Ontogeny of sexual size dimorphism in the spotted hyena (*Crocuta crocuta*)

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Body size and growth rate are among the most important traits characterizing an organism, influencing niche occupancy, life-history patterns, mortality rates, and many other fitness components. Sexual size dimorphism is common among animals; in most species females are on average larger than males. In contrast, male mammals are usually larger on average than females of the same species, and the spotted hyena (*Crocuta crocuta*) may be one of the rare species of mammal in which females are generally larger than males. Nevertheless, some have argued that the evidence is equivocal regarding this reversal. This disagreement may reflect differences in traits measured, methods used, or ontogenetic differences among individuals sampled for these studies. We quantified size at various points during ontogeny in 651 individuals, the largest sample used in size analyses of spotted hyenas to date. We measured 14 morphological traits as well as 4 linear combinations of the traits that provide multivariate estimates of size; these were used to examine growth patterns among males and females measured in a free-living population in Kenya. We demonstrate that female spotted hyenas are larger than males for most, but not all traits, and that females are larger because they grow faster, rather than exhibiting a prolonged period of growth. Early in life males and females appear to grow similarly, but between weaning and reproductive maturity their multivariate ontogenetic trajectories diverge. Traits that mature before divergence of these ontogenetic trajectories are monomorphic, whereas traits that mature later are dimorphic. Furthermore, dimorphism is generally greatest in traits that cease development latest. We propose that later-maturing traits are more dimorphic because of a systemic increase in female growth rates during adolescence that persists through morphological maturity, which varies among traits. We also assess body-size data obtained from captive hyenas to show that adult female hyenas are larger than adult males for some traits even when they are fed identical diets throughout development, allowing us to rule out a strictly environmental explanation for this dimorphism.

Key words: *Crocuta crocuta*, growth, morphology, ontogeny, sexual size dimorphism, spotted hyenas

Intersexual variation in body size, or sexual size dimorphism, is common in animals, and has a variety of ecological and life-history implications (Promislow 1992; Fairbairn 1997; Fairbairn et al. 2007). Sexual size dimorphism is generally attributed to different fitness optima for adult body size in males and females, and is of special interest in part because it occurs despite a strong genetic correlation between the sexes (Fairbairn 2007), although the degree or presence of sexual size dimorphism also responds to variation in food availability or survivorship (e.g., Powell and King 1997). Female-biased sexual size dimorphism, in which females are the larger sex, is the norm in most animal taxa, and is often explained as an adaptation to increase fecundity (Andersson 1994; Fairbairn 2007; reviewed in Fairbairn et al. 2007). Male-biased sexual size dimorphism is the general pattern in mammals, probably due to sexual selection among competing males (Darwin 1871;

TABLE 1.—Published accounts of sexual dimorphism, or lack thereof, in wild *Crocuta crocuta*. BL represents body length, CBL represents skull condylobasal length, HBL represents head–body length, SH represents shoulder height, and ZB represents zygomatic breadth. For van Jaarsveld et al. (1988), total sample size was 30; numbers of males and females were not reported. Matthews (1939) did not perform statistical analyses, but did demonstrate that the median size of females was larger than that of males for HBL. Sample sizes for Matthews (1939) were not given in the original paper, but were determined by direct examination of the collected material (McElhinny 2009). Asterisks represent traits where the difference between males and females corresponds: * $P \leq 0.05$; ** $P < 0.01$; and *** $P < 0.001$.

Females > males	Females = males	No. males	No. females	Location	Reference
HBL	CBL, ZB	63	40	Tanzania	Matthews (1939)
Mass**		12	8	Tanzania	Kruuk (1972)
BL*, CBL*, ZB**	Mass, SH	5	5	South Africa	Skinner (1976)
	Mass, HBL	13	12	South Africa	Whately (1980)
Mass***		5	5	Kenya	Neaves et al. (1980)
Mass*, girth*	HBL	25	18	Kenya	Hamilton et al. 1986
Mass*, girth*	SH	8	6	South Africa	Henschel (1986)
	HBL, SH			South Africa	van Jaarsveld et al. (1988)
Mass***, girth*	HBL	9	7	South Africa	Mills (1990)
	Mass, girth, HBL	5	9	Kenya	Sillero-Zubiri and Gottelli (1992)

Ralls 1976; Alexander et al. 1979; Weckerly 1998; Fairbairn et al. 2007; Lindenfors et al. 2007).

A putative exception to the general mammalian pattern of male-biased sexual size dimorphism is the spotted hyena (*Crocuta crocuta*), a large mammalian carnivore that exhibits a variety of rare and unusual role-reversed traits. Spotted hyenas live in social groups, called clans, that may contain as many as 120 individuals ordered in a linear dominance hierarchy in which females and their offspring are dominant to breeding males (Frank 1986; Smale et al. 1993). Breeding males are usually immigrants from other clans, but females are philopatric (Smale et al. 1997; Van Horn et al. 2003; Honer et al. 2007). Both sexes reach physiological sexual maturity at around 24 months (Glickman et al. 1992), but females often fail to give birth until after 36 months of age (Holekamp et al. 1996; Hofer and East 2003). Adult female spotted hyenas have preferential access to feeding sites (Kruuk 1972; Tilson and Hamilton 1984; Frank 1986; Mills 1990), are more aggressive than adult males (Szykman et al. 2003; Van Meter 2009), and bear uniquely masculinized genitalia (Matthews 1939; Kruuk 1972; Skinner 1976; Neaves et al. 1980; Glickman et al. 1987; Drea and Frank 2003). In addition to these well-documented sex-role reversals, the spotted hyena is arguably the only terrestrial member of the order Carnivora that exhibits female-biased sexual size dimorphism (Ralls 1976), although some other hyaenid species also may exhibit female-biased sexual size dimorphism (Gittleman and VanValkenburgh 1997). Female-biased dimorphism in the spotted hyena was 1st described more than 70 years ago (Matthews 1939), yet in the intervening years researchers have disagreed with regard to whether or not females are truly larger than males (Table 1).

Although many researchers have documented dimorphism in some (Matthews 1939; Skinner 1976; Hamilton et al. 1986; Henschel 1986; Mills 1990) or all (Kruuk 1972; Neaves et al. 1980) morphological traits measured, others find that males and females are the same size on average for every trait measured (van Jaarsveld et al. 1988; Sillero-Zubiri and Gottelli 1992; Gottelli et al. 1994).

Perhaps because of the controversy regarding whether or not females are larger than males, virtually no empirical research exists on the evolutionary and developmental underpinnings of sexual size dimorphism in spotted hyenas, despite a great deal of evolutionary and developmental research on the other sex-role–reversed traits expressed in this species (e.g., Kruuk 1972; Glickman et al. 1987; Frank et al. 1990; Smale et al. 1993; Holekamp and Smale 2000; Drea and Frank 2003; Van Meter 2009; Watts et al. 2009). Detailed documentation of the ontogeny of any trait represents an important 1st step toward understanding the developmental processes mediating its expression. Such documentation also is critical to our understanding of the evolution of sexual size dimorphism, because dimorphism in adult size cannot arise independently of development. Rather, the evolution of sexual size dimorphism occurs through alteration of sex-specific ontogenetic trajectories, and recognizing this represents an important step toward understanding evolutionary patterns of dimorphism among adults (Badyaev 2002). Specifically, knowledge of the developmental program underlying sexual size dimorphism can shed considerable light on the mechanisms by which complex adaptations respond to selection, the evolutionary origins of dimorphism, the proximate neuroendocrine mecha-

nisms mediating dimorphism, and the environmental factors influencing sexual size dimorphism.

Our goals in the current study were 4-fold. First, we wanted to determine unequivocally whether or not spotted hyenas in our study population exhibit female-biased sexual size dimorphism during the time studied, and how the degree of dimorphism varies among morphological traits. Here we define sexual size dimorphism as a statistically significant difference in the means of size measures taken from males and females. Second, we wanted to elucidate the developmental trajectories in males and females that result in the respective body-size distributions observed among adults in our study population. Specifically, we inquired whether female spotted hyenas exhibit more-rapid growth than males, continue growing longer than males during ontogeny, or both. Third, we wanted to identify and test hypotheses explaining why earlier researchers were unable to settle the question of whether or not spotted hyenas exhibit female-biased sexual size dimorphism. Finally, we compared free-living hyenas to a captive population in which both sexes were fed identical diets to test whether any sexual size dimorphism observed in nature might be caused by differential food access. If sexual size dimorphism in our population could be largely attributed to differential food access, we would expect to find no sex difference among captive hyenas.

To accomplish our 1st and 2nd goals, we measured sexual dimorphism in adult size, growth rate during ontogeny, and growth duration in 14 morphological traits using a large set of cross-sectional and longitudinal data collected during immobilizations of free-living spotted hyenas in Kenya. We also tested for dimorphism in overall "body size," a common approach that also is more difficult than commonly appreciated. The 2 most widely used approaches to quantifying overall body size involve either using univariate measures such as mass or body length, or using scores from the 1st principal component (PC) in a principal component analysis (PCA) of all size traits measured in each animal. Both of these approaches are problematic for reasons detailed in Swanson et al. (2011). Therefore, in addition to our univariate, "trait-by-trait" approach to investigating sexual size dimorphism, we investigated dimorphism in the 1st PC axis (PC1) from a PCA on all traits measured, and also utilized a novel approach to defining size based on allometric relationships. This approach, which groups traits based on their multivariate allometric coefficients, was recently used to quantify size and its fitness consequences among adult female hyenas (Swanson et al. 2011).

To test for dimorphism we fitted growth models to the morphological data collected from the free-living hyena population. These are sigmoidal models that fit a growth rate parameter as well as an asymptotic parameter representing adult size. Sex was then fitted as a predictor of adult size and relative growth rate to simultaneously test for dimorphism in adult size and growth rate during ontogeny. Finally, to test the hypothesis suggesting that female-biased sexual size dimorphism in spotted hyenas results from differential food access mediated by female dominance over males, we analyzed a 2nd,

smaller data set collected from adult members of a captive colony where males and females experienced identical feeding and environmental conditions throughout the life span.

In relation to our 3rd goal of addressing why researchers have yet to unequivocally determine whether or not female spotted hyenas are larger than males, we noted that many of the previous studies on both sides of this controversy had small sample sizes, which may have hampered researchers' ability to detect mild to moderate differences in size. We suggest this possibility because a well-known consequence of small sample size in statistical tests is low statistical power, the ability to detect a difference between 2 groups when the 2 groups are in fact different. We therefore performed bootstrapped power analyses using our data to test the hypothesis that previous studies have merely had insufficient statistical power to reliably find size differences between males and females. Finally, we suggest that the degree of dimorphism for different traits varies, and this also plays a role in determining researchers' ability to detect sexual dimorphism.

Materials and Methods

Data were collected during 799 immobilizations of 651 individuals between 1990 and 2011, including 352 females and 299 males, largely from 3 contiguous clans in the Masai Mara National Reserve, Kenya. Of the 651 individuals, 551 were measured only once. The mean number of measurements of a single individual was 1.23, the median was 1, and the maximum number of times an individual was measured was 5. The mean age (in months $\pm$ SD) of measurement was 48.09 $\pm$ 41.79 months; the youngest hyena was 0.20 months and the oldest was 207.58 months. Immobilizations were conducted in Kenya using Telazol (6.5 mg/kg; Fort Dodge Animal Health, Overland Park, Kansas) administered via a lightweight plastic dart fired from a CO_2-powered rifle (Telinject Inc., Saugus, California). All immobilizations were carried out in accordance with guidelines of the American Society of Mammalogists (Sikes et al. 2011), and our protocols also were approved by the Institutional Animal Care and Use Committee at Michigan State University. Ages of most hyenas residing in their natal clans were determined based on known emergence dates from natal dens ($\pm$ 7 days—Holekamp et al. 1996), but ages of some adults born in clans outside our study population were based on patterns of tooth wear ($\pm$ 6 months—Van Horn et al. 2003). During each immobilization several morphological measurements were taken, including 4 cranial and 9 postcranial measurements, in addition to body mass. Measurements are shown in Fig. 1, and a detailed description of each of these measures is given by Van Horn et al. (2003).

Allometric relationships among traits over ontogeny.—We used 3 approaches to quantify size in order to compare ontogenetic patterns of size change between male and female spotted hyenas. First, we computed thePC1 from a PCA of all measured morphological traits except mass, and used this composite score as an estimate of overall size. This measure included all individuals in all ontogenetic stages, and the scores
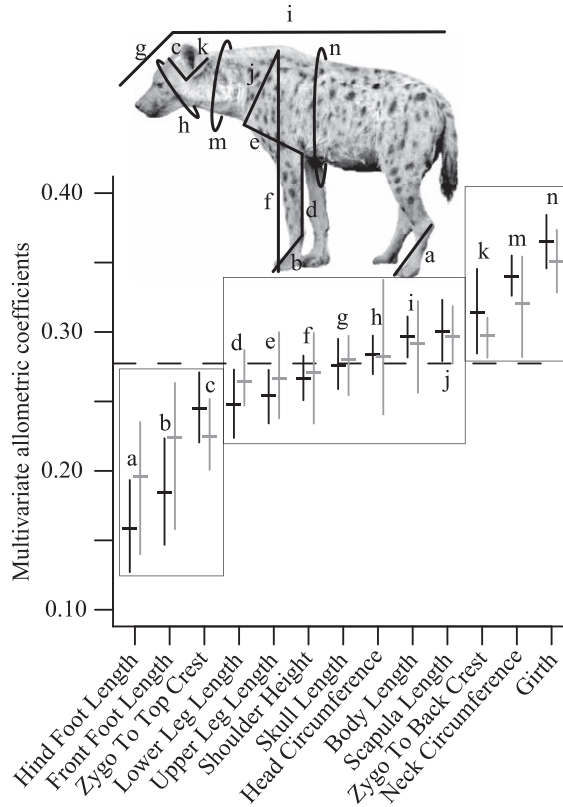
FIG. 1.—Bootstrap means (horizontal lines) and 95% confidence intervals (*CI*s; vertical lines) for multivariate allometric coefficients for univariate morphological traits for spotted hyenas (*Crocuta crocuta*). Lines representing males are gray and lines representing females are black. Boxes around traits represent groupings for multivariate traits chosen by whether or not the allometric *CI* overlaps the isometric hypothesis (horizontal dotted line). Letters above each allometric *CI* correspond to measures on the hyena diagram. Any letters for which the corresponding morphological trait on the hyena diagram is ambiguous refer to the line directly below the letter.

thus apply to all individuals in the population. Traits were log-transformed before PCA. Henceforth we refer to this composite score as "overall body size." Second, in addition to the PC1 score, we analyzed the ontogeny of each univariate trait separately. Finally, we adopted the approach suggested by Swanson et al. (2011), in which traits are grouped based on their multivariate allometric coefficients, estimated as the loadings of each individual trait on PC1. Morphological allometries represent the log–log ratios, or ratios of 2 log-transformed traits, at which the size of specific traits increase with increasing overall body size. Multivariate allometric coefficients calculated in this way specifically represent the log–log ratio at which traits increase with increasing PC1. Traits that increase at log ratios greater than 1 are generally referred to as hyperallometric, traits that increase at log ratios equal to 1 are called isometric, traits that increase at log ratios of less than 1 are called hypoallometric.

To obtain the multivariate size measures suggested by Swanson et al. (2011), we resampled our data with replacement 10,000 times (Efron and Tibshirani 1986), performed a PCA on

the 13 log-transformed morphological traits (again excluding mass) for each resampled data set, and estimated 95% bootstrap confidence interval (*CI*) on the trait loadings (Jackson 1993; Tzeng and Yeh 2002). Following Swanson et al. (2011) we next assigned traits to groups based on whether or not their 95% bootstrap *CI* overlapped the expected value for isometry. The expected isometric value, or "isometric hypothesis," is equal to $1/(p^{1/2})$ where p is the number of traits in the PCA, and is equivalent to the trait loadings in the hypothetical situation where every trait included in the PCA increases isometrically. Finally, we performed PCAs on each of the resulting groups, and used the PC scores associated with the 1st eigenvalue of each of these PCAs as a new multivariate trait, referred to respectively as the hypoallometric, isometric, and hyperallometric size traits. Although we recognize that the allometric variation is continuous, this method provides a useful basis for separation. These and all following analyses were carried out in R version 2.13.1 (R Development Core Team 2009).

Sex differences in ontogenetic vectors.—Sexual size dimorphism only arises through a limited number of developmental routes, and each route is suggestive of certain physiological mechanisms mediating the dimorphism. Specifically, members of 1 sex may achieve a larger size because they grow for a longer period of time, at a greater rate, or both (Alberch et al. 1979; Leigh 1996; Setchell et al. 2001; Altmann and Alberts 2005; Derocher et al. 2005). If a dimorphism results from a disparity in growth rates between males and females, this disparity may be present throughout development, or it may occur in the form of a "growth spurt," where growth rates differ between the sexes only during a limited period of time (Leigh 1996). Growth spurts, particularly during the final stages of sexual maturation, are common among mammals, especially in some orders, such as primates (Leigh 1996). In addition to using the multivariate allometric coefficients to determine trait grouping, we estimated the angular difference between the allometric vectors (PC1 on all traits—see Pitchers et al. 2013) calculated separately for males and females to test for overarching differences between the sexes with respect to the multivariate ontogenetic trajectory (Zelditch et al. 2003). We performed this analysis on resampled data in order to estimate 95% bootstrap *CI*. Increases away from 0° in the angle between the ontogenetic vectors for males and females suggest divergence in growth rates among the sexes. We partitioned ontogeny into 3 separate time periods for comparison: individuals younger than 13.5 months, individuals between 13.5 and 24 months, and individuals between 24 and 36 months. Thirteen and one-half months is the mean weaning age in this population (Holekamp et al. 1996), 24 months is the age at which females are physiologically competent to breed (Matthews 1939; Glickman et al. 1992), and 36 months represents a conservative estimate for complete morphological and reproductive maturity (Tanner et al. 2010) and the age after which females generally start to reproduce. Our intention with this analysis was to isolate the phases of development during
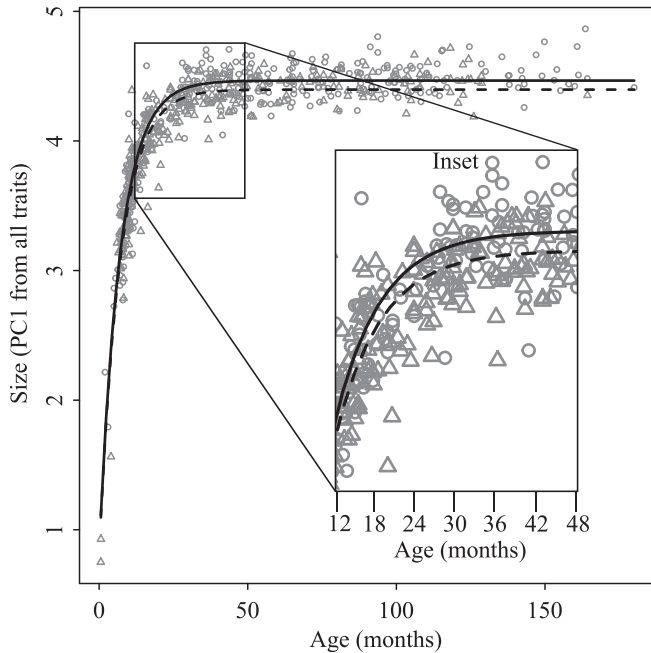
Fig. 2.—Plot of size of spotted hyenas (*Crocuta crocuta*) as estimated from the 1st principal component axis (PC1) taken from a principal component analysis on all traits except mass (size), predicted by age. A solid line plotted through data represents the female growth curve taken from best-fitting monomolecular growth curve, and dashed line represents the male growth curve from the best-fitting monomolecular function. Data points for females are represented by circles and for males by triangles. Inset is magnified between 12 and 48 months of age to better exhibit the dimorphic growth period.

which males and females exhibited notably similar or different ontogenetic vectors.

Sexual dimorphism and growth in free-living spotted hyenas.—To test for sexual dimorphism in adult size and relative growth rate, we fitted several flexible, commonly used sigmoidal growth models for each univariate variable, as well as for the hypoallometric, isometric, and hyperallometric multivariate traits, and for overall body size. The models we fitted included a saturating "monomolecular" model (Gaillard et al. 1997), the Gompertz model of Zullinger et al. (1984), the Gompertz model as formulated by Fiorello and German (1997), the Von Bertalaffy model (Zullinger et al. 1984), and the logistic model (Zullinger et al. 1984). Equations were parameterized as in Zelditch et al. (2003). Each of these models includes an asymptotic value representing adult size that is approached as age increases, a relative growth rate parameter representing the rate at which adult size is approached, and an age at which size is equal to 0 (see Fig. 2 for an example of a growth curve with adult size for males and females modeled separately). Because we were fitting models to mixed cross-sectional and longitudinal data, we faced a potential issue of pseudoreplication, in which using multiple data points from the same individuals can bias results, or violate the assumptions of parametric statistical tests. To address the problem of bias, we first tested whether the combination of cross-sectional and longitudinal data resulted in

a bias by estimating the variance in each morphological variable explained by individual identity. To do so we fitted nonlinear growth models with and without a random effect of individual as a predictor of asymptotic adult size and relative growth rate using the "nls" and "nlme" functions for modeling nonlinear responses in R. We then used likelihood ratio tests calculated from model deviance to compare models. In no case was the model that included the effect of individual identity a significantly better fit to the data than models lacking this variable, indicating that consistent similarities among measures on the same individuals do not explain a significant amount of variation in adult size or relative growth rate. This may be because repeated measures on the same individual almost always took place more than a year apart, so replicated measures within individuals were generally distributed widely over the life span. To further ensure that use of all our data, including replicated samples within individuals, did not bias our results, we reestimated all *P*-values using the same parameter estimates, but using the total number of individuals as the sample size rather than the total number of immobilizations. Throughout the remainder of this manuscript we indicate when using this smaller sample size resulted in a difference. We then refitted the models using maximum-likelihood estimation with the "bbmle" package in R (Bolker and R Development Core Team 2012). Because the monomolecular model fit our data best for 11 of 14 univariate traits compared (including mass), we present all results using the monomolecular model to facilitate comparison among results for different traits. To make certain this did not bias our results, we also repeated all tests using the best model for the 3 traits where a different model fit better. Specifically, the Von Bertalaffy curve fit better for skull length and upper-leg length, whereas the logistic curve fit better for lower-leg length. Repeating all relevant analyses using an alternative growth model had no effect on the results for any trait.

To test for differences in relative growth rate and adult size between males and females, we fit 4 separate monomolecular models. No sex difference in relative growth rate or adult size was fit for the 1st model ("no dimorphism"). For the 2nd model a sex difference was fit to adult size ("adult size dimorphism"). The 3rd model was fit with a difference in relative growth rate (the "b" parameter in the monomolecular equation; "relative growth dimorphism"), and the 4th model was fit with a difference between the sexes in both adult size and relative growth rate ("size and relative growth dimorphism"). We again performed model selection using sample-size–corrected Akaike's information criterion (AIC_c). We also wanted to evaluate whether the degree of dimorphism is influenced more strongly by variation in growth rate or duration of growth. Therefore, we tested for a correlation between the length of development of a trait and the degree of dimorphism, as well as a correlation between the degree of dimorphism in a trait and its absolute rate of growth (cm/day) estimated from the best growth model. Both tests were performed using a nonparametric Spearman rank correlation.
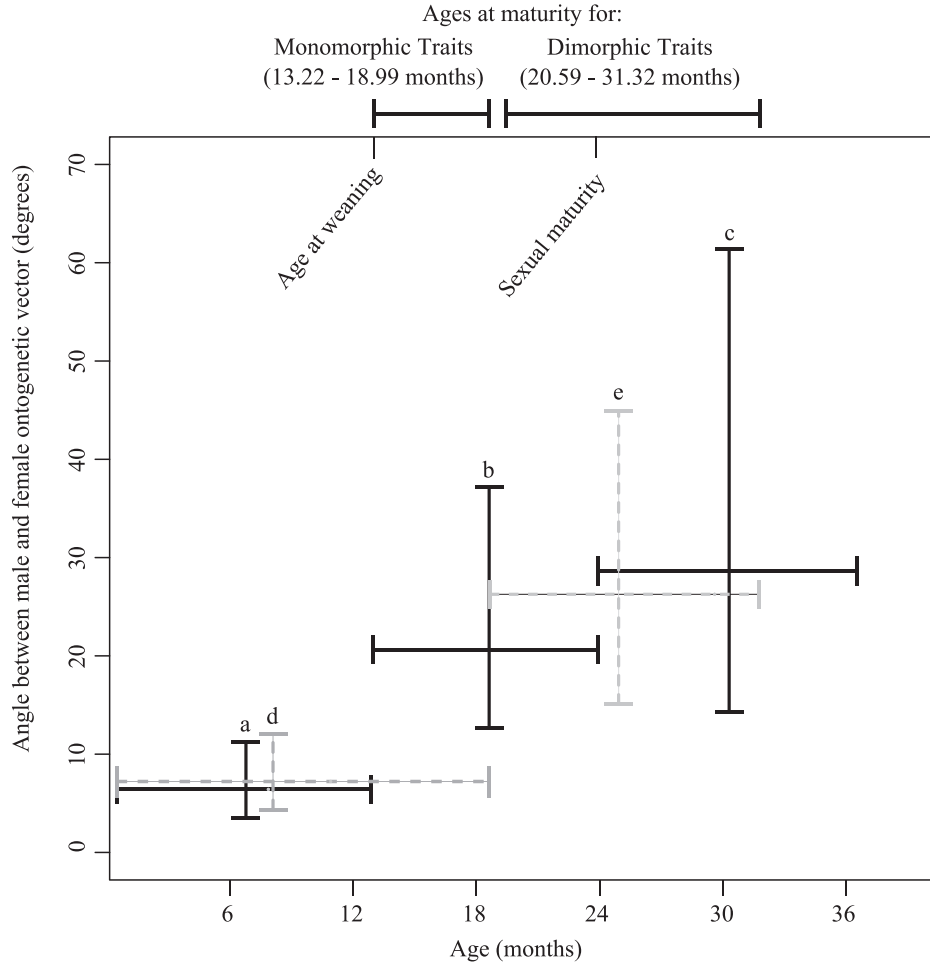
FIG. 3.—Angles between ontogenetic vectors for male and female spotted hyenas (*Crocuta crocuta*) calculated from the 1st principal component axis (PC1) on all traits for each sex individually. Vertical bars on the plot represent 95% bootstrap confidence intervals (*CIs*; vertical bars) from 10,000 bootstrap replicates of estimation of the ontogenetic angle; horizontal bars show the age ranges themselves. Black bars with a–c) solid lines represent the a priori choices for age ranges (0–13.5 months, 13.5–24 months, and 24–36 months, respectively), and gray bars with dashed lines represent post hoc choices for age ranges based upon our proposed d) "monomorphic" growth period (0–18.99 months) and e) "dimorphic" growth period (18.99–31.23 months).

Sexual dimorphism in adult captive spotted hyenas.—To determine whether size differences between the sexes have a genetic basis, or are instead merely a result of females' priority of access to food, we collected data from 32 captive adult spotted hyenas fed on uniform diets in the absence of feeding competition at the University of California–Berkeley Field Station for the Study of Behavior, Ecology, and Reproduction. Measurements were taken from 19 adult male and 13 adult female hyenas of similar age ($t_{30} = -0.51$, $P = 0.612$), descended from animals collected near our study area in the Masai Mara National Reserve. Individual hyenas were immobilized using a blowgun dart (darts: Telinject Inc., Agua Dulce, California; blowgun: Addison Biological Laboratory, Inc., Fayette, Missouri) to administer a mixture of ketamine (10 mg/kg; 100 mg/ml), xylazine (1 mg/kg; 100 mg/ml), and atropine (0.045 mg/kg; 15 mg/ml), after which total mass, head–body length, and shoulder height were measured. Sedation was then reversed using yohimbine (0.075–0.12 mg/kg; 2 mg/ml; Lloyd Incorporated,

Shenandoah, Iowa). We compared male and female size for mass, head–body length, and shoulder height using Student's *t*-tests.

Statistical power of previous studies.—To ask whether previous studies had insufficient statistical power to adequately address the question of sexual size dimorphism, we used our field data to perform power analyses. Using only data from wild adults older than 36 months, we separated males from females, resampled our data with replacement separately for the 2 sexes, and performed *t*-tests to assess our ability to find a significant difference in size between males and females for the trait in question at a variety of sample sizes. We started at a sample size of 5, and increased sample size by 1 until all 500 replicates for each run found the difference in size to be statistically significant at an $\alpha = 0.05$. We replicated this process 10,000 times and estimated 95% bootstrap *CI* on the sample size for each sex at which 80% of the runs found a statistically significant difference in size for males and females. The value 80% was selected a priori as an estimate of statistical

Table 2.—Difference in sample-size–corrected Akaike's information criterion (ΔAIC_c) values for sex model selection for multivariate and univariate morphological traits. ΔAIC_c values > 2 are generally considered to represent evidence that the model does not fit the data as well. Generally this is used to determine whether a parameter is a useful addition to a model given the complexity it adds. Columns represent: "No dimorphism," a model with no difference in either adult size or relative growth rate; "Adult size dimorphism," a model denoting a difference in adult size between the sexes, but no difference in relative growth rate; "Relative growth dimorphism," a model denoting dimorphism in relative growth rate, but not adult size; and "Size + relative growth dimorphism," a model denoting a difference in both adult size and relative growth rate. Boldface type represent the "best" model, or the model that most closely fits the data. Zygo to back crest = distance between the widest point on the zygomatic arch and the back of the sagittal crest; Zygo to top crest = distance from the zygomatic arch to the top of the sagittal crest.

	No dimorphism	Adult size dimorphism	Relative growth dimorphism	Size + relative growth dimorphism
Size	21.6	**0**	17.8	1.7
Hypoallometric size	1.7	**0**	2.8	2
Isometric size	20.3	**0**	14.3	2
Hyperallometric size	29	**0**	22.8	1.5
Zygo to top crest	9.6	**0**	6	2
Zygo to back crest	5.2	**0**	4.9	1.8
Skull length	12.8	**0**	11.6	1.1
Head circumference	51.1	**0**	36.7	1.2
Girth	33	**0**	27.7	0.2
Lower-leg length	**0**	1.9	1.7	3.8
Upper-leg length	2	**0**	0.5	1.3
Scapula length	7.8	**0**	7.5	1.8
Shoulder height	3.4	**0**	4.2	1.9
Front-foot length	**0**	1.8	2	3.7
Hind-foot length	**0**	1.6	1.4	3.4
Neck circumference	36	**0**	28.6	0.7
Body length	23.4	**0**	10.3	1.2
Mass	78.5	0	52.9	1.1

power, that is, the percent of times one would expect to find a statistically significant difference in size between males and females; 80% was used simply because it is commonly considered a high degree of statistical power, although it is an arbitrary threshold. Use of alternative thresholds did not affect our results qualitatively. We only performed these power analyses for traits that our growth models found to differ significantly between adult males and females in the wild; these included mass, the distance between the widest point on the zygomatic arch and the back of the sagittal crest (henceforth "zygo to back crest"), the distance from the zygomatic arch to the top of the sagittal crest (henceforth "zygo to top crest"), skull length, body length, head circumference, girth, neck circumference, shoulder height, upper-leg length, and scapula length.

RESULTS

Allometric relationships.—We compared the bootstrap *CI*s for the multivariate allometric coefficients for the univariate variables to determine where they fell in relation to the isometric hypothesis. The allometric *CI*s for front-foot length, hind-foot length, and zygo to top crest fell below the isometric hypothesis, whereas *CI*s for lower-leg length, upper-leg length, scapula length, body length, skull length, head circumference, and shoulder height overlapped the isometric hypothesis (indicated by the dashed line in Fig. 1). The allometric *CI*s for girth, neck circumference, and zygo to back crest all fell above the isometric hypothesis. Ontogenetic allometries did not generally correspond with static allometries (which describe variation among individuals in the same ontogenetic stage, rather than over the course of development) from earlier work (Swanson et al. 2011), but in a few cases they did. Specifically, the same traits were hyperallometric using both approaches. Based on their multivariate allometric *CI*s, we grouped together the traits for which entire *CI*s fell below the isometric hypothesis, and we refer to PC1 from this group as "the hypoallometric trait" (Fig. 1). We also grouped the traits for which the *CI*s overlapped the isometric hypothesis; we refer to PC1 from a PCA on these traits as "the isometric size trait." Finally, we grouped the traits for which the entire *CI* fell above the isometric hypothesis, and we refer to PC1 from a PCA on these traits as "the hyperallometric trait."

Sex differences among allometric vectors.—Allometric *CI*s across the entirety of ontogeny generally differed little between males and females, although hyperallometric traits did appear to be slightly more hyperallometric, and hypoallometric traits slightly more hypoallometric among females (Fig. 1). When comparing angles between male and female allometric vectors over specific periods of ontogeny, it is nonetheless apparent that as individuals approach sexual maturity the angle increases, suggesting that some traits are growing differently in males than in females during this period (Fig. 3). It seems likely that this represents the period of dimorphic growth.

Sexual dimorphism and growth among free-living hyenas.— To assess the ontogeny of sexual size dimorphism we fitted several different growth models that capture key parameters such as relative growth rate and adult size. The monomolecular model fit best for 11 of 14 univariate models, and for all 4 of the growth models using multivariate traits (Supporting Information S1, DOI: 10.1644/12-MAMM-A-277.S1). The 3

traits for which the monomolecular was not the best model included lower-leg length, upper-leg length, and skull length. Although the monomolecular model differed slightly from the best model with respect to the quantitative estimates of adult size and growth rate, in no case did these differences lead to different conclusions. We therefore present results from the monomolecular model here to maintain consistency regarding the meaning of the parameters discussed.

Adult females were larger than adult males for 10 of 13 univariate traits (Tables 2 and 3), as well as 3 of 4 multivariate traits, including the isometric and hyperallometric traits and total size (Tables 2 and 3). For the 3 monomorphic univariate traits (hind-foot length, front-foot length, and lower-leg length), the best model was the monomolecular model, with no difference between males and females fitted for either relative growth rate or adult size. For the hypoallometric trait, the best model was the model with sex fitted as a predictor to adult size, but the difference was not quite significant at an $\alpha = 0.05$ (Table 3). For traits that we identify as dimorphic, perhaps a more useful question than the statistical significance of dimorphism is the degree of sexual dimorphism expressed, and the biological significance of this dimorphism; these questions are addressed in the "Discussion." Of the 3 monomorphic univariate traits, front-foot length and hind-foot length were in the hypoallometric group, whereas lower-leg length was the most hypoallometric trait in the isometric trait group (Fig. 1). All of the skeletal measures in our study reached 95% of their adult size before 32 months of age. Mass, the only measure that did not mature by this point, reached 95% of its adult value at 45 months (Table 3). Finally, we found that degree of dimorphism was correlated with the age at maturity for traits using a nonparametric Spearman rank correlation ($n = 13$, $R_s = 83.06$, $P = 0.002$) but not with average absolute postnatal growth rate for different traits ($n = 13$, $R_s = 336.81$, $P = 0.808$).

Sexual dimorphism among adult captive spotted hyenas.— As with the free-living hyenas, female hyenas from the captive colony were heavier than males (females: 55.6 kg ± 2.0 SE, males: 49.0 ±1.3 kg, $t_{30} = 2.89$, $P = 0.0071$), and longer (head–body length—females: 131.4 cm ± 1.2 SE cm, males: 127.2 ± 1.1 cm, $t_{30} = 2.24$, $P = 0.0193$). In contrast to our results from the free-living population, we were unable to detect dimorphism in shoulder height (females: 82.0 cm ± 0.54 SE, males: 81.7 ± 0.4 cm, $t_{30} = 0.53$, $P = 0.5996$). Interestingly, for the free-living population, shoulder height exhibited perhaps the least dimorphism of those univariate traits exhibiting statistically significant differences in male and female size as adults (Fig. 4; Table 3).

Statistical power of previous studies.—Our analysis suggested that the sample size required to achieve sufficient power to detect a statistically significant difference in size between males and females varies greatly depending on the trait of interest. For example, reliably detecting dimorphism in body mass in our power analysis required only 14.4 individuals of each sex (bootstrap SD: 0.683). Other traits required larger samples, ranging from 33.85 individuals to more than 350 individuals of each sex to achieve a statistical power of 0.80

(Fig. 4). Upper-leg length was an extreme case, requiring more than 2,500 individuals in each sex to reach a power of 0.80 and representing barely detectable dimorphism. Even with very large sample sizes, the traits for which dimorphism appears to be of the greatest biological significance, assessed relative to the average trait size, are the traits for which it is easiest to detect statistical significance.

DISCUSSION

Our results demonstrate that when large sample sizes are available, female-biased sexual size dimorphism is apparent for most morphological traits we measured in our study population of spotted hyenas (Table 3). Nevertheless, we found marked variation among traits regarding both the degree of dimorphism and the sample size needed to reliably detect dimorphism (Fig. 4). Some traits, such as hind-foot length, front-foot length, and lower-leg length, do not exhibit dimorphism even when statistical power is enormous, such as in our analyses (Tables 2 and 3). Thus, earlier studies that disagree on the question of dimorphism in spotted hyenas may do so simply because the researchers made different decisions about which traits to measure.

Variation in degree of dimorphism among sampled traits cannot explain all the variation among prior studies. Body and skull length, for example, both exhibit clear, if moderate, dimorphism in our data. Nevertheless, only one-third of previous studies found dimorphism in skull length (CBL in Table 1), body length (BL in Table 1), or the combination of the 2, head–body length (HBL in Table 1). Factors other than variation in degree of dimorphism must therefore contribute to the variation among previous studies with respect to the presence of sexual size dimorphism in the spotted hyena. Although hypotheses suggesting geographic or temporal variation in sexual size dimorphism cannot be ruled out, the results of our analyses are fully consistent with the explanation that the controversy over whether spotted hyenas exhibit female-biased sexual size dimorphism largely results from insufficient statistical power in most previous studies. In only 1 study in Table 1 was a combined sample size greater than 50 available for the 2 sexes, and in that case, no statistics were actually calculated (Matthews 1939). Most researchers, in fact, measured fewer than 10 individuals of each sex (Table 1; median = 8.5 individuals), which the results of our power analyses suggest is insufficient to detect sexual dimorphism in spotted hyenas for even the most dimorphic traits (Fig. 4). Even body mass, the trait exhibiting the greatest degree of dimorphism of all those we measured (Fig. 4; Table 3), required an average of 14.4 (± 0.683 bootstrap SDs) individuals of each sex to reliably find a significant difference. Interestingly, the monomolecular growth models we fitted to our data appear more likely to detect statistically significant differences in adult size between males and females than t-tests comparing only adults (Supporting Information S2, DOI: 10.1644/12-MAMM-A-277.S2). We assume this is due to the inclusion of large numbers of nearly mature individuals

TABLE 3.—Model parameters for "best" fitted models. Asymptote refers to the estimate for adult size for females ($\pm$ *SE*), whereas "Male effect" is the difference in adult size estimated for males compared to the estimated adult size for females ($\pm$ *SE*). *z* is the test statistic for the comparison of male and female adult size and *P* is the associated *P*-value. *b* represents the relative growth rate of each trait and t0 is the estimated age at onset of development of the trait. Age at maturity for each trait is the age in months at which the predicted size for the trait is equal to 95% of the asymptotic value, or adult size. Units for mass are kilograms (kg), and units for all other univariate traits are centimeters (cm). Letters preceding trait names correspond to Fig. 1. Asterisks (*) designate *P*-values no longer significant at $\alpha \leq 0.05$ after correcting *z*-scores for reduced sample sizes.

Trait	Female size (asymptote)	Male effect	z	P	b	t0	n	Age at maturity
All size	4.466 ± 0.011	−0.070 ± 0.014	−4.911	< 0.001	0.142 ± 0.003	−1.447 ± 0.222	621	19.65
Hyperallometric size	2.139 ± 0.008	−0.058 ± 0.010	−5.647	< 0.001	0.115 ± 0.004	−1.831 ± 0.366	659	24.22
Isometric size	3.269 ± 0.007	−0.046 ± 0.010	−4.773	< 0.001	0.142 ± 0.003	−1.262 ± 0.197	649	19.83
Hypoallometric size	2.099 ± 0.006	−0.015 ± 0.008	−1.936	0.053	0.206 ± 0.006	−0.544 ± 0.33	669	14
Mass	59.386 ± 0.467	−5.721 ± 0.612	−9.352	< 0.001	0.069 ± 0.003	1.865 ± 0.310	631	45.28
k. Zygo to back crest	17.392 ± 0.082	−0.283 ± 0.104	−2.708	0.007	0.078 ± 0.004	−7.085 ± 0.873	679	31.32
g. Skull length	30.103 ± 0.098	−0.493 ± 0.127	−3.878	< 0.001	0.089 ± 0.003	−6.076 ± 0.516	686	27.58
n. Girth	83.937 ± 0.374	−2.938 ± 0.488	−6.018	< 0.001	0.099 ± 0.004	−2.833 ± 0.474	681	27.43
h. Head circumference	53.097 ± 0.152	−1.453 ± 0.195	−7.450	< 0.001	0.094 ± 0.003	−5.369 ± 0.458	683	26.5
m. Neck circumference	50.607 ± 0.222	−1.808 ± 0.288	−6.277	< 0.001	0.099 ± 0.004	−3.565 ± 0.547	678	26.69
c. Zygo to top crest	13.001 ± 0.065	−0.291 ± 0.085	−3.438	< 0.001	0.102 ± 0.007	−6.035 ± 0.989	682	23.33
i. Body length	98.170 ± 0.353	−2.368 ± 0.464	−5.097	< 0.001	0.100 ± 0.003	−4.255 ± 0.409	690	25.7
j. Scapula length	28.458 ± 0.103	−0.430 ± 0.136	−3.149	0.002	0.113 ± 0.004	−2.911 ± 0.367	687	23.6
f. Shoulder height	78.431 ± 0.207	−0.645 ± 0.276	−2.339	0.019	0.130 ± 0.003	−2.013 ± 0.262	678	21.03
e. Upper-leg length	25.458 ± 0.097	−0.262 ± 0.130	−2.017	0.044*	0.131 ± 0.005	−2.282 ± 0.333	688	20.59
d. Lower-leg length	25.911 ± 0.077	—	—	—	0.146 ± 0.004	−1.526 ± 0.041	687	18.99
b. Front-foot length	19.157 ± 0.066	—	—	—	0.190 ± 0.007	−1.210 ± 0.264	687	14.56
a. Hind-foot length	23.395 ± 0.066	—	—	—	0.207 ± 0.007	−1.255 ± 0.209	688	13.22

exhibiting partial but incomplete dimorphism that cannot be included in simple 2-group comparisons of fully mature adults. This suggests that fitting such models in general may be good practice when data are available for species in which the sexes diverge to some extent before full maturity, even to answer questions that directly involve only adults, such as the degree of sexual size dimorphism among adults.

Food limitation in the environment can have a variety of effects on dimorphism in a species. For example, if both sexes have similar access to food, food limitation could reduce dimorphism by allowing the smaller sex to reach its full adult size, but not the larger sex. Because female spotted hyenas have complete priority access to feeding at kills, it might be argued that they are larger because they generally get more food than males, especially when food is limiting in the environment. An important consideration, however, is that

young hyenas of both sexes retain the same ranks as their mothers as long as they remain in their birth clan, so females and males in the same cohort have similar access to food until males disperse (Smale et al. 1993). Male hyenas rarely disperse before the end of the growth period; the mean age of emigration in our study area is 42.1 months $\pm$ 10.5 *SD* (Van Horn et al. 2003). Adult body size is reached long before this average dispersal time; skeletal measures in our study all reach 95% of adult size before 31.6 months, 1 *SD* below the mean dispersal age. In addition, comparison of male and female hyenas fed identical diets in captivity demonstrates that captive females are both longer (head–body length) and heavier than captive males. Shoulder height was monomorphic in the captive population, but our power analysis suggested that enormous sample sizes would be required to reliably distinguish a sex difference in this trait. Thus, it seems likely
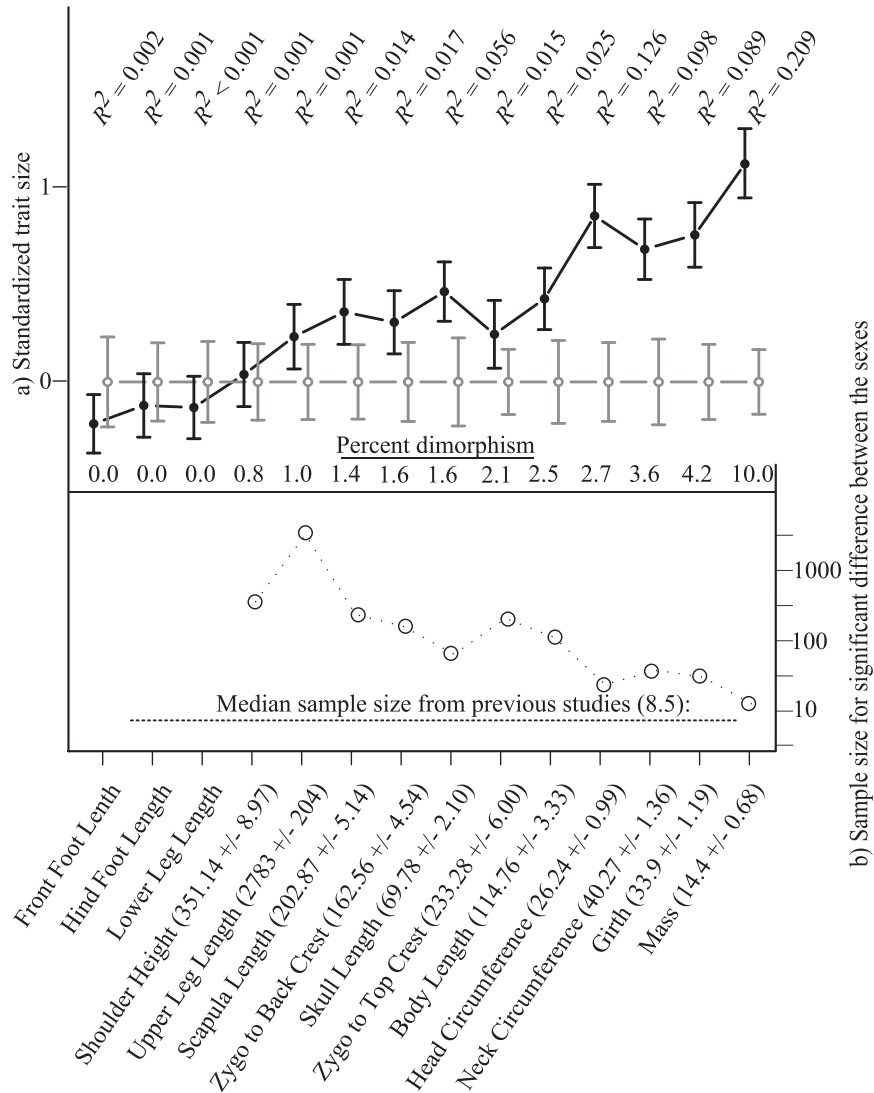
Fig. 4.—Size differences between male and female spotted hyenas (*Crocuta crocuta*) and sample sizes required to detect the differences. a) Size differences between males and females shown using standardized line plots (using the "sciplot" package in R—Morales et al. 2011) of male and female size distributions for each univariate trait. Females are in black and males are in gray. Data for each trait are mean-centered to the male mean for that trait, and standardized by dividing all data for the trait by the pooled standard deviation of the trait calculated for each sex separately and weighted by sample size for each sex (Nakagawa and Cuthill 2007). For this figure we only used data from immobilizations for which measurements from every trait are available ($n = 261$). Circles represent means, error bars represent $1.96*SEM$ (95% confidence intervals [*CIs*]) using pooled standard errors. *R*-squared values given above each trait represent the percent variance in the trait explained by the sex difference between males and females among adults over 36 months. b) Statistical power required to reliably detect a significant difference between males and females. Hollow circles represent the sample size at which 0.80 power is reached for each variable. The secondary y-axis (right-hand axis) is on a log base 10 scale, with actual sample sizes given in x-axis labels with bootstrap standard deviations. Median sample size from previous studies is represented by horizontal dotted line.

that the failure to discern dimorphism in shoulder height among captive hyenas simply reflects a lack of sufficient statistical power in our captive sample. These results also suggest that female-biased sexual size dimorphism in spotted hyenas has a genetic basis, and is not simply a result of better nutrition for free-living females, because naturally occurring dimorphism persists in a laboratory population where feeding conditions are identical for both sexes.

A key consideration here is the biological importance of this sexual size dimorphism; female spotted hyenas are hardly any larger than males for some traits, and other traits, such as lower-leg length, hind-foot length, and front-foot length, do not appear to be dimorphic at all. Traits associated with overall length nevertheless exhibit fairly clear dimorphism, and traits associated with "robustness," such as head circumference, neck circumference, and girth, exhibit marked dimorphism (Fig. 4; Table 3). Mass, in particular, exhibits notable dimorphism (see Table 3; Fig. 4). The functional significance of dimorphism is not fully clear in this species, because we know little about the performance consequences of body size in

spotted hyenas with reference to hunting, intraspecific fighting, or interspecific interactions with other large predators. Nevertheless, the mass difference (about 10% of adult size) is large enough to suggest the possibility of functional consequences to sexual size dimorphism.

For all traits we measured, male and female spotted hyenas appear to grow at the same rate relative to their respective adult sizes (Table 3). We found no difference between the age at which male and female hyenas cease growth, so sex differences in adult traits must result from differences in absolute growth rate. Thus, our data supported the hypothesis that females are larger because they grow more rapidly, rather than for a longer period of time. Our results further suggest that females do not grow more rapidly than males throughout their development, but rather that female growth rates increase relative to those of males as animals approach sexual maturity. The greater angle between allometric vectors for males and females in later than earlier development indicates that growth differences between males and females arise sometime after weaning. If we repeat the allometric angle analysis, using 0–18.99 months and 19.0–31.32 months as our time periods, we find essentially the same result (gray dashed lines in Fig. 3). The 1st time period lasts from the onset of growth at 0 months to the age at maturity of the last-maturing sexually monomorphic trait, lower-leg length at 18.99 months of age. The 2nd time period spans from the end of the 1st time period to age at maturity of the latest maturing sexually dimorphic trait excluding mass, zygo to back crest at 31.32 months of age. For the angle between the male and female allometric vectors over the time period of 0–18.99 months we found an estimate of 6.41° with a 95% bootstrap *CI* of 3.53°–11.21°. Because we use the absolute value of the dot product of the 2 vectors, these angle measures cannot overlap 0, so one can only make relative comparisons among them. For the time period from 18.99 to 31.32 months we found an angle of 25.46° with a 95% bootstrap *CI* of 14.27°–44.11°. The 95% *CI*s do not overlap here, suggesting that the developmental trajectory differs most between males and females between approximately 19 and 24 months of age, compared to the trajectories before 19 months, and after 24 months.

Our recent work suggested that body length, shoulder height, lower-leg length, head circumference, and scapula length were under positive selection among females in this population, and that the observed sexual size dimorphism might result from this selection (Swanson et al. 2011). If so, these traits should be the most dimorphic traits. Some traits under selection, such as body length and head circumference, are indeed among the most dimorphic traits and support this hypothesis. Others are weakly dimorphic or not dimorphic at all, such as shoulder height or lower-leg length, respectively. Because many traits are dimorphic, we suggest that the developmental factors mediating dimorphism affect body size as an integrated unit. If true, there are 2 possibilities: that traits respond differently to the same developmental factors, or that traits are influenced for different lengths of time. Our

results here provide evidence for the latter hypothesis. Specifically, the degree of dimorphism among measured traits was significantly correlated with age at trait maturity, but not with average absolute growth rate. This suggests that the degree of dimorphism in different traits depends on how long the trait continues to develop after the onset of divergent growth, and although not definitive, supports our hypothesis.

Evolutionary history, rather than contemporary selection, may yet explain some of the observed dimorphism. Hypotheses concerning evolutionary history are notoriously difficult to falsify, and our analyses do not address this. We propose instead that investigations into potential neuroendocrine mechanisms such as growth hormone and insulin-like growth factor may be fruitful, because both these hormones play important roles in mitogenesis and cell growth (reviewed in Froesch et al. 1985; Zapf and Froesch 1999; Kappeler et al. 2008; Dantzer and Swanson 2011). The question of the physiological mechanism mediating sexual size dimorphism in spotted hyenas is especially interesting because of the number of ways in which the "masculinized" endocrine profiles of female spotted hyenas might mediate anabolic growth in a sex-specific manner. Gonadal steroids generally have sex-specific profiles and also can influence the release of growth hormones (e.g., Veldhuis et al. 1995; Mauras et al. 1996; Muniyappa et al. 2007). Androstenedione in particular represents an interesting potential mediator of growth rates in spotted hyenas. Androstenedione is a testosterone precursor that can have anabolic effects of its own (Chen et al. 2004). Circulating androstenedione concentrations are very high in female spotted hyenas during infancy, and they subsequently remain higher in females than in males throughout development, although levels decline in females across ontogeny (Glickman et al. 1987, 1992). The timing of peak androstenedione in females does not appear to coincide with dimorphic growth. Nevertheless, interactions with other hormones or organizational effects could set up conditions for faster growth during pubertal development. Addressing such physiological hypotheses should help us understand the mechanisms mediating sexual size dimorphism in spotted hyenas and suggest specific hypotheses concerning the role that evolutionary history plays in patterns of sexual size dimorphism.

ACKNOWLEDGMENTS

Supporting Information

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