical significance.

#### Brain Size/Body Size Correlations: Meta-Analyses

Rosenthal [1984; p. 94] provided a method for combining probabilities, when similar measurements are tak-

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en on samples derived from different populations. Overall, this analysis offers statistical support for the general pattern of results described above. The results, from combining the probabilities for data from each of the 3 samples are: in terms of absolute sex differences, adult male spotted hyenas had significantly larger brains (p < 0.05), housed in significantly smaller bodies (p < 0.001), than adult female hyenas. In addition, when brain weights (or cranial volumes) of male and female hyenas were plotted against body weights (or body lengths), a statistically significant (p < 0.003 for weight; p < 0.004 for length) negative slope emerged. Although the trends were generally similar, statistical significance was not found for males and females considered separately.

## Some Regional Allometry

As noted above, the brains obtained in Moyale were blocked and dispersed before volumetric analyses of telencephalic structures in the cerebral hemispheres could be undertaken. However, limited measurements of external features were obtained from photographs taken in the field in Kenya (Tables 4, 5, summary). In particular, we focused on 3 measures: (a) PTW, (b) BSW, and (c) an omnibus index of the neocortical surface area calculated by adding the measures of cortical length, width, and

**Table 4.** Correlation value (r) and probability (p) for brainstem width and pyramidal tract width as functions (f) of body weight and brain weight

	BSW	PTW	
$V = f(\mathbf{P})$	r = 0.90 p < 0.002*	r = 0.94 p < 0.0002*	
V = f(E)	r = -0.43 p < 0.29	r = -0.69 $p < 0.038^*$	

BSW, brainstem width; PTW, pyramidal tract width; **P**, body weight; **E**, brain weight. \* Significant by the usual criteria.

**Table 6.** Prenatal body weight  $(\mathbf{P})$  and brain weight  $(\mathbf{E})$  data for females and males according to gestational age

Females			Males		
age	<b>P</b> , g	E, g	age	<b>P</b> , g	E, g
45 days	11.67	0.747	45 days	12.54	_
45 days	12.31	0.830	65 days	137.9	4.44
65 days	134.3	3.96	95 days	1,122.6	29.5
95 days	1,124.5	31.0	_ ,	_	_
110 days	1,540.0	52.2	-	-	-

height (Br L + W + H). The anterior-posterior length of the cerebral cortex was measured from a dorsal view of each brain, as the greatest length parallel to the mid-sagittal sulcus. Cerebral cortex width was measured at the point of greatest width across both hemispheres from a dorsal view. The point of measurement occurred at  $0.64 \pm 0.026$  of the way from the anterior pole to the posterior pole, and the line of measurement was perpendicular to the midline. Cortical height was measured on a lateral view of each brain, along a line starting at the anterior margin of the pons and running approximately parallel to the posterior end of the lateral fissure. Positions of the measurements are illustrated in Figure 1. Landmarks of the brain surface in hyenas have been described by Arsznov et al. [2010].

Reference to the plots of PTW and body weight (Fig. 7a), and BSW and body weight (Fig. 7b), reveals very strong and highly significant positive correlations. However, when we plot our index of cortical surface area and body weight (Fig. 7c), the graph returns to the more familiar hyena pattern, i.e., a modest negative correlation that fails to achieve statistical significance.

**Table 5.** Relations between sex, neocortical volume, brainstem width, and index of cortical surface, and probability that the males and females were drawn from the same population

Sex	Br L + W + H	BSW	Br L + W + H/BSW
Female Male	203.54 215.2	25.32 25.2	8.04 8.41
	<i>p</i> < 0.047*	<i>p</i> < 0.86	<i>p</i> < 0.37

Br L + W + H, neocortical volume; BSW, brainstem width; Br L + W + H/BSW, index of cortical surface. \* Significant by the usual criteria.

An Index of "Encephalization"

Passingham [1975] used the ratio of neocortical-tomedullary volume as an index of encephalization. The rationale involved the assumption that medullary volume constituted a reasonable measure of neural tissue devoted to essential vegetative functions and that a larger ratio of neocortical-to-medullary volume could function as an index of encephalization. We calculated an analogous index by dividing the neocortical surface measures (Br L + W + H) for each subject by the BSW for that subject (Table 5). Females had the same BSW as males (p < 0.86), whereas males had a significantly larger index of neocortical surface area (p < 0.047). Consequently, it is not surprising that males were more "encephalized" than females, in terms of the ratio of cortex-to-BSW, although this was not significant (p < 0.37).

## Fetal/Neonatal Brain and Body Weights

Table 6 contains available data on brain and body growth in our small sample of male and female spotted hyena fetuses obtained during cesarian sections. They included mixed-sex litters of twins (at days 65 and 95 of a 110-day gestation), as well as mixed-sex triplets at 45 days of gestation. Although the sample sizes are very small, the results provide some sense of the typically rapid fetal growth rate, and suggest that there are no obvious sex differences in absolute brain/body weights or growth trajectories during gestation. This result was reinforced (regarding body weight) by examining 4 male and 4 female neonatal hyenas (Table 7) born into mixed-sex litters, with weights collected within 2 days after birth. The mean body weights were 1,510 g for females and 1,570 g for males; the probability that they were drawn from the same population is p = 0.47. Brains were also collected from a set of 3 male and 3 female full-term stillborn hy-

**Table 7.** Postnatal body weight  $(\mathbf{P})$  and brain weight  $(\mathbf{E})$  data for females and males

Females		Males		
<b>P</b> , g	E, g	<b>P</b> , g	E, g	
1,460	52.2	1,540	48.4	
1,380	46.1	1,500	53.25	
1,680	45.7	1,700	41.5	
1,520	_	1,540	-	

enas on the day of birth. There was no obvious indication of a significant sex difference in brain weight between males and females.

#### Discussion

In sexually dimorphic mammalian species, the sex with the larger body typically has a larger brain. However, female spotted hyenas have smaller brains than male spotted hyenas, despite having bodies that are (on average) longer and heavier. We observed similar trends in 3 separate samples derived from different populations in Kenya and northern Tanzania, significant when probabilities from the 3 samples were combined. Our measures of regional allometry, necessarily limited to the Moyale sample, revealed that linear measurements of the hyena cerebral cortex are also negatively correlated with body size, although the BSW of the hyena shows a strong positive relationship with body size.

Arsznov et al. [2010] computed brain volume (i.e., total endocast volume) from 3-dimensional CT endocasts made from 23 female and 21 male adult spotted hyenas, members of a single clan from the Talek region of the Masai Mara National Reserve in Kenya. Although they concluded that "overall brain volume did not differ between the sexes" (p = 0.184), their measurements were based on individual skull volumes adjusted for individual skull length. The actual body sizes were not presented. Instead, they used skull length as a "proxy" for body size, and all the values presented in their article are adjusted accordingly. However, "skull length" is not equivalent to the individual body weight values that have dominated the allometric literature [e.g., Jerison, 1973]. Nevertheless, it is noteworthy that, although not significantly so, males did have larger endocast volumes. Males had significantly larger anterior cerebrum volumes than females did [Sakai et al., 2011]. These re-

**Fig. 7.** Scatter plots of body weight against pyramidal tract width (PTW) (**a**), body weight against brainstem width (BSW) (**b**), and body weight against an index of cortical surface for the Moyale sample of hyena materials. Circles, males; squares, females. The regression lines for combined males and females have slopes of a = +0.039 (**a**), a = +0.048 (**b**), and a = -0.051 (**c**). The slopes in **a** and **b** are significantly different from zero by the usual criteria; the slope in **c** is not.

sults are in line with the often slightly larger brains as described here. Perhaps the different measures used, i.e., intracranial volume and skull basal volume instead of brain weight and body weight, explain the different results.

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<sup>6.8</sup> 6.6 6.4 шш 6.2 6.0 PTW, I 5.8 5.6 С 0 5.4 52 50 70 40 60 80 Body weight, kg а 26.5 26.0 0 3SW, mm 25.5 П 25.0 C 24 5 50 60 70 80 40 b Body weight, kg 230 Index of cortial surface, mm 0 220 0 210 200 n 190 50 70 40 60 80 С Body weight, kg

The kind of explanation that is required to account for our data depends on whether there is a significant sex difference in the magnitude of negative slope when brain size is plotted against body size. If there is no difference in slope, i.e., if females and males are drawn from a common population, differing only in body size, then any explanation would focus on the overall negative correlation. No special explanatory mechanisms concerning sex differences in physiology/lifestyle would need to be invoked. Such proved to be the case in a prior report by Towe and Mann [1995], who studied habitat-related variations in brain and body size in pocket gophers. The male gophers had larger brains and larger bodies than female gophers, and the gophers living in an energy-rich habitat had even larger brains and larger bodies than those living in a habitat that was less provident. But a single allometric relationship accounted for all the data. Differences in brain size, correlated with sex or caloric intake, could be accounted for by assuming that increments in brain size reflected the minimum additional brain required "... to operate a body of increased size, with no change of lifestyle" [Towe and Mann, 1995, p. 195].

Although the power of our statistical tests is not as robust as one might wish, there were no significant sex differences in slope for the relationship between brain size and body weight or brain size and body length. In the 2 samples where brain weight or cranial volume could be plotted against body weight, there were negative correlations or slopes for both sexes (although the actual slope was negligible in the MVZ males). In the 3 populations where slopes could be plotted for brain size against body length, correlations or slopes were negative in all the male samples and in 2/3 of the female samples. The only failure to find a "hint" of a negative relationship was in the BMNH female sample.

When analysis failed to show significance when the 2 sexes were treated separately, significance was often found when the sexes were treated together. Presumably this is because of the resulting increase in sample size. Some of the negative slopes were significantly different from zero and some were not, but they were all negative. It seems that this consistency of negative slopes is more important and more convincing than the few failures to reach significance.

Negative relationships between brain size and body size have sporadically appeared in the allometric literature. For example, Holloway [1980] described a negative correlation between brain size and body size in female but not male gorillas. Mann et al. [1988] found a negative brain/body correlation in *Microtus montanus* (r = -0.54),

but it represented an overall relationship for males and females. Review of these data indicates that the coefficient for females was r = -0.69 (p < 0.006) but r = +0.01 (p > 0.10) for males. Martin and Harvey [1985] provide several additional examples of negative correlation coefficients in primate brain/body allometry, using data from Holloway [1980]. However, the occurrence of the odd, unreplicated, negative correlation coefficient in large surveys of brain/body allometry did not inspire a search for explanatory mechanisms.

Our data, however, do beg for understanding. Given the essential similarity between female and male patterns, we might begin by searching for a common explanation, which could account for the inverse relationship between brain size and body size in both sexes of spotted hyenas.

## Costs and Benefits of a Large Brain

In general, it has been assumed that animals with larger brains, relative to body size, would be more intelligent, i.e., more flexible in their capacity to interact with the environment and possessing problem-solving abilities [Benson-Amram et al. 2016]. There are many reasons to view this assumption with suspicion. Species differences in regional allometry of cerebral structures, in the details of synaptic pathways and allocation of neurotransmitters, would result in brains of similar size having very different information-processing characteristics. Moreover, although "information-processing capacity" and "flexibility" are reasonable orienting terms, the behavior patterns regulated by the nervous system are highly differentiated. Intelligence, in any of its guises, is surely not a unitary concept that translates easily across species.

On the other hand, it is also important not to discard the baby with the bathwater. Several decades ago, Passingham [1975] calculated the ratio of neocortical-tomedullary volume for a variety of primate species (n<sup>3</sup>/m<sup>3</sup>; with the latter indexed by the area of the foramen magnum). His work began with the assumption that such a ratio fulfilled the need for an index relating the size of the brain to its inputs and outputs. Using data reviewed by Hodos [1970] and Kintz et al. [1969], he found that the ratio of neocortical-to-medullary volume predicted performance of learning sets in 9 species of primates (including humans). He also found that this index predicted exploration of novel objects in 10 different primate species, as studied in an array of animals housed in zoos [Glickman and Sroges, 1966].

Glickman and Sroges [1966], after examining reactions to novel objects in >100 mammalian species, concluded that the best predictor of persistent exploratory behavior was a varied diet or one that required complex dexterous motor sequences for capturing prey (i.e., carnivores). In the 1980s, a new set of studies appeared, linking large relative brain size with varied, nutrition-rich diets [Mace et al., 1980; Towe and Mann, 1995]. Several more recent publications have offered strong support for linking encephalization, or relative brain size, with "innovation" in primates [Reader and Laland, 2002; Marino, 2005; Sol et al. 2008].

Armstrong [1983], Aiello and Wheeler [1995], Martin [1996], and Isler and van Shaik [2009] have argued that the metabolic costs of neural tissue are a potentially limiting factor, restraining the growth of the brain. They noted that neural tissue is exceptionally expensive in metabolic terms, and suggested that brain size ultimately represents an energetic compromise with the different systems of the body competing for limited energetic resources. This argument is compatible with the fact that folivorous rodents, locked into low-quality diets, tend to have smaller brains (relative to body size) than rodents subsisting on diets providing calorie-dense diets [Mace et al., 1980; Mann et al., 1988; Towe and Mann, 1995]. Similar arguments have been made for primates [e.g., Milton, 1993]. Isler and van Shaik [2009]: "... the energetic cost of a large brain must be met by reduced energy allocation to another expensive function such as digestion, locomotion, or production (growth or reproduction)". Aiello and Wheeler [1995] argued that as primate (especially human) brains have increased in size, there has not been a corresponding increase in basal metabolic rate. This is curious for a tissue that has such high energy demands. They noted that the size of the gut (also with high energy demands) has decreased because of the adoption of a diet of more easily digested, higher-energy foods. The reduction of gut size has "allowed" the brain size to increase, for whatever reason. A similar argument could explain why female hyenas have bigger bodies but smaller brains than males. Females "should" have bigger brains than males because they have bigger bodies, but they are involved in extended lactation, another activity with a high energy requirement. In other words, the females have given up the amount of extra brain they would have had on account of having a bigger body because lactation would not allow them to support this. Males, of course, do not have this particular constraint. Presumably, hyenas cannot gain any basal metabolic rate by changing diet because they already have a highenergy diet. This argument is based on the assumption that there is a positive relation between brain and body size in hyenas, an assumption which is, however, not

supported by the negative relation that also exists in males (that do not lactate).

A different view is suggested by possible differential effects on body and brain during prenatal and postnatal growth. Riska and Atchley [1985] suggested that adaptive change affecting prenatal growth would affect both the body and brain whereas change that affects postnatal growth would affect the body only with little effect on the brain. If some selection had occurred to increase the postnatal growth of body exclusively in female hyenas, then we might expect to find that females have larger bodies than males. If that selection were applied at a time during development when females had (or still had) smaller brains, our results of differences between males and females would occur. Swanson et al. [2013] found that female hyenas weigh more because they grow faster after birth. Shea et al. [1987] found no enlargement of the brains of "giant transgenic mice" relative to those of litter-mate controls though most other structures were enlarged by the process that occurs in postnatal development. Though this mechanism could explain the sexual dimorphism of brain and body in hyenas, it does not explain the overall negative slope of the brain-body relations that occurs in both males and females.

#### Costs and Benefits of a Large Body

As Simpson [1960] observed many years ago, there has been a general trend toward increased body size, within diverse mammalian lineages, across evolutionary time. Hypothetical reasons for such selection are equally diverse and linked to lifestyle. For temperate-zone mammals, larger bodies have a lower surface-to-volume ratio, and the maintenance of core temperature is more efficient. In other cases, there may have been a competitive race between predators and prey [Jerison, 1973].

In addition to the preceding general pressures, there are more specific selective issues for female mammals. Ralls [1976] notes that in 25% of mammalian families, one finds species where females are larger than their male conspecifics: "big mothers" may have been in a better position to deal with the severe energetic demands of lactation as well as being better equipped to defend/support their offspring. But large bodies are also energetically costly, may require special structural modifications, and could interfere with speed and agility.

## The Case of the Spotted Hyena

The puzzling observation concerning the inverse relationship between brain size and body size in spotted hyenas has led us down a very speculative road. The following scenario is offered:

- 1. There has been strong selection for increased body size, with the pressures particularly pronounced in females.
- 2. All females are dominant over males, and there is strong dominance among the females within a clan.
- 3. With dependable caloric intake limited by availability and lifestyle, mechanisms were selected that insured that the total metabolic demands of the organism did not exceed the available food supply.
- 4. The inverse relationship between brain size and body size, observed in spotted hyenas, is a consequence of the rules of allocation, i.e., there were sufficient calories to support a very large body or a very large brain, but not both.

With regard to body size, spotted hyenas are the largest of the 4 extant species in the family Hyaenidae. They are the only hyaenids that prey on animals as large as zebra and buffalo. Presumably, large body size facilitates the capture of prey. As in wolves and wild dogs, hunting in social groups was also a critical evolutionary step, as was the development of an exceptionally powerful jaw musculature and specialized bone-crunching teeth [Binder and Van Valkenburgh, 2000]. The latter permitted access to the nutritionally rich marrow and fat in bone [Marean et al., 1992]. Large body size, formidable jaws/teeth, and social feeding also assist spotted hyenas to defend a kill against scavenging lions, subordinate hyenas, and neighboring hyena clans [Kruuk, 1972].

As noted by Hofer and East [1993], lactation constitutes a particular burden for female spotted hyenas. Among the social canids, only the dominant-female breeds and the burdens of nursing are distributed because other pack members regurgitate food for pups [Marten and Marten, 1982; Mech, 1999]. In spotted hyenas, all females breed but each mother assumes sole responsibility for nursing her own offspring. Moreover, the burden of nursing lasts for a year or more. By the end of the first year, the twin hyenas that commonly comprise a spotted hyena litter have grown to 30 kg each, and both are nursed by a 60-kg mother. Such large females would also be better equipped to compete with males and other females for food at a kill, and to defend their offspring against infanticide by other hyenas. The preceding array of benefits could offer the confluence of selective forces required to produce "big mothers" [Ralls, 1976].

If it is easy to identify a set of factors that would make a large body advantageous, we are on somewhat more tenuous ground in postulating caloric limitations that force a choice between brains and bodies. A proper assessment of this hypothesis would require a detailed knowledge of the temporal allocation of daily activities as well as a precise understanding of the energetic costs of such activities and also information regarding the available caloric supply.

Finally, there is the question of brain size. On average, spotted hyenas have relatively large brains, as might be predicted from their carnivorous lifestyle [Gittleman, 1986], the size and complexity of their social relationships [Dunbar, 1998], and the exceptional maternal commitment of female hyenas [Gittleman, 1994]. They communicate through an impressively broad array of vocalizations [Kruuk, 1972; East and Hofer, 1991; Mathoven et al., 2010; Benson-Amram et al., 2011], and modulate their behavior via a range of olfactory stimuli [Drea et al., 2002a, b]. Their ability to cooperate on a food acquisition task challenges that of the chimpanzee [Drea and Frank, 2003; Drea and Carter, 2009], although this probably reflects the nature of cooperative hunting. It would be of interest to administer a battery of intellectual assays to hyenas, correlating individual differences in problemsolving ability with individual variations in brain/body relationships. Have large hyenas with small brains really sacrificed any intellectual capacity?

## Physiological Mechanisms

Ultimately, understanding the mechanisms of species-characteristic allometry involves tracking the underlying mechanisms. Deacon [1997] has made a first step in that direction, observing that sets of highly conserved genes appear to regulate the development of the brain and the body in invertebrate and vertebrate organisms. Of particular interest, he has described disparate early genetic mechanisms that differentially regulate the growth of the cerebral hemispheres and the brainstem. The existence of such differentiated genetic control provides exactly the sort of opportunity for divergent selection required for the brainstem of hyenas to correlate positively with body size, while the cerebral hemispheres present an inverse pattern of correlation. One could postulate multiple mechanisms whereby this could occur. A negative relationship between brain and body could result if: the effects of growth-promoting agents were more pronounced in skeletal tissue than in neural tissue; the mix of circulating androgens and estrogens stimulated the growth of cerebral tissue more than skeletal tissue; and/or a negative feedback system developed whereby high concentrations of IGF-1 inhibit the secretion of gonadal steroids.

These mechanisms, singly or in combination, illustrate that available physiology provides routes that could in theory produce the pattern of results described in this paper. The actual mechanism is apt to be more complex and probably involves genes, growth factors, hormones, binding proteins, and tissue-specific receptors not mentioned in the preceding description.

As noted earlier, the slope of the brain-body relation within species is usually thought to be positive [Gould, 1975]. It is possible that other species (perhaps some in which the female is bigger than the male) also have brainbody relations that are negative. Recently, an extraordinarily comprehensive survey of brain/body allometry appeared [Tsuboi et al., 2018], but the sample includes only 1 species of carnivore, not the hyena. Of interest to the current discussion, the data show species of birds and mammals for which the allometric slopes are negative. Furthermore, they show that the negative slopes amongst mammals are of recent origin, none appeared before 1 million years ago. They do not mention or discuss either of these observations, however. Though these observations do not impact hyenas directly, they may suggest that there are other species with negative brain-body slopes, and that examining them further could offer comparative information that could lead to an understanding of the reason for their existence in hyenas.

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The authors have no conflicts to declare.

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Mann/Frank/Glickman/Towe