

Sexual selection on skeletal shape in Carnivora

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Lifetime reproductive success of males is often dependent upon the ability to physically compete for mates. However, species variation in social structure leads to differences in the relative importance of intraspecific aggression. Here, we present a large comparative dataset on sexual dimorphism in skeletal shape in Carnivora to test the hypotheses that carnivorans exhibit sexual dimorphism in skeletal anatomy that is reflective of greater specialization for physical aggression in males relative to females and that this dimorphism is associated with the intensity of sexual selection. We tested these hypotheses using a set of functional indices predicted to improve aggressive performance. Our results indicate that skeletal shape dimorphism is widespread within our sample. Functional traits thought to enhance aggressive performance are more pronounced in males. Phylogenetic model selection suggests that the evolution of this dimorphism is driven by sexual selection, with the best-fitting model indicating greater dimorphism in polygynous versus nonpolygynous species. Skeletal shape dimorphism is correlated with body size dimorphism, a common indicator of the intensity of male–male competition, but not with mean body size. These results represent the first evidence of sexual dimorphism in the primary locomotor system of a large sample of mammals.

KEY WORDS: Aggression, functional trade-offs, locomotion, sexual dimorphism.

Physical aggression is an essential component of the life histories of many animals. Aggressive performance is adaptive in the contexts of both natural and sexual selection and has profound influence on individual fitness (Andersson 1994). While fighting ability may be important to some degree for both sexes (e.g., for resource acquisition and survival), there are multiple reasons to expect male mammals to be more specialized for physical aggression than females. Because paternal care is limited or absent in most mammals, male reproductive success depends largely on the ability to gain mating opportunities and sire offspring (Trivers 1972). These actions are often dependent on fighting ability (e.g., Le Boeuf 1974; Clutton-Brock et al. 1982; Campagna and Le Boeuf 1988). Thus, intraspecific aggressive performance may directly correlate with resource holding power (Parker 1974), resulting in greater variance in lifetime reproductive success in males than in females (Bateman 1948; Emlen and Oring 1977; Clutton-Brock 1988; Le Boeuf and Reiter 1988; Clutton-Brock 1989). This relationship between aggression and reproductive success has led to evolution of pronounced male weaponry (e.g., canines,

antlers) and fatal fighting among the males of many species (Southwick 1970; Wilson and Daly 1985; Huntingford and Turner 1987; Chagnon 1988; Clutton-Brock 1988; Enquist and Leimar 1990; Andersson 1994; Wrangham and Peterson 1996; Sherrow 2012), emphasizing the importance of aggressive performance.

Male aggressive ability is adaptive for multiple sexually selected behaviors such as: (1) acquiring and defending territories and/or resources (resource-defense polygyny; Emlen and Oring 1977); (2) directly competing with males congregated near an estrous female (scramble-competition polygyny; Farentinos 1972; Thompson 1977; Koford 1982; Michener 1983; Fisher and Lara 1999) or preventing access by other males (female-defense polygyny; Davies 1991); (3) carrying out or preventing infanticide (Hausfater and Hrdy 1984; Pusey and Packer 1994; Van Schaik and Janson 2000); (4) securing or preventing extra-pair copulations; and (5) facilitating sexual coercion of females (i.e., forced copulation, harassment, intimidation, and punishment; Smuts and Smuts 1993; Clutton-Brock and Parker 1995). In social species, male fighting performance may improve the ability to maintain



social dominance through aggression (Packard et al. 1985; Haley et al. 1994; Creel et al. 1997; Kays and Gittleman 2001; Minami et al. 2009) and increases the chances of winning territorial disputes (Cassidy 2013). Additionally, in many mammal species, females show a strong preference for associating with males that control territories, have large harems, or are socially dominant as this may increase the likelihood that her male offspring will have high fitness (reviewed in Clutton-Brock and Parker 1995). Finally, aggressive ability may be important during dispersal, a male-biased and inherently risky behavior given the high incidence of dispersal-related mortality from intraspecific aggression in many species (Waser 1996; Smale et al. 1997).

Aggressive performance is considered a primary driver of the evolution of sexual dimorphism, in which sexual selection alters a male trait (Darwin 1874; Andersson 1994) and, subsequently, viability selection causes that same trait in females to evolve to be closer to a natural selection optimum (Lande 1980). Sexual dimorphism is thought to be slow to evolve because of a high degree of genetic correlation in phenotypic traits between the sexes (Lande 1980; Reeve and Fairbairn 1996; Bonduriansky and Chenoweth 2009). For example, dimorphism in body size may evolve several orders of magnitude more slowly than body size itself (Lande 1980; Rogers and Mukherjee 1992; Reeve and Fairbairn 1996). Combined with the maladaptive nature of many sexually selected traits in regard to natural selection (Darwin 1874), the presence of sexual dimorphism indicates the evolutionary importance of male competition for mates.

Larger body size in males occurs in approximately 45% of mammals (Lindenfors et al. 2007) and is the sexually dimorphic trait that has received the most attention from evolutionary biologists. Functionally, larger body size may confer advantages during intraspecific contests by increasing total momentum, power, and force applied to a competitor or by increasing energy reserves important during endurance rivalry (Darwin 1874; Ghiselin 1974; Andersson 1994). Male body mass is positively correlated with individual reproductive success within many mammalian species, from slightly sexually dimorphic (e.g., bridled nailtail wallabies, *Onychogalea fraenata*; Fisher and Lara 1999) to highly dimorphic taxa (e.g., red deer, *Cervus elaphus*, and brown bears, *Ursus arctos*; Clutton-Brock et al. 1988; Kruuk et al. 1999; Zedrosser et al. 2007). However, larger body size in males may incur a fitness cost in the context of natural selection by driving body mass away from an ecological optimum (Peters 1983; Blanckenhorn 2000). Sexual selection has led to the males of some species (e.g., kudu, *Tragelaphus strepsiceros*, and stoats, *Mustela erminea*) being larger than their ecologically optimal size (e.g., increased susceptibility to malnutrition, starvation, and predation; Owen-Smith 1993; Powell and King 1997), leading to greater rates of male-biased juvenile and adult mortality, particularly in polygynous species (Clutton-Brock et al. 1985; Promislow 1992).

In addition to overall body size, specific anatomical and physiological traits may improve aggressive ability. For example, in several territorial lizard species, bite force is the best measured predictor of contest outcome between males (Lailvaux et al. 2004; Huyghe et al. 2005), number of females within a territory (Lappin and Husak 2005), and number of progeny sired (Husak et al. 2009). Jumping velocity and sprint speed are correlated with winning in contests between size-matched competitors in other lizards (Garland et al. 1990; Robson and Miles 2000; Lailvaux et al. 2004). Similarly, agility and maneuverability may be important in arboreal contests among primates (Lawler et al. 2005). Thus, the type of male–male combat in a given species may lead to selection on specific functional traits (Jarman 1983, 1989; Lailvaux et al. 2004; Lailvaux and Irschick 2006; Lassek and Gaulin 2009; Carrier and Morgan 2015). In a comparative study on kangaroos, Jarman (1983, 1989) found widespread male-biased sexual dimorphism in forelimb morphology (forearm length and muscle mass) that he associated with grappling and pushing actions that occur when males fight each other over dominance status or access to females. These differences were most pronounced in polygynous species and were likened to the cranial weaponry of many artiodactyls (Jarman 1983). Likewise, carnivorans use their teeth, jaws, and forelimbs as primary weapons during aggressive encounters. Male-biased sexual dimorphism in canine size and muscle moment arms in the jaw-closing muscles (Gittleman and Van Valkenburgh 1997), traits also common in primates (Plavcan 2001), indicate their importance during male–male competition. Similarly, sexual dimorphism is expected in other functional traits important during male contests. Traits such as robust limb bones, high mechanical advantages, and relatively powerful distal limb muscles may improve aggressive performance by increasing stability, resisting high limb loading in variable directions, and increasing force output for striking or manipulating opponents (Pasi and Carrier 2003; Kemp et al. 2005).

Alternatively, locomotor constraints may limit or entirely preclude adaptation for aggressive performance in the postcranial skeleton (Carrier 2002). Carnivorans have greater daily travel distances than most other mammalian groups (Garland 1983; Carbone et al. 2005), implying that locomotor economy is an important performance trait. However, characters associated with locomotor economy (e.g., elongated limbs with reduced distal mass; Gambaryan 1974; Hildebrand 1985b; Steudel 1990) may represent a functional trade-off with traits that improve aggressive performance (Pasi and Carrier 2003; Kemp et al. 2005). Thus, sexual dimorphism in the primary locomotor system (i.e., postcranial skeleton) of carnivorans may be limited or absent. Furthermore, differences in locomotor zone (e.g., terrestrial vs. arboreal) may impose different constraints on the postcranial skeleton among taxa.

Our first aim in this study was to test the hypothesis that carnivores exhibit sexual dimorphism in skeletal anatomy that is reflective of greater specialization for physical aggression in males relative to females. We evaluate sexual dimorphism in skeletal shape using a set of characters thought to improve aggressive ability (Morris and Brandt 2014). Specifically, we predicted that males, as compared to females, would have: (1) relatively broader skulls to house larger jaw-closing muscles that increase bite force (Biknevicius and Van Valkenburgh 1996); (2) relatively broader necks to accommodate more robust musculature on the cervical vertebrae that functions to resist torsional loading of the neck (Radinsky 1981) and increase force capacity for jerking the skull and tearing with the teeth; (3) broader scapulae that facilitate greater musculature that functions to transmit force from the trunk to the forelimbs and to stabilize the shoulder joint (Goslow et al. 1981); and (4) more robust limbs with greater anatomical mechanical advantages. More robust limbs increase safety factors (Alexander 1981) of bones that, during aggressive interactions, may experience bending loads greater than an animal's own muscular capacity (Kemp et al. 2005). Additionally, broader distal ends of long bones increase surface areas for muscle attachment (Hildebrand 1985a), allowing for greater distal limb musculature. This may function to improve balance control, rapid turning and acceleration, and opponent manipulation (Pasi and Carrier 2003). Greater mechanical advantages function to increase force (Maynard Smith and Savage 1956; Hildebrand 1985b) that may be applied to the substrate or an opponent. When fighting, many mammals rear up on their hindlimbs as this reorients the powerful locomotor muscles in the forelimbs to be used against a competitor (Carrier 2011). However, this causes the hindlimbs to be oriented at high angles in relation to their principal axis of force transmission, diminishing the effective mechanical advantage. Greater anatomical mechanical advantages around hindlimb joints would function to circumvent this constraint on force production; this may be important for accelerating the body and gaining leverage during aggressive contests.

Our second aim was to test alternative models for the evolution of skeletal shape dimorphism. To do this, we used a direct modeling approach (Hansen 1997; Butler and King 2004) to compare evolutionary models incorporating different selective regimes (i.e., diet, locomotor zone, group size, mating system, and parental care) to each other and to a model of random drift. To determine if dimorphism in our set of traits is related to other functions (e.g., prey capture), we include species with a variety of feeding niches, from hypercarnivores to insectivores and frugivores, and mating systems, from socially monogamous to highly polygynous. Our third aim was to examine the relationship between skeletal shape dimorphism and the intensity of male–male competition. For this, we use sexual dimorphism in body size as a proxy, given that it is positively correlated with the inten-

sity of male–male competition in carnivores (Weckerly 1998; Lindenfors et al. 2002; Cullen et al. 2014) and other mammals (Clutton-Brock et al. 1977; Leutenegger and Kelly 1977; Alexander et al. 1979; Jarman 1983; Clutton-Brock 1985; Ford 1994; Mitani et al. 1996; Loison et al. 1999).

Materials and Methods

SPECIMENS

We measured male ($N = 371$) and female ($N = 319$) specimens of 26 carnivore species from collections at seven natural history museums listed in the Acknowledgments. All specimens were osteologically mature, as determined by complete fusion of long bone epiphyses (Evans 1993). Though individuals may gain or lose mass throughout adulthood, comparative studies on terrestrial carnivores have shown geometric scaling of joint surface areas (Godfrey et al. 1991), long bone length (Christiansen 1999), and minor deviations from geometric similarity in long bone mid-shaft diameters (Bertram and Biewener 1990) and circumferences (Christiansen 1999). Thus, the metrics used in the present study should be minimally affected by changes in body mass after an animal reaches adulthood. We collected data for specimens that were at least 80% complete and had sex and geographic origin information available. Species names and specimen identification numbers are provided in the electronic supplementary material (Table S1).

MORPHOLOGICAL TRAITS AND INDICES

Twenty length and breadth measurements (Table 1) were taken for each specimen to the nearest 0.01 cm using digital calipers (Mitutoyo Corporation, Japan) or Vernier calipers (for lengths > 20 cm; Phase II Machine and Tool, USA). We used physiological length (distance between articular surfaces) for postcranial measurements, which describes the effective working length of a bone during use (Wilder 1920). Digital imaging software (ImageJ; Rasband 2015) was used to measure surface area of the scapula. From the metrics listed in Table 1, we calculated 13 morphological indices that quantify relative proportions, robusticity, and anatomical mechanical advantages in the cranial and postcranial skeleton (Morris and Brandt 2014; Table 2). These functional indices are ratio values that are predicted to increase with specialization for physical aggression.

Statistical Analysis

We first tested all functional indices for evidence of allometry using an analysis of covariance (ANCOVA) with functional index values as the dependent variable, body size (geometric mean of

Table 1. Skeletal morphometrics taken for carnivoran specimens.

Metric	Definition and functional significance
Skull width	Zygomatic width of skull
Skull length	Basal length of skull (basion to prosthion)
Occipital width	Greatest width of the bases of the paraoccipital processes
Atlas width	Greatest width of atlas across the wings
C2 length	Physiological length of second cervical vertebra
Scapula length	Height of scapula along spine
Scapula area	Surface area of lateral aspect of scapula ^a
Humerus length	Physiological length of humerus
Radius length	Physiological length of radius
Olecranon length	Length from estimated center of rotation of trochlear notch to proximal extent of olecranon process
Metacarpal length	Physiological length of 3rd metacarpal
Pisiform length	Length of pisiform from midpoint on border of ulnar carpal/styloid articular surfaces to palmar surface
Humerus epicondyle width	Epicondylar width of distal end of humerus
Styloid width	Width of distal end of articulated radius/ulna
Ischium length	Length from estimated center of rotation of acetabulum to medial angle of ischiatic tuberosity
Femur length	Physiological length of femur
Tibia length	Physiological length of tibia
Calcaneus length	Length of calcaneal process from proximo-dorsal border of articulation with talus to the insertion of the calcaneal tendon
Metatarsal length	Physiological length of 3rd metatarsal
Femur epicondyle width	Epicondylar width of distal end of femur
Hindlimb malleolus width	Width of distal end of articulated tibia/fibula

^aCalculated using digital imaging software (ImageJ; Rasband 2015).

all 20 individual skeletal measurements; GM; Jungers et al. 1995) as the independent variable, and sex as a covariate. A significant ($P < 0.05$) interaction term indicated allometric scaling and the given functional index data for a given species was removed from further analysis.

For each functional index within each species, we quantified sexual dimorphism in functional indices (SD_{FI}) as (Lovich and Gibbons 1992; Smith 1999):

$SD_{FI} = (\text{mean male value}/\text{mean female value})$, when the male mean was greater, and

$SD_{FI} = 2 - (\text{mean female value}/\text{mean male value})$, when the female mean was greater.

All SD_{FI} values were ln-transformed. We tested each functional index for evidence of phylogenetic signal by comparing log likelihood values of models incorporating no phylogenetic signal ($\lambda = 0$) against an optimized Pagel's λ (optimized by maximum likelihood of PGLS models; Pagel 1999; Freckleton et al. 2002). For indices with significant phylogenetic signal (likelihood ratio test; $P < 0.05$), we used phylogenetic paired t -tests (Lindenfors et al. 2010) with optimized λ to test for consistent sex differences across our dataset. For indices with no significant

phylogenetic signal, we used nonphylogenetic two-tailed paired t -tests. P -values were adjusted to correct for multiple comparisons using the false discovery rate procedure (Benjamini and Hochberg 1995). Significance levels were set at $\alpha = 0.05$ for all statistical tests. The phylogeny used for analyses was taken from a recent species-level Carnivora supertree (Nyakatura and Bininda-Emonds 2012).

We then calculated mean skeletal shape dimorphism for each species (SD_{MEAN}) by taking the mean of SD_{FI} values. We used these values to compare alternative models for the evolution of skeletal shape dimorphism using the phylogenetic comparative modeling approach of Butler and King (2004). Specifically, we compared six adaptive (Ornstein-Uhlenbeck; OU) models based on different evolutionary scenarios, one OU model with a single global optimum (implying stabilizing selection), and one model of pure random drift (Brownian motion; BM). These methods use maximum likelihood to estimate the strength of selection (α) and random drift (σ) on a continuous trait (here, mean skeletal shape dimorphism), as well as adaptive optimum values (θ) for that trait. The six adaptive OU models were based on discretely (all binary) coded life history traits, representing different selective regimes. The number of species in each category for each model is shown

Table 2. Morphological indices, definitions, and functional interpretations associated with morphological specialization for aggression.

Index	Definition
Skull shape index	Skull width relative to total length (Skull width/Skull length). Indicates relative ability to generate bite force, given that a wider skull is associated with larger jaw-closing muscles and/or a shorter skull (i.e., shorter snout) increases the mechanical advantage of the jaw-closing muscles (Biknevicius and Van Valkenburgh 1996).
Occipital width index	Occipital width relative to length of second cervical vertebra (Occipital width/C2 length). Indicates relative size of cervical neck musculature.
Atlas width index	Atlas width relative to length of second cervical vertebra (Atlas width/C2 length). Indicates relative surface area for attachment of cervical neck musculature.
Scapula area index	Surface area of lateral aspect of scapula relative to scapula length ($(\sqrt{\text{Scapula area}})/\text{Scapula length}$). Indicates relative size of muscles involved in the transfer of forces from the trunk to the forelimbs (Carrier et al. 2006) and in stabilizing the shoulder joint (Hildebrand and Goslow 2001).
Forelimb proportions index	Length of proximal forelimb relative to length of distal forelimb ($(\text{Scapula length} + \text{Humerus length})/(\text{Radius length} + \text{Metacarpal length})$). Indicates degree of morphological specialization for producing large out-forces in the forelimb (Hildebrand and Goslow 2001).
Humerus epicondyle index	Humerus epicondyle width relative to humerus length (Humerus epicondyle width/Humerus length). Indicates relative surface area for attachment of wrist and digit flexor, extensor, pronator, and supinator muscles (Evans 1993; Meachen-Samuels and Van Valkenburgh 2009; Samuels et al. 2013).
Olecranon mechanical advantage	Length of olecranon process relative to length of distal forelimb ($\text{Olecranon length}/(\text{Radius length} + \text{Metacarpal length})$). Indicates anatomical mechanical advantage of triceps brachii, an elbow extensor (Samuels et al. 2013).
Styloid width index	Styloid width relative to radius length (Styloid width/Radius length). Indicates relative robusticity of distal forelimb.
Pisiform mechanical advantage	Length of pisiform relative to length of manus ($\text{Pisiform length}/\text{Metacarpal length}$). Indicates anatomical mechanical advantage of flexor carpi ulnaris, a wrist flexor (Evans 1993).
Ischium mechanical advantage	Length of ischium relative to total hindlimb length ($\text{Ischium length}/(\text{Femur length} + \text{Tibia length} + \text{Metatarsal length})$). Indicates anatomical mechanical advantage of main hindlimb retractor muscles (e.g., biceps femoris, semimebranosus, semitendinosus; Evans 1993).
Femur epicondyle index	Femur epicondyle width relative to femur length ($\text{Femur epicondyle width}/\text{Femur length}$). Indicates relative surface area for attachment of hip extensor, knee flexor, and foot plantarflexor muscles (e.g., semimembranosus, gastrocnemius, extensor digitorum longus; Evans 1993; Samuels et al. 2013).
Hindlimb malleolus index	Hindlimb malleolus width relative to tibia length ($\text{Hindlimb malleolus width}/\text{Tibia length}$). Indicates relative robusticity of distal hindlimb.
Calcaneus mechanical advantage	Length of calcaneal process relative to length of pes ($\text{Calcaneus length}/\text{Metatarsal length}$). Indicates anatomical mechanical advantage of ankle extensors (e.g., gastrocnemius).

Indices are calculated from measurements listed in Table 1.

in parenthesis. The first adaptive model was based on the presence ($N = 12$ species) or absence ($N = 14$) of polygyny, with polygyny defined as more than one female per male, either within a breeding group or within an exclusive territory. The second adaptive model (parental care) differentiated between species in which only the female provides care for young ($N = 14$) versus those in which the female has adult helpers of any sort ($N = 12$). The third adaptive model (diet) distinguished between species that are truly carnivorous ($> 60\%$ of diet is meat; $N = 12$) or not primarily carnivorous (omnivores, insectivores, frugivores; $N = 14$). The fourth adaptive model (locomotor zone) separated species that are

primarily terrestrial ($N = 17$) from those that are both terrestrial and frequently arboreal ($N = 9$). The fifth adaptive model (social group size) separated strictly solitary species ($N = 13$) from those in which unrelated adults regularly associate and share a common home range ($N = 13$). The sixth adaptive model (foraging group size) distinguished between species in which individuals forage alone ($N = 20$) or in groups ($N = 6$). Life history trait categories were derived from previous comparative analyses of Carnivora (Gittleman 1985; Gittleman 1986; Creel and Macdonald 1995; Gittleman and Van Valkenburgh 1997). Life history data was obtained from these sources and other references (Nowak 1999;

Table 3. Mean sexual dimorphism (SD_{FI}) and descriptive statistics for functional indices across 26 Carnivora species.

Index	Mean SD_{FI} (std. dev.)	t	df	P
Skull shape index	1.036 (0.038)	-5.040	25	0.0001***
Occipital width index	0.993 (0.028)	1.257	24	0.2210
Atlas width index	1.025 (0.037)	-3.523	25	0.0027**
Scapula area index	1.008 (0.012)	-3.318	22	0.0044**
Forelimb proportions index ^a	1.012 (0.018)	-1.950	25	0.0688
Humerus epicondyle index	1.025 (0.026)	-4.801	25	0.0002***
Olecranon MA	1.027 (0.023)	-6.196	25	< 0.0001***
Styloid width index	1.026 (0.029)	-4.573	25	0.0002***
Pisiform MA	1.021 (0.033)	-3.217	24	0.0044**
Ischium MA	1.034 (0.032)	-5.323	23	0.0001***
Femur epicondyle index	1.020 (0.024)	-4.234	25	0.0005***
Hindlimb malleolus index	1.027 (0.025)	-5.444	25	0.0001***
Calcaneus MA	1.019 (0.029)	-3.244	23	0.0044**

MA, mechanical advantage.

^aPhylogenetic paired T -test.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

T -test statistics are from two-tailed paired T -tests unless otherwise indicated. All P -values were corrected for multiple comparisons using the false discovery rate procedure.

Wilson and Ruff 1999; Hutchins et al. 2004; Garbutt 2007; Smith and Xie 2008; Hunter 2011; Kingdon and Hoffmann 2013). For each adaptive model, we reconstructed ancestral character states based on maximum likelihood estimates using data from as many terrestrial Carnivora species as possible for which we could find reliable information ($N = 84, 125, 203, 184, 163,$ and 164 species for the first through sixth adaptive models, respectively, as described above). We then fit each model to SD_{MEAN} values from our set of 26 species. Model fits were compared using the Akaike Information Criterion corrected for small sample size (AICc) and $\Delta AICc$ values. A $\Delta AICc$ score of < 4 indicates strong support for a candidate model (Burnham and Anderson 2002). Analyses were performed in the R statistical environment (R Development Core Team 2015) using the “ape” (Paradis et al. 2004), “geiger” (Harmon et al. 2008), “ouch” (Butler and King 2004), and “phytools” (Revell 2012) packages.

Finally, we used Spearman rank correlations to examine relationships between mean skeletal shape dimorphism (SD_{MEAN}) and mean body size dimorphism (SD_{GM} ; calculated using the same method as SD_{FI} values), a proxy for the intensity of male-male competition (see above), as well as male mass, female mass, and mean mass for each species. To graphically summarize the data set, we plotted SD_{GM} and SD_{FI} values for each species onto the Carnivora phylogeny used in the analysis above. We plotted a given value onto the phylogeny only when a univariate ANOVA indicated sexual dimorphism was present ($P < 0.05$) and no evidence of allometry was found.

Results

Of 338 total comparisons (13 functional indices each for 26 species), nine were removed from further analysis due to evidence of allometric scaling. One of 13 functional indices was found to have significant phylogenetic signal: the forelimb proportions index ($\lambda = 0.889$; $2 LR = 4.728$; $P = 0.030$). For all other functional indices, no significant phylogenetic signal was detected ($P > 0.05$). Phylogenetic (for the forelimbs proportions index) and nonphylogenetic (for all others) paired t -tests indicated significant sexual dimorphism in 11 of 13 functional indices (Table 3). In all significant results, males had greater mean functional index values.

Phylogenetic model comparison indicated one model with strong support ($\Delta AICc < 4$) over all other candidate models (Table 4). The best-fitting model was based on the presence or absence of polygyny. This model also received the largest proportion of Akaike weights (0.750) whereas all other candidate models had weights < 0.1 , indicating strong support for the polygyny model over others. The single optimum model had the second best fit and the BM model had the poorest fit. Parameter estimates for all adaptive models are shown in Table 5. Each of these showed strong selection (i.e., large α values) with low levels of drift (i.e., small σ values). For the best-fitting model, evolutionary optima estimates show greater optimum values for SD_{MEAN} in polygynous ($\theta = 1.029$) versus nonpolygynous ($\theta = 1.011$) species.

Across species, SD_{MEAN} was positively correlated with SD_{GM} whether including (Spearman $r = 0.430$, $P = 0.029$;

Table 4. AICc scores and Akaike weights for BM and OU models fit to mean skeletal shape dimorphism data.

Model	AICc	Δ AICc	Akaike weights
Polygyny	-146.586	0	0.750
Single optimum	-142.114	4.472	0.080
Locomotor zone	-140.888	5.698	0.043
Social group size	-140.801	5.785	0.042
Foraging group size	-139.970	6.616	0.027
Parental care	-139.906	6.680	0.027
Diet	-139.711	6.875	0.024
Brownian motion	-137.117	9.469	0.007

Δ AICc values are relative to the best-fitting model.

Table 5. Model parameters for all models of selective regimes fit to mean skeletal shape dimorphism data.

Model	α	σ	Selective optima	
			Character state	θ
Polygyny	9.692	0.053	Nonpolygynous	1.011
			Polygynous	1.029
Single optimum	4.606	0.045	Single state	1.020
Locomotor zone	14.607	0.072	Terrestrial	1.017
			Arboreal	1.029
Social group size	5.175	0.045	Solitary	1.024
			More than 1	1.015
Foraging group size	4.626	0.044	Solitary	1.019
			More than 1	1.029
Parental care	5.021	0.046	Female only	1.022
			Female plus helpers	1.016
Diet	4.987	0.046	Noncarnivorous	1.022
			Carnivorous	1.017

α = strength of selection.

σ = strength of random drift.

θ = estimated optimum for a given selective regime.

Fig. 1A) or not including (Spearman $r = 0.413$, $P = 0.037$; Fig. S1) the one trait with significant phylogenetic signal. SD_{MEAN} was not correlated with mean species mass (Spearman $r = 0.167$, $P = 0.413$; Fig. 1B), male mass (Spearman $r = 0.160$, $P = 0.432$; Fig. S2A), or female mass (Spearman $r = 0.139$, $P = 0.496$; Fig. S2B). A graphical summary showing the presence and degree of dimorphism in each functional index in each species is presented in Figure 2. Means, standard deviations, sample sizes, and descriptive statistics for all comparisons are included in the electronic supplementary (Table S2).

Discussion

Our results indicate that sexual dimorphism in skeletal shape is widespread in Carnivora. When testing for differences among the

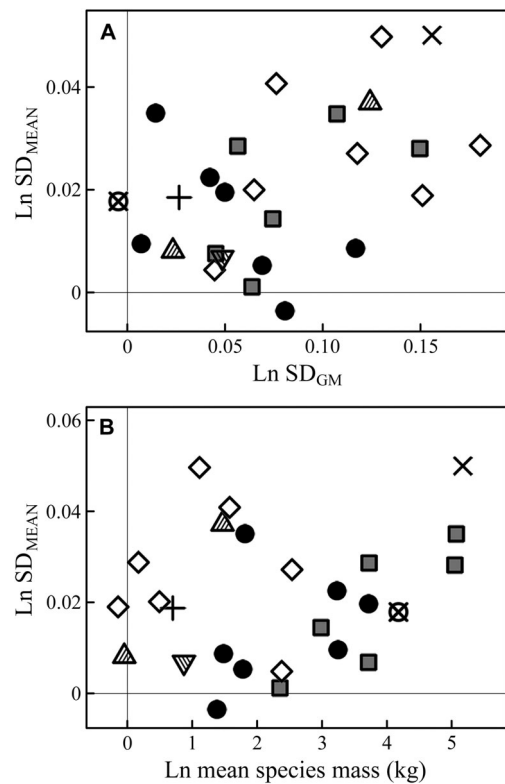


Figure 1. Mean skeletal shape dimorphism (SD_{MEAN}) plotted against (A) sexual dimorphism in body size (SD_{GM}) and (B) mean species mass for 26 Carnivora species. Spearman rank correlations indicate that SD_{MEAN} is positively correlated with SD_{GM} ($r = 0.430$, $P = 0.029$) but not with mean species mass ($r = 0.167$, $P = 0.413$). Unique symbols represent families: ● Canidae, ■ Felidae, ⊗ Hyaenidae, ▽ Mephitidae, ◇ Mustelidae, + Nandiniidae, ▲ Procyonidae, × Ursidae.

26 species in our dataset, males exhibited greater mean values in 11 of 13 functional indices thought to improve aggressive performance. Phylogenetic comparative model selection indicated that the evolution of skeletal shape dimorphism is associated with sexual selection, specifically the presence or absence of polygyny in the mating system. Models based on locomotor zone, social and foraging group sizes, parental care, diet, and pure random drift received substantially less support. Skeletal shape dimorphism was positively correlated with sexual dimorphism in body size, a proxy of the intensity of male–male competition, but not with mean species mass, male mass, or female mass. Along with testing each metric for evidence of allometric scaling, this demonstrates that skeletal shape dimorphism is not a consequence of body size scaling relationships. Together, these results support the hypothesis that male carnivorans exhibit greater morphological specialization for aggression than females and that skeletal shape dimorphism in Carnivora is associated with selection on improved performance in male–male contests that are more frequent and intense in polygynous mating systems (e.g., Kay et al.

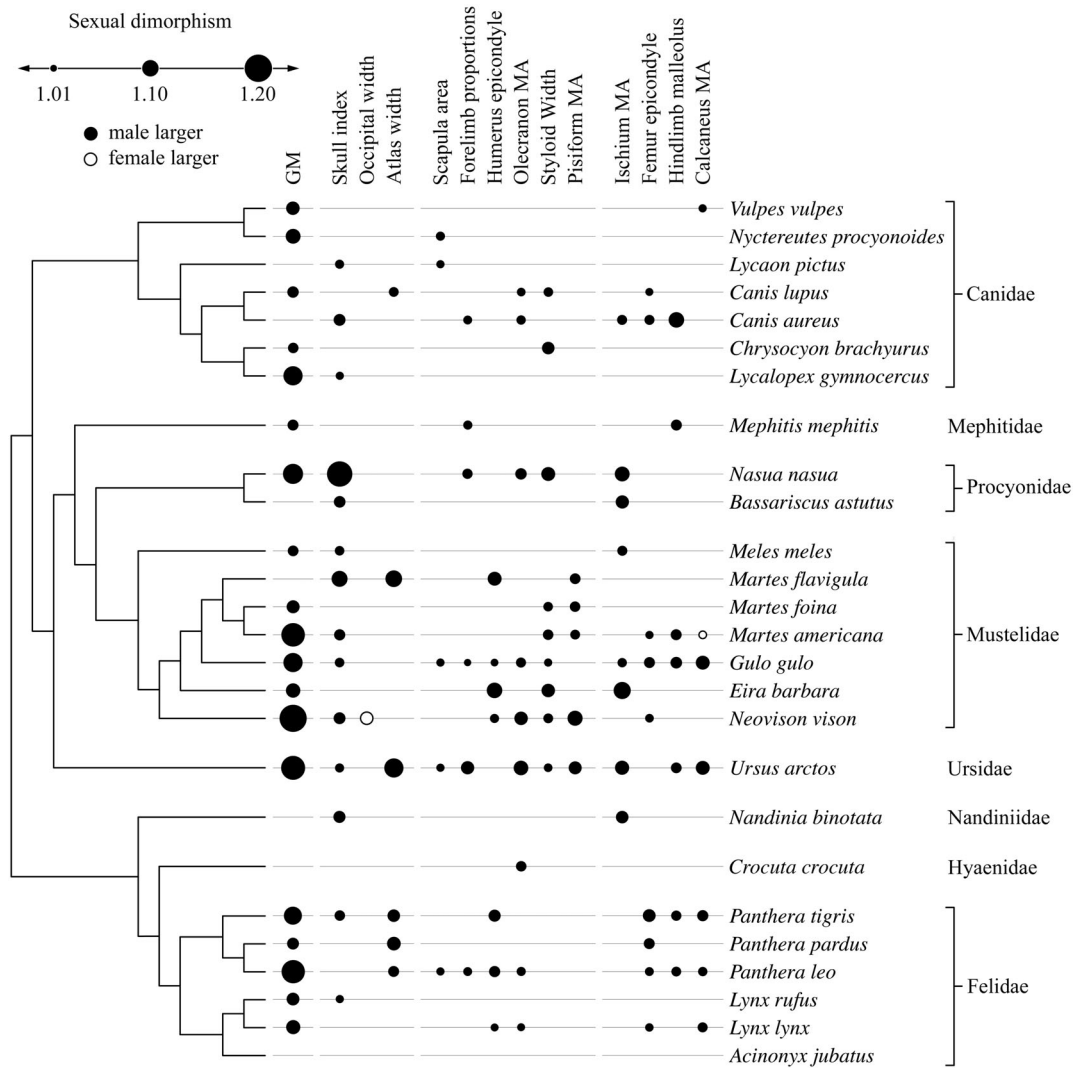


Figure 2. Graphical summary of all data used in the analysis. Plotted SD_{FI} points indicate traits that were sexually dimorphic ($P < 0.05$; ANOVA). The size of a point indicates the degree of sexual dimorphism. Geometric mean (GM) is provided as indicator of the degree of sexual dimorphism in overall body size. See text for details of methodology. The phylogeny is pruned from a recent Carnivora supertree (Nyakatura and Bininda-Emonds 2012).

1988; Mitani et al. 1996; Weckerly 1998; Bro-Jørgensen 2007). The prevalence of skeletal dimorphism in our dataset indicates the evolutionary significance of male–male competition in carnivorans, given that sexual dimorphism is both slow to evolve and often maladaptive in regard to natural selection (Darwin 1874; Lande 1980; Rogers and Mukherjee 1992; Reeve and Fairbairn 1996).

Sexually dimorphic traits in the skull and neck identified by our analysis include relatively broader skulls (skull shape index) and necks (atlas width index). Broader skulls allow greater bite force by increasing the size of the jaw-closing muscles (masseter and temporalis; Biknevicius and Van Valkenburgh 1996). Similarly, a broader neck allows more robust cervical musculature that increases force capacity for tearing with the teeth by jerking the

skull. More robust cervical musculature increases safety factors (Alexander 1981) by providing a greater ability to resist torsional loading (Radinsky 1981) that occurs during aggressive interactions. Cervical neck muscles are also involved in protraction of the forelimbs (Evans 1993) that may be important when grappling or striking. In postcranial anatomy, males had relatively broader scapulae (scapula area index), allowing greater mass of muscles involved in stabilizing the shoulder joint (Goslow et al. 1981). Males also had larger mechanical advantages (anatomical muscle in-lever/out-lever) in all lever systems that we measured. In the forelimbs, these were associated with the triceps (olecranon mechanical advantage) and flexor carpi ulnaris (pisiform mechanical advantage) muscles, allowing greater force output during elbow extension and wrist flexion, respectively. More robust forelimb

bones (humerus epicondyle index and styloid width index) increase areas for muscle attachment and provide larger safety factors for bones experiencing high loading. Functionally, these traits increase total forces available for striking or manipulating opponents and may improve balance control, turning, and acceleration. In the hindlimbs, males had more robust distal limb bones (femur epicondyle index and hindlimb malleolus index) and larger mechanical advantages associated with hindlimb retraction (ischium mechanical advantage) and ankle extension (calcaneus mechanical advantage). Similar to those found in the forelimbs, these traits increase forces available for accelerating the body and may increase stability.

Many of these traits may be adaptive by providing functional advantages during behaviors other than male–male competition (e.g., when capturing prey is physically demanding; Morris and Brandt 2014). Our inclusion of species with a broad range of life history traits allows the direct comparison of alternative scenarios driving the evolution of skeletal shape dimorphism. Specifically, our dataset includes species spanning a broad range of body masses, from less than 1 kg (*Martes americana*) to greater than 200 kg (*Ursus arctos*), a variety of social systems, from generally monogamous canids to highly polygynous mustelids and ursids (Wilson and Reeder 2005), and disparate dietary niches, including hypercarnivorous felids, insectivores (*Mephitis mephitis* and *Meles meles*), frugivores (*Nandinia binotata*), and omnivores (e.g., *Chrysocyon brachyurus*, *Nyctereutes procyonoides*, *Bassariscus astutus*). The results of our model selection analysis indicate strong support for the polygyny model over all other candidate models. This indicates that behaviors associated with mating system are under stronger selective pressure than the other life history traits included in our analysis. The greater evolutionary optimum value for skeletal shape dimorphism in polygynous species as compared to nonpolygynous species indicates that behaviors associated with polygyny are under strong selection. Greater values for functional indices in males are expected to be highly adaptive because of their importance in male–male competition, which is both more intense and more frequent in polygynous species. Evidence from correlational analysis provides further support for this. Sexual size dimorphism is a commonly used proxy for the intensity of sexual selection because it is positively correlated with the degree of male–male competition in carnivorans (Weckerly 1998; Lindenfors et al. 2002; Cullen et al. 2014), primates (Clutton-Brock et al. 1977; Leutenegger and Kelly 1977; Clutton-Brock 1985; Ford 1994; Mitani et al. 1996; Plavcan 2012), ungulates (Jarman 1983; Loison et al. 1999), and other mammals (Alexander et al. 1979). In our data set, skeletal shape dimorphism and sexual size dimorphism were positively correlated, suggesting that skeletal shape is under strong selection in males, leading to more pronounced dimorphism in species characterized by more intense male–male competition. This positive correla-

tion appears to be followed by most taxa in our dataset with the exception of the canids. Though lacking adequate power ($N = 7$ species for Canidae) for proper analysis, skeletal shape dimorphism among our canid species appears to decrease with size dimorphism. Because there are no patterns between the degree of shape dimorphism in canids in relation to any other life history traits considered (e.g., diet, degree of sociality), this result remains unresolved.

At least one sexually dimorphic skeletal shape index was identified in nearly all species that we measured. As discussed earlier, differences in the number and degree of dimorphic traits is largely predicted by the presence or absence of polygyny in the mating system. Variability in which traits are dimorphic among species may be a product of differences in the mechanics of male–male combat, as has been suggested for lizards (Lailvaux et al. 2004; Lailvaux and Irschick 2006; Cameron et al. 2013), kangaroos (Jarman 1983, 1989), and humans (Morgan and Carrier 2013; Carrier and Morgan 2015; Horns et al. 2015). These differences may also reflect constraints on trait evolution imposed by other behaviors (Maynard Smith et al. 1985; Lauder 1991; Carrier 2002; Oufiero and Garland 2007). For example, the lack of dimorphism in the cheetah (*Acinonyx jubatus*), the only species for which no dimorphism was detected, may be an extreme example of a conflict between the demands of terrestrial locomotion and characters that improve aggressive performance (discussed below). The lack of female-biased dimorphic traits in the spotted hyena (*Crocuta crocuta*) is somewhat surprising, given that females are the dominant and more aggressive sex (Kruuk 1972). These results agree, however, with other studies showing limited or absent dimorphism in this species (reviewed in Swanson et al. 2013). The evolution of female-biased dimorphism in aggression-based traits may be limited by differences in the expression of testosterone-mediated traits in males and females (Ketterson et al. 2005).

Though less pronounced than in polygynous species, many socially monogamous species were found to be dimorphic in skeletal shape. This result is interesting given that many of these species are only weakly dimorphic in body mass (e.g., *Canis aureus*). Improved male aggressive performance in these species may be adaptive for limiting extra-pair copulations through behaviors such as mate-guarding or direct control of conspecific competitors or packmates (see Jennions and Petrie 2000; Brotherton and Komers 2003; Clutton-Brock and Isvaran 2006; Cohas et al. 2006). An increasing amount of evidence suggests that genetic monogamy is rare, even among socially monogamous species (e.g., Cohas and Allainé 2009). To date, extra-pair paternity has been identified in seven socially monogamous canid species, including several in this study (*Canis lupus*, *Lycan pictus*, and *Vulpes vulpes*; reviewed in Morris and Brandt 2014). Thus, skeletal dimorphism in these species may indicate the adaptive significance of male aggression and male–male competition

even in species with socially monogamous mating systems. This is supported by an evolutionary optimum value > 1 for nonpolygynous species in the best-fitting model. Male aggressive performance in these species may also be beneficial when establishing and defending territories or for the increased burden on males to capture prey in order to provision the female after a litter is born (Mech 1999; Morris and Brandt 2014). Alternatively, the low level of skeletal dimorphism in socially monogamous species may be associated with factors unrelated to intraspecific aggression.

Our results are in agreement with previous studies on sexual dimorphism in skeletal morphology in mammals. In a comparative study on 45 carnivoran species, Gittleman and Van Valkenburgh (1997) found widespread male-biased sexual dimorphism in canine size and muscle moment arms in the jaw-closing muscles. These dimorphic traits were related predominantly to mating system and not to mean species mass, diet, or habitat. Jarman (1983, 1989) reported male-biased sexual dimorphism in forearm bone length and muscle mass in a broad sample of kangaroos and associated these differences with the use of the forelimbs as weapons during male–male competition. Warburton et al. (2013) extended these results in one species of kangaroo (*Macropus fuliginosus*), showing that the most dimorphic muscles were those associated with grappling (shoulder adductors, arm retractors, and elbow flexors). Similarly, pronounced dimorphism is present in the forelimbs of western lowland gorillas (*Gorilla gorilla*; Zihlman and McFarland 2000) and humans (Fuller et al. 1992; Nindl et al. 2002; Abe et al. 2003; Lassek and Gaulin 2009), species that also use their forelimbs as weapons during conflict (Wrangham and Peterson 1996). Male contest competition is the best supported life history variable for dimorphism in weapon size in other taxa: canines in primates (Plavcan and van Schaik 1992; Plavcan 2001, 2012), antlers in cervids (Clutton-Brock et al. 1980), and horns in bovids (Bro-Jørgensen 2007).

In contrast to previous studies, here we have found evidence of dimorphism in the primary locomotor system. Interestingly, several of these aggression-based traits may directly conflict with locomotor performance (Carrier 2002). Elongated distal limb elements with reduced distal mass are associated with economical and high speed locomotion (Gambaryan 1974; Hildebrand 1985b; Van Valkenburgh 1987; Steudel 1990; Garland and Janis 1993; Samuels et al. 2013) but these traits are in direct contrast to the aggression-based traits in our analysis. Similarly, greater mechanical advantages increase force output but at the cost of decreased velocity when swinging the limbs (Maynard Smith and Savage 1956; Hildebrand 1985b). Thus, traits that improve aggressive performance may represent a functional trade-off with locomotor performance (Pasi and Carrier 2003; Kemp et al. 2005) in the musculoskeletal system of male carnivorans. This is particularly interesting when considering that carnivorans typically have much greater daily movement distances, and therefore possibly a

greater dependence on locomotor economy, than other mammal groups (Garland 1983). Locomotor-aggression trade-offs may be common among animals but are rarely examined. In two studies testing for these trade-offs in territorial lizard species, the authors found decreased locomotor performance in individuals with larger head size (López and Martín 2002) and in individuals with both larger head size and greater bite force (Cameron et al. 2013). Though the adaptive model based on locomotor zone in the present study received substantially less support than the best model, the high α value (strength of selection) and greater evolutionary optimum value for arboreal species suggests that terrestrial locomotion may impose a stronger constraint on postcranial trait evolution than arboreal locomotion. The lack of skeletal shape dimorphism in the cheetah may be an example of this constraint. Alternatively, the greater degree of skeletal dimorphism in arboreal species may be associated with sex-based differences in arboreal locomotor behavior (Doran 1993; but see Isler 2005).

In summary, we found evidence of skeletal shape dimorphism among a sample of 26 species within Carnivora. Skeletal proportion traits that are predicted to enhance performance in physical competition tend to be sexually dimorphic in carnivorans, making males better equipped for intraspecific competition. The evolution of this dimorphism appears to have been driven mainly by sexual selection, specifically the presence or absence of polygyny in the mating system. Variability in dimorphic traits among species may reflect different fighting tactics, social contexts (e.g., dyads vs. coalitions; Plavcan et al. 1995), or other behavioral or phylogenetic constraints. Many of the postcranial traits in our analysis may functionally conflict with locomotor economy. This functional trade-off may impose greater limits on trait evolution in the primary locomotor system of terrestrial as compared to arboreal species.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Figure S1. Mean skeletal shape dimorphism (SD_{MEAN}) plotted against sexual dimorphism in body size (SD_{GM}) for 26 Carnivora species.

Figure S2. Mean skeletal shape dimorphism (SD_{MEAN}) plotted against body mass (in kg) for 26 Carnivora species.

Table S1. Specimen identification numbers, listed by species and sex.

Table S2. Means and standard deviations (std. dev.), sample sizes, and descriptive statistics for functional indices and geometric means (GM) of all skeletal measurements for all carnivoran species in the study.