

Specialization for aggression in sexually dimorphic skeletal morphology in grey wolves (*Canis lupus*)

Jeremy S. Morris and Ellissa K. Brandt

Department of Biology, University of Utah, Salt Lake City, UT, USA

Abstract

Aggressive behaviour is important in the life history of many animals. In grey wolves (*Canis lupus*), territory defence through direct competition with conspecifics is severe and often lethal. Thus, performance in aggressive encounters may be under strong selection. Additionally, grey wolves frequently kill large dangerous prey species. Because both sexes actively participate in aggressive activities and prey capture, wolves are expected to exhibit a low level of musculoskeletal sexual dimorphism. However, male wolves more often lead in agonistic encounters with conspecifics and must provision the nursing female during the pup-rearing period of the breeding season. These behaviours may select for males that exhibit a higher degree of morphological adaptation associated with aggression and prey capture performance. To test this prediction, we assessed skeletal sexual dimorphism in three subspecies of grey wolves using functional indices reflecting morphological specialization for aggression. As expected, sexual dimorphism in skeletal shape was limited. However, in two of three subspecies, we found sexually dimorphic traits in the skull, forelimbs and hindlimbs that are consistent with the hypothesis that males are more specialized for aggression. These characters may also be associated with selection for improved prey capture performance by males. Thus, the sexually dimorphic functional traits identified by our analysis may be adaptive in the contexts of both natural and sexual selection. Several of these traits may conflict with locomotor economy, indicating the importance of aggression in the life history of male grey wolves. The presence of functional specialization for aggression in a generally monogamous species indicates that sexual dimorphism in specific musculoskeletal traits may be widespread among mammals.

Key words: aggression; *Canis lupus*; functional trade-offs; locomotion; prey capture; sexual dimorphism.

Introduction

Aggressive behaviour plays a key role in many aspects of the life history and ecology of animals. Though relatively rare, violent interactions occur in most vertebrate species (Sherrow, 2012), and have profound effects on individual fitness through survival, resource acquisition and access to mates (Andersson, 1994). In mammals, the evolution of sexual dimorphism is generally associated with sexual selection acting on males to improve their ability to compete for mates (Darwin, 1871; Andersson, 1994), whereas the female phenotype is closer to a natural selection optimum (Lande, 1980). The degree of sexual dimorphism among mammalian species is positively correlated with the intensity of male–

male competition (Weckerly, 1998) and degree of polygyny (Gittleman & Van Valkenburgh, 1997), and inversely correlated with the amount of male parental investment (Trivers, 1972).

Male reproductive success is often linked to fighting ability (Le Boeuf, 1974; Clutton-Brock et al. 1982). Sexual size dimorphism is typically attributed to sexual selection for greater body mass in males that improves performance during male–male contests (Andersson, 1994), putatively by increasing the absolute forces and momentum that may be applied to a competitor. In predatory species, greater body mass in males may also improve prey capture performance (MacNulty et al. 2009) and allow males to hunt larger prey (Caro & Fitzgibbon, 1992; Sand et al. 2006). In addition to body mass, other musculoskeletal characteristics often play an important role in determining the outcome of agonistic encounters. In studies on territorial lizard species, bite force is the strongest predictor of the outcome of male–male contests (Lailvaux et al. 2004; Huyghe et al. 2005), female density within a territory (Lappin & Husak, 2005), and number of progeny sired (Husak et al. 2009). Similarly, agility

Correspondence

Jeremy S. Morris, Department of Biology, University of Utah, 257 S 1400 E, Salt Lake City, UT 84112, USA. T: 423 208 2975; E: j.s.morris@utah.edu

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and manoeuvrability may be more important than large body size in aerial male contests among species of shorebirds (Székely et al. 2000) and bustards (Raihani et al. 2006), and during arboreal male contests in primates (Lawler et al. 2005). Among terrestrial species, high force production and agility play important roles during agonistic encounters. Jumping ability (velocity and acceleration) is correlated with winning in contests between size-matched 'lightweight' male anoles (*Anolis carolinensis*; Lailvaux et al. 2004). Similarly, sprint speed is correlated with winning in paired contests between size-matched males in other territorial lizard species (Garland et al. 1990; Robson & Miles, 2000). Thus, the relative importance of specific functional traits varies with the type of male–male combat (Lailvaux et al. 2004; Lailvaux & Irschick, 2006).

Male mammals in the order Carnivora use their teeth, jaws and forelimbs as primary weapons when fighting with conspecifics (for an example in grey wolves, see Landis, 2010). The importance of the skull and teeth in male contests among carnivorans is indicated by male-biased sexual dimorphism in canine size and muscle moment arms in the temporalis and masseter muscles (Gittleman & Van Valkenburgh, 1997). These dimorphic traits are also found in multiple species of primates in which males compete (reviewed in Plavcan, 2001). Pushing, grappling and striking events occur during aggressive encounters that involve force application in highly variable directions (Kemp et al. 2005), increasing the risk of injury (Alexander, 1981). Morphological specialization for these interactions likely results in broad body plans that increase stability, robust limb bones that resist bending and torsional moments, and high mechanical advantages that increase forces available to strike or manipulate opponents or to quickly reorient and accelerate the body (Pasi & Carrier, 2003; Kemp et al. 2005). Many of these traits are also expected to improve performance when carnivorans attack and kill large prey species. Thus, these morphological characters may be adaptive in the contexts of both sexual and natural selection.

In the context of specialization for physical aggression, grey wolves (*Canis lupus*) are an interesting species. Both male and female grey wolves hunt and kill dangerous prey animals (e.g. moose, bison, elk; Mech, 1999), and defend against kleptoparasitism by other carnivorans such as cougars and bears (Murie, 1944; Mech & Boitani, 2003). Furthermore, both sexes aggressively defend against territorial incursions by conspecifics (Mech, 1993). Contrary to typical mammalian social patterns, parental investment from both sexes is high and dominance/leadership roles are shared by the breeding pair (Mech, 2000). Because both males and females actively engage in all of these activities, wolves are expected to exhibit a low level of musculoskeletal sexual dimorphism. Indeed, dimorphism in body mass in *C. lupus* is limited (males approximately 20% larger than females; Mech, 1970) as compared with other carnivorans (Bekoff et al. 1981).

However, behavioural differences between the sexes have been described. Among aggressive behaviours, males lead more often than females in agonistic encounters and territorial disputes with conspecifics (reviewed in Mech, 2000), and are more likely to chase and attack individual wolves (Yellowstone Wolf Project, unpublished data, in Cassidy, 2013). Conflicts among packs and/or lone individuals are often lethal (Mech, 1994), with intraspecific strife responsible for up to 65% of natural wolf mortality (Mech et al. 1998). Recent evidence from Yellowstone National Park indicates that the number of adult males in a pack increases the likelihood of winning in interpack aggressive encounters, suggesting that adult males influence the outcome of territorial contests more than other pack members (Cassidy, 2013). Male wolves may also constitute a larger percentage of dispersers, 1- to 3-year-old individuals leaving their natal packs in search of mates and available territory (Ballard et al. 1987). Dispersal is an inherently dangerous activity (Waser, 1996; Smale et al. 1997) because territorial intrusions may occur and grey wolves commonly attack and kill trespassers within their territories (reviewed in Mech & Boitani, 2003). Additionally, males may join established packs to become dominant breeders, while this behaviour is rare or absent in females (VonHoldt et al. 2008). This process may take weeks, with the immigrant male frequently being attacked by pack members (Yellowstone Wolf Project, unpublished data). Because wolf–wolf conflict is frequent and severe, and given the associated behavioural differences, selection on morphology associated with intraspecific aggression is expected to be stronger in males than in females.

In the context of feeding ecology, a 'division of labour' system (Mech, 1999) occurs for a period during the breeding season in which the female remains near the den to nurse and defend pups while the male forages and provisions the female. Because the energetic cost of lactation is so high, females must increase their food intake substantially. In *Canis familiaris* breeds of similar body size and litter size to that of grey wolves, females increase food intake by 300–400% while lactating (Scantlebury et al. 2000). In a typical wolf pack (a breeding pair and their prior offspring; Mech, 1999), the breeding male carries out the majority of provisioning the nursing female (Mech et al. 1999). Thus, it is possible that selection may act on males to increase prey capture performance (e.g. greater body mass; MacNulty et al. 2009) during this critical stage of reproductive life history. However, prey animals killed by wolves during this seasonal stage are predominantly small (e.g. neonate ungulates; Mech, 1970; Sand et al. 2008; Metz et al. 2012) and likely are not physically demanding to capture (*sensu* MacNulty et al. 2009). This may allow prey capture rates to increase (Metz et al. 2012), while mitigating selective pressure on prey capture performance. In wolf populations with greater pack sizes, female reproductive success (both litter size and pup survival) increases with the number of males in

a pack, likely a result of the greater effectiveness of males at prey capture (MacNulty et al. 2009), territory defence, and protection of offspring from intra- and interspecific threats (Stahler, 2011). Thus, morphological traits that improve performance in multiple behaviours may be under stronger selection in males.

Here, we test the hypothesis that grey wolves exhibit sexual dimorphism in functional traits likely to be important during aggressive interactions. An important caveat of this study is that morphological adaptations associated with aggression are also expected to improve performance when capturing large dangerous prey. First, we predicted that males, as compared with females, would have relatively broader skulls to house larger temporalis muscles that increase bite force (Biknevicius & Van Valkenburgh, 1996). Second, we predicted that males would have relatively broader necks that facilitate more robust cervical musculature on the cervical vertebrae and skull. This would function to increase forces available for jerking the skull in order to tear with the teeth and would also provide a greater ability to resist torsional loading of the neck (Radinsky, 1981), increasing safety factors (Alexander, 1981) and decreasing the risk of injury. Additionally, the cervical vertebrae are the origin site for extrinsic appendicular muscles that protract the forelimb (Evans, 1993), and may be important during grappling or pushing. The third prediction was that males would have broader scapulae, capable of housing larger muscles associated with the transmission of forces from the trunk to the forelimbs, providing stability and doing work at the shoulder joint (Carrier et al. 2006). Finally, we predicted that males would have more robust limbs with greater anatomical mechanical advantages. Robust bones are expected because the forelimbs function as levers for force application and because, during grappling, these bones may experience bending loads that exceed the animal's own muscular capacities (Kemp et al. 2005). Broader distal ends of long bones (e.g. humeral epicondyle) allow for greater surface areas for muscle attachment (Hildebrand, 1985a). Larger distal limb muscles may improve balance control, rapid turning and acceleration, and opponent manipulation (Pasi & Carrier, 2003). Greater anatomical mechanical advantages (anatomical muscle in-lever/out-lever) around the limb joints function to increase muscle forces (Maynard Smith & Savage, 1956; Hildebrand, 1985b) that may be applied to the substrate or an opponent. During fighting, the limbs are often oriented at high angles relative to the principal axis of force transmission, decreasing the effective mechanical advantage. Increasing the anatomical mechanical advantages of the limbs may circumvent this constraint on force production. While grey wolves are certainly adapted for efficient locomotion as indicated by gracile forelimbs (Gambaryan, 1974; Hildebrand, 1985b; Steudel, 1990) with limited lateral joint mobility (Andersson & Werdelin, 2003; Andersson, 2004), they are nonetheless capable of creating large forces with

the forelimb muscles (Walter & Carrier, 2007, 2009). By rearing up to fight, they reorient these forces to apply to a competitor (Carrier, 2011). This is likely important for gaining leverage during fights, which may be advantageous for toppling a competitor to the ground. We also tested these predictions on the hindlimb bones given that broader hindlimbs may increase stability and high mechanical advantages increase forces available for accelerating the body.

Materials and methods

Specimens

Skeletal metrics were taken from prepared specimens of culled wolves obtained from the Idaho and Wyoming Departments of Fish and Game, and from the collections at the natural history museums listed in the Acknowledgements. Specimen identification numbers are provided in the electronic supplementary material (Table S1). All specimens measured were osteologically mature, as determined by complete fusion of epiphyses in the long bones (Evans, 1993). Though wolves may gain mass throughout adulthood (MacNulty et al. 2009), ontogenetic studies have shown geometric scaling patterns (i.e. length and width dimensions scale in direct proportion to each other) or slightly negative allometric patterns (i.e. width dimensions increase at a lower rate than length dimensions) of skeletal growth in domestic dogs (Casinos et al. 1986; Wayne, 1986). Analysis of adult specimens has shown similar patterns of geometric similarity in limb bone lengths and widths between domestic dogs and wild canids (Wayne, 1986). Additionally, broad comparative studies of terrestrial carnivorans have indicated geometric scaling of long bone length (Christiansen, 1999) and joint surface areas (humeral and femoral heads; Godfrey et al. 1991), and small deviations from geometric similarity in long bone mid-shaft diameters (Bertram & Biewener, 1990) and circumferences (Christiansen, 1999). Thus, morphological indices used in the present study should be minimally affected by increases in body size after an animal reaches adulthood. We measured all available museum specimens that were at least 80% complete skeletons with the requirement that sex and location information was available. Because this limited the number of specimens, we included data from three subspecies: *C. l. lupus* ($n=15$ females, 15 males); *C. l. lycaon* ($n=10$ females, 10 males); and *C. l. occidentalis* ($n=8$ females, 9 males). However, these subspecies were analysed separately after statistical testing revealed differences in skeletal morphology between each taxa (see below).

Morphological traits and indices

For each specimen, 20 length and breadth measurements (Table 1) were taken to the nearest 0.01 cm using digital callipers (Mitutoyo Corporation, Japan) or Vernier callipers (for lengths > 20 cm; Phase II Machine and Tool, USA). Measurement methods were adapted from von den Driesch (1976). Physiological length (Kiesewalter, 1888; von den Driesch, 1976) was used for postcranial bone length measurements. Physiological length is measured as the length between articular surfaces and describes the effective working length of a bone during use (Wilder, 1920). Additionally, we used digital imaging software (ImageJ; Rasband, 2013) to determine the surface area of the scapula. From the measurements listed in Table 1, we calculated 14 morphological indices (as in Van

Table 1 Skeletal morphometrics taken for *Canis lupus* 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*
Humerus length	Physiological length of humerus
Radius length	Physiological length of radius
Olecranon length	Length from estimated centre 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 centre 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

*Calculated using digital imaging software (ImageJ; Rasband, 2013).

Valkenburgh, 1987; Samuels & Van Valkenburgh, 2008; Meachen-Samuels & Van Valkenburgh, 2009b; Samuels et al. 2013) that quantify relative proportions, shape differences, robusticity and anatomical mechanical advantages in the skull and postcranial skeleton (Table 2). These indices reflect traits likely to be important during aggressive interactions.

Statistical analysis

Prior to analysis, we confirmed that all morphological index values were normally distributed ($P > 0.05$; Shapiro–Wilk tests) with similar variances between groups ($P > 0.05$; Bartlett's tests). We tested for shape differences between subspecies using a multivariate analysis of variance (MANOVA) with all indices included and sexes pooled. To limit the total number of comparisons (and the Type 1 error) for within-subspecies analysis, we first used MANOVAS to test for

differences in skeletal robusticity indices of the neck (included morphological indices OWI and AWI from Table 2), forelimbs (HEI, StWI) and hindlimbs (FEI, HMI). When differences in shape were indicated by a MANOVA, we then used univariate ANOVAS on the individual morphological indices included. Otherwise, those metrics were discarded from the analysis, decreasing the total number of comparisons. All mechanical advantages and limb proportions indices were tested using univariate ANOVAS. Additionally, to examine the relative contribution of skull metrics to dimorphism in the skull shape index (SSI), we examined linear regressions of skull length and skull width against the geometric mean (GM; Jungers et al. 1995) of all metrics. Sexual dimorphism was calculated as male value/female value (Lovich & Gibbons, 1992; Smith, 1999). Significance levels for ANOVAS were set at 0.10, given that we had a priori directional expectations (males larger) for all tests. To control for the false discovery rate in multiple comparisons, we used the Benjamini–Hochberg method (Benjamini & Hochberg, 1995) to determine significance levels. Finally, given the constraints imposed by correction for multiple comparisons (Moran, 2003), we used an exact binomial test to calculate the probability of our results for each subspecies due to chance alone (as in Butler & Losos, 2002). All analyses were carried out in the R statistical package (R Development Core Team, 2013).

Results

Differences between all subspecies were significant ($P < 0.05$; MANOVA), so for the main analysis of sexual dimorphism we analysed all subspecies separately. Males were significantly larger than females in nearly all morphometric variables ($P < 0.05$ in 20 of 21 metrics in *C. l. lupus*, 21 of 21 in *C. l. lycaon*, and 19 of 21 metrics in *C. l. occidentalis*; two-tailed *t*-tests; Table S2). Sex-based differences in morphological indices were limited ($P < 0.10$ in 4 of 14 indices in *C. l. occidentalis* and 5 of 14 in *C. l. lupus*; Table 3). In *C. l. occidentalis*, ANOVAS indicated sexual dimorphism in SSI, scapula shape (ScWI), a mechanical advantage in the manus (PMA), and the hindlimb proportions index (HPI), with males larger in all (SD values from 1.02 to 1.06). The binomial probability of obtaining four sex-based differences (out of 14 indices) in the predicted direction ($\alpha = 0.10$) was significant ($P = 0.044$). In *C. l. lupus*, MANOVAS indicated sex differences in forelimb shape (Wilks' Lambda = 0.79; $F_{2,27} = 3.59$; $P = 0.042$) and hindlimb shape (Wilks' Lambda = 0.84; $F_{2,27} = 2.55$; $P = 0.096$), with subsequent ANOVAS indicating a relatively wider styloid process (StWI) and femoral epicondyle (FEI) in males than in females. Males also had a larger SSI and greater mechanical advantages in the manus (PMA) and forelimb (OMA). Linear regression analyses of individual skull metrics indicated that dimorphism in the SSI is primarily due to broader skulls in males, though this was only significant for *C. l. occidentalis* [ANCOVA with GM as a covariate for skull width: $F_{1,13} = 6.16$; $P = 0.028$; $P > 0.05$ in ANCOVAS for skull width (*C. l. lupus*) and skull length (both subspecies); $P > 0.05$ for all interaction terms]. After correction for multiple comparisons, only the sexually dimorphic traits in *C. l. occidentalis* remained significant. However, we include results from *C. l. lupus* because we

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

Index	Definition
Skull shape index (SSI)	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 a shorter skull (i.e. shorter snout) increases the mechanical advantage of the jaw-closing muscles (Biknevicius & Van Valkenburgh, 1996).
Occipital width (OWI)	Occipital width relative to length of second cervical vertebra (occipital width/C2 length). Indicates relative size of cervical neck musculature.
Atlas width (AWI)	Atlas width relative to length of second cervical vertebra (atlas width/C2 length). Indicates relative size of cervical neck musculature.
Scapula width (ScWI)	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 (e.g. supraspinatus, infraspinatus; Carrier et al. 2006).
Forelimb proportions index (FPI)	Length of proximal forelimb relative to length of distal forelimb [(scapula length + humerus length)/(radius length + metacarpal length)]. Indicates degree of morphological specialization for producing large out-forces in the forelimb (Hildebrand, 1985b).
Humerus epicondyle index (HEI)	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 (Hildebrand, 1985a; Evans, 1993).
Olecranon mechanical advantage (OMA)	Length of olecranon process relative to length of distal forelimb [olecranon length/(radius length + metacarpal length)]. Indicates anatomical mechanical advantage of triceps brachii, an elbow extensor (Maynard Smith & Savage, 1956; Carrier, 1983).
Styloid width index (StWI)	Styloid width relative to radius length (styloid width/radius length). Indicates relative robusticity of distal forelimb.
Pisiform mechanical advantage (PMA)	Length of pisiform relative to length of manus (pisiform length/metacarpal length). Indicates anatomical mechanical advantage of flexor carpi ulnaris, a wrist flexor (Carrier, 1983; Evans, 1993).
Ischium mechanical advantage (IMA)	Length of ischium relative to total hindlimb length [ischium length/(femur length + tibia length + metatarsal length)]. Indicates anatomical mechanical advantage of main hindlimb retractor muscles (e.g. biceps femoris, semimembranosus, semitendinosus; Emerson, 1985; Evans, 1993).
Hindlimb proportions index (HPI)	Length of proximal hindlimb relative to length of distal hindlimb [femur length/(tibia length + metatarsal length)]. Indicates degree of morphological specialization for producing large out-forces in the hindlimb (Hildebrand, 1985b).
Femur epicondyle index (FEI)	Femur epicondyle width relative to femur length (femur epicondyle width/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 (HMI)	Hindlimb malleolus width relative to tibia length (hindlimb malleolus width/tibia length). Indicates relative robusticity of distal hindlimb.
Calcaneus mechanical advantage (CMA)	Length of calcaneal process relative to length of pes (calcaneus length/metatarsal length). Indicates anatomical mechanical advantage of ankle extensors (e.g. gastrocnemius; Carrier, 1983).

Indices are calculated from measurements listed in Table 1.

believe they are biologically meaningful, and because the binomial probability of obtaining five sex-based differences is highly significant ($P = 0.009$). No differences were found between male and female *C. l. lycaon*. Means and standard deviations for all morphological indices are included in the electronic supplementary material (Table S3).

Discussion

Overall, sex-based differences in skeletal shape in *C. lupus*, as determined by a set of morphological indices, were limited. This result was expected, given the generally monogamous mating system and the high level of parental investment from both sexes of this species (reviewed in Mech & Boitani, 2003). However, in two of three subspecies,

we found sexual dimorphism in skeletal traits that appear to reflect morphological specialization for aggression. In both *C. l. occidentalis* and *C. l. lupus*, all of the dimorphic traits identified by our analysis are consistent with the hypothesis that males are more specialized for aggression than females. These dimorphic traits are also likely to improve the capture of large prey animals.

Male *C. l. occidentalis* and *C. l. lupus* had relatively broader skulls than females, a trait that increases bite force by increasing the cross-sectional area of the jaw-closing muscles (Biknevicius & Van Valkenburgh, 1996). Grey wolves kill prey by repetitive bites to the body, producing large lacerations that cause massive blood loss or evisceration (Mech, 1970). Biting is also the primary method of attack when wolves fight each other (reviewed in Mech & Boitani,

Table 3 Descriptive statistics of sexually dimorphic morphological variables in *Canis lupus* subspecies.

Index	Means (SD)		Sexual dimorphism	ANOVA statistics		
	Female	Male		df	F	P
<i>Canis lupus occidentalis</i>						
Skull shape index (SSI)	0.564 (0.027)	0.588 (0.014)	1.04	1,14	4.96	0.043
Scapula width index (ScWI)	0.718 (0.021)	0.744 (0.022)	1.04	1,15	6.03	0.027
Pisiform MA (PMA)	0.227 (0.011)	0.241 (0.009)	1.06	1,14	7.05	0.019
Hindlimb PI (HPI)	0.687 (0.008)	0.698 (0.011)	1.02	1,14	5.78	0.031
<i>Canis lupus lupus</i>						
Skull shape index (SSI)	0.602 (0.011)	0.615 (0.017)	1.02	1,19	3.92	0.062
Olecranon MA (OMA)	0.176 (0.003)	0.179 (0.005)	1.02	1,24	3.12	0.090
Styloid width index (StWI)	0.196 (0.007)	0.203 (0.007)	1.04	1,28	6.64	0.016
Pisiform MA (PMA)	0.265 (0.010)	0.273 (0.011)	1.03	1,24	4.08	0.055
Femur epicondyle index (FEI)	0.179 (0.006)	0.183 (0.005)	1.02	1,28	5.3	0.029

MA, mechanical advantage; PI, proportions index. See Table 2 for description of variables.

Bold type *P*-values indicate variables that were significant after correction for multiple comparisons using the false discovery rate procedure (Benjamini & Hochberg, 1995). Note that no traits in *C. l. lupus* were significant after correction. However, we include these results because the binomial probability of five sex-based differences (out of 14 indices) in the predicted direction ($\alpha = 0.10$) is highly significant ($P = 0.009$).

Values are means and standard deviations (SD). Sexual dimorphism was calculated as the ratio of male/female values. Significant results from ANOVA tests are given. Significance levels were set at 0.10, given that males *a priori* were predicted to have larger values in all morphological indices.

2003). Thus, the capability of generating larger bite forces in males likely improves performance in encounters with both prey and conspecifics.

Dimorphic characters were also found in postcranial morphology. In *C. l. occidentalis*, males had relatively broader scapulae, capable of housing larger muscles associated with the transmission of forces from the trunk to the forelimbs (e.g. *m. serratus*, *m. rhomboideus*; Carrier et al. 2006), providing stability and doing work at the shoulder joint (e.g. *m. supraspinatus*, *m. infraspinatus*), and, hence, may assist in the grappling and dragging aspects of aggressive and prey capture behaviours. Male *C. l. occidentalis* also had a larger mechanical advantage in the manus associated with the pisiform bone, an insertion point for the *m. flexor carpi ulnaris* that flexes the forepaw at the wrist joint (Carrier, 1983; Evans, 1993). Greater force application in the forepaw may be advantageous during grappling or during the braking behaviour that occurs when being dragged forward with teeth gripping a prey animal. The HPI was also larger in males, indicating greater specialization for producing large out-forces in the hindlimbs (Hildebrand, 1985b) that may increase performance when quickly reorienting and accelerating the body. In addition to a larger mechanical advantage associated with wrist flexion (as in *C. l. occidentalis*), male *C. l. lupus* had a larger mechanical advantage associated with the *m. triceps brachii*, allowing greater force application during elbow extension (Maynard Smith & Savage, 1956; Carrier, 1983; Hildebrand, 1985b; Van Valkenburgh, 1987) that may be important when grappling with the forelimbs or to resist being dragged forward. Males in

this subspecies also had a more robust styloid process (wrist joint) and broader femoral epicondyles, traits that reflect greater robusticity and provide larger safety factors (Alexander, 1981), and are likely to be important when large bending and torsional loads are placed on the limb bones. A broader femoral epicondyle increases attachment area for several hip extensor, knee flexor and foot plantarflexor muscles (e.g. *m. semimembranosus*, *m. gastrocnemius*, *m. extensor digitorum longus*; Evans, 1993) and, thus, may increase burst acceleration capacity. More robust limb bones with larger safety factors and greater mechanical advantages in males support our hypothesis given that, during aggressive interactions, grey wolves use their forelimbs for grappling while the hindlimbs are important for stability, body reorientation and burst acceleration (for an example, see Landis, 2010). These traits are also likely to be advantageous when restraining and pulling down large prey (e.g. large ungulates).

Larger canines and muscle moment arms in the jaw-closing muscles of males have been identified in many species of carnivorans (Gittleman & Van Valkenburgh, 1997) and primates (Plavcan, 2001) in which males compete. Our results for skull morphology agree with these previous studies. However, few studies have explicitly tested aggression-based hypotheses in postcranial morphology. In a comparison between domestic dog breeds under different artificial selection criteria (high-speed locomotion in greyhounds vs. fighting ability in pit bulls), Carrier and associates found that pit bulls have relatively more forelimb muscle mass, larger distal muscles in the limbs and more

robust, stronger limb bones than greyhounds (Pasi & Carrier, 2003; Kemp et al. 2005). In a recent study on sexual dimorphism in the western grey kangaroo (*Macropus fuliginosus*), males were found to have relatively larger muscles in the forelimbs, and these differences were most pronounced in the shoulder adductor, arm retractor and elbow flexor muscles that are likely to be important during male–male combat (Warburton et al. 2013). Our results are in agreement with these studies. However, in grey wolves, similar actions (e.g. grasping, grappling, biting) are carried out during both prey capture and intraspecific contests. Thus, the sexually dimorphic functional traits identified by our analysis are likely adaptive in the contexts of both natural and sexual selection.

Improved aggressive performance in mated males may also be adaptive for limiting extra-pair copulations by conspecific competitors (Jennions & Petrie, 2000; Cohas & Allainé, 2009). An increasing number of studies combining behavioural and genetic data indicates that extra-pair paternity is common among socially monogamous species (Clutton-Brock & Isvaran, 2006; Cohas & Allainé, 2009). Among canids, extra-pair paternity has been found in multiple socially monogamous species: the Ethiopian wolf (*Canis simensis*; Randall et al. 2007); the African wild dog (*Lycaon pictus*; Girman et al. 1997); and four species of foxes (Roemer et al. 2001; Baker et al. 2004; Kitchen et al. 2006; Weston Glenn et al. 2009). Current research at Yellowstone National Park indicates that up to 25% of wolf packs show non-monogamous mating structure (all forms of polygamy and promiscuity; D. Stahler, personal communication). Behaviours to limit extra-pair activity, such as mate-guarding (Brotherton & Komers, 2003; Clutton-Brock & Isvaran, 2006) or the direct control of competitors and/or packmates (Cohas et al. 2006), may select for improved aggressive ability in males.

While the dimorphic traits indicated by our analysis are likely to improve aggressive performance in males, several of these characters may functionally conflict with locomotor performance. Morphological specialization for economical locomotion results in elongation of the limbs, particularly the distal elements, and reduced distal limb mass, including smaller humeral and femoral epicondyles, that lower the cost of transport by decreasing the energy required to swing the limbs (Gambaryan, 1974; Hildebrand, 1985b; Van Valkenburgh, 1987; Steudel, 1990; Garland & Janis, 1993; Samuels et al. 2013). Additionally, the out-force and out-velocity of the lever systems around limb joints are inversely correlated (Maynard Smith & Savage, 1956; Hildebrand, 1985b), such that the greater mechanical advantages in the limbs of male *C. l. occidentalis* and *lupus* increase force output at the cost of decreased angular velocity of swinging the limbs. Thus, the increased distal mass and greater mechanical advantages of the limb bones of male wolves are traits that likely increase the cost of transport and decrease locomotor efficiency, reflecting a

functional trade-off (Maynard Smith et al. 1985; Lauder, 1991; Vanhooydonck et al. 2001; Van Damme et al. 2002; Cameron et al. 2013) in the musculoskeletal system whereby simultaneous specialization for aggression and efficient locomotion is impossible (Pasi & Carrier, 2003; Kemp et al. 2005). This trade-off is interesting given the presumed importance of economical locomotion in grey wolves, as indicated by their large daily travel distances (average of 14.4–27.4 km, up to 72 km, per day; reviewed in Mech & Boitani, 2003) and vast home ranges (up to 4335 km²; Mech et al. 1998), and implies strong selection on aggressive performance. Though rarely tested, functional trade-offs between locomotion and aggression may be widespread (Carrier, 2002; Pasi & Carrier, 2003; Kemp et al. 2005). In two species of territorial lizards, studies found that locomotor performance in males decreases with head size (López & Martín, 2002), and with both head size and bite force (Cameron et al. 2013). Future studies of other species characterized by intense male–male competition would improve our understanding of the prevalence and importance of these trade-offs.

Our analysis did not identify any sexually dimorphic functional traits in *C. l. lycaon*. One possible explanation is the frequent hybridization of *C. l. lycaon* with coyotes (*Canis latrans*; VonHoldt et al. 2011; Benson et al. 2012). While wolf–coyote hybrids are intermediate in size (Benson et al. 2012), the effects of coyote DNA introgression on specific morphological traits, behaviour and sexual dimorphism are unknown. Another possible explanation is the disparity in prey characteristics killed by each grey wolf subspecies. During the 'division of labour' (Mech, 1999) period following parturition (May–June), *C. l. lycaon* primarily kills white-tailed deer (*Odocoileus virginianus*; Theberge & Theberge, 2004), a small species relying on speed and agility to escape predation (Mech & Boitani, 2003). In contrast, *C. l. occidentalis* and *C. l. lupus* kill larger prey species during this period, with elk (*Cervus canadensis*) and moose (*Alces alces*) being the most common prey items, respectively, though most individuals killed are juveniles (62% of elk and 90% of moose prey; Sand et al. 2008; Metz et al. 2012). Additionally, bison (*Bison bison*) were abundant prey throughout much of the historical range of *C. l. occidentalis* (Mech & Boitani, 2003). These large ungulates rely on large size and aggressiveness for defence, and are capable of injuring and killing wolves (MacNulty, 2002; Mech & Boitani, 2003). The sexually dimorphic characters in *C. l. occidentalis* and *lupus* may improve a male's ability to kill these dangerous prey species, whereas these characters may not be as important for killing small, fleet-footed prey by male *C. l. lycaon*. Similar results have been reported by Van Valkenburgh and associates, who found that large prey specialists in Canidae have relatively broader skulls (Van Valkenburgh & Koepfli, 1993), and that large prey specialists in Felidae have relatively broader skulls (Meachen-Samuels & Van Valkenburgh, 2009a), broader

humeral epicondyles, larger olecranon processes and relatively shorter radii as compared with small prey specialists (Meachen-Samuels & Van Valkenburgh, 2009b). In an excellent study on wolf predation of elk in Yellowstone National Park, MacNulty et al. (2009) proposed a trade-off between pursuit and handling abilities based on wolf body size. While the larger body size of males was found to improve performance of prey handling and killing (strength-based tasks), it did not improve performance of chasing individual elk (a locomotor-based task; MacNulty et al. 2009).

In summary, we found sexual dimorphism in skeletal traits that reflect morphological specialization for aggression in two of three subspecies of *C. lupus*. While overall differences in skeletal shape were limited, we found dimorphism in functional traits that may improve performance during intraspecific aggressive encounters or prey capture by males or both. Additionally, skeletal sexual dimorphism in wolves could be influenced by the evolution of a flexible mating system (Moehlman, 1989) such that, under certain socioecological conditions, a population may demonstrate greater male–male competition. These aggression-related characters may represent a functional trade-off with locomotor economy, indicating the importance of aggression in the life history of grey wolves. The presence of sexually dimorphic musculoskeletal traits in *C. lupus*, a generally monogamous species, indicates that these traits may be widespread in mammals, given that most mammalian species have a polygynous mating system and that the intensity of male–male competition generally increases with the level of polygyny (reviewed in Andersson, 1994). Further research on sexual dimorphism in functional traits will improve our understanding of the prevalence and degree of specialization for aggression and the functional trade-offs that may result. Future studies would be improved by including a large number of species with different mating systems and food ecology in order to provide resolution on the relative importance of sexual vs. natural selection in sexually dimorphic skeletal morphology.

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References

- Alexander RM (1981) Factors of safety in the structure of animals. *Sci Prog* **67**, 109–130.
- Andersson M (1994) *Sexual Selection*. Princeton: Princeton University Press.
- Andersson K (2004) Elbow-joint morphology as a guide to forearm function and foraging behaviour in mammalian carnivores. *Zool J Linn Soc* **142**, 91–104.
- Andersson K, Werdelin L (2003) The evolution of cursorial carnivores in the Tertiary: implications of elbow-joint morphology. *Proc Biol Sci* **270**, S163–S165.
- Baker PJ, Funk SM, Bruford MW, et al. (2004) Polygynandry in a red fox population: implications for the evolution of group living in canids? *Behav Ecol* **15**, 766–778.
- Ballard WB, Whitman JS, Gardner CL (1987) *Ecology of an Exploited Wolf Population in South-Central Alaska*. Bethesda: The Wildlife Society.
- Bekoff M, Diamond J, Mitton JB (1981) Life-history patterns and sociality in canids: body size, reproduction, and behavior. *Oecologia* **50**, 386–390.
- Benjamini Y, Hochberg Y (1995) Controlling the false discovery rate: a practical and powerful approach to multiple testing. *J Roy Stat Soc Ser B (Stat Method)* **57**, 289–300.
- Benson JF, Patterson BR, Wheeldon TJ (2012) Spatial genetic and morphologic structure of wolves and coyotes in relation to environmental heterogeneity in a *Canis* hybrid zone. *Mol Ecol* **21**, 5934–5954.
- Bertram JE, Biewener AA (1990) Differential scaling of the long bones in the terrestrial Carnivora and other mammals. *J Morphol* **204**, 157–169.
- Biknevicius A, Van Valkenburgh B (1996) Design for killing: craniodental adaptations of predators. In: *Carnivore Behavior, Ecology, and Evolution*. (ed. Gittleman JL), pp. 393–428. Ithaca: Cornell University Press.
- Brotherton PN, Komers PE (2003) Mate guarding and the evolution of social monogamy in mammals. In: *Monogamy: Mating Strategies and Partnerships in Birds, Humans and Other Mammals*. (eds Reichard U, Boesch C), pp. 42–58. Cambridge: Cambridge University Press.
- Butler MA, Losos JB (2002) Multivariate sexual dimorphism, sexual selection, and adaptation in Greater Antillean *Anolis* lizards. *Ecol Monogr* **72**, 541–559.
- Cameron SF, Wynn ML, Wilson RS (2013) Sex-specific trade-offs and compensatory mechanisms: bite force and sprint speed pose conflicting demands on the design of geckos (*Hemidactylus frenatus*). *J Exp Biol* **216**, 3781–3789.
- Caro T, Fitzgibbon CD (1992) Large carnivores and their prey: the quick and the dead. In: *Natural Enemies: The Population Biology of Predators, Parasites and Diseases*. (ed. Crawley M), pp. 117–142. Oxford: Blackwell Scientific Publications.
- Carrier DR (1983) Postnatal ontogeny of the musculo-skeletal system in the black-tailed jack rabbit (*Lepus californicus*). *J Zool* **201**, 27–55.
- Carrier DR (2002) Functional tradeoffs in specialization for fighting versus running. In: *Topics in Functional and Ecological Vertebrate Morphology*. (eds Aerts P, D'Aout K, Herrel A, Van Damme R), pp. 237–255. Maastricht: Shaker.

- Carrier DR (2011) The advantage of standing up to fight and the evolution of habitual bipedalism in hominins. *PLoS One* **6**, e19630.
- Carrier DR, Deban SM, Fischbein T (2006) Locomotor function of the pectoral girdle 'muscular sling' in trotting dogs. *J Exp Biol* **209**, 2224–2237.
- Casinos A, Bou J, Castiella M, et al. (1986) On the allometry of long bones in dogs (*Canis familiaris*). *J Morphol* **190**, 73–79.
- Cassidy KA (2013) Group composition effects on inter-pack aggressive interactions of gray wolves in Yellowstone National Park. MS thesis. University of Minnesota.
- Christiansen P (1999) Scaling of the limb long bones to body mass in terrestrial mammals. *J Morphol* **239**, 167–190.
- Clutton-Brock T, Isvaran K (2006) Paternity loss in contrasting mammalian societies. *Biol Lett* **2**, 513–516.
- Clutton-Brock TH, Guinness FE, Albon S (1982) *Red Deer: Behavior and Ecology of Two Sexes*. Chicago: University of Chicago Press.
- Cohas A, Allainé D (2009) Social structure influences extra-pair paternity in socially monogamous mammals. *Biol Lett* **5**, 313–316.
- Cohas A, Yoccoz N, Da Silva A, et al. (2006) Extra-pair paternity in the monogamous alpine marmot (*Marmota marmota*): the roles of social setting and female mate choice. *Behav Ecol Sociobiol* **59**, 597–605.
- Darwin C (1871) *The Descent of Man, and Selection in Relation to Sex*. London: John Murray.
- von den Driesch A (1976) *A Guide to the Measurement of Animal Bones from Archaeological Sites*. Cambridge: Harvard University.
- Emerson S (1985) Jumping and leaping. In: *Functional Vertebrate Morphology*. (eds Hildebrand M, Bramble DM, Liem KF, Wake DB), pp. 58–72. Cambridge: Harvard University Press.
- Evans HE (1993) *Miller's Anatomy of the Dog*. Philadelphia: WB Saunders.
- Gambaryan P (1974) *How Mammals Run: Anatomical Adaptations*. New York: John Wiley.
- Garland T Jr, Janis CM (1993) Does metatarsal/femur ratio predict maximal running speed in cursorial mammals? *J Zool* **229**, 133–151.
- Garland T Jr, Hankins E, Huey R (1990) Locomotor capacity and social dominance in male lizards. *Funct Ecol* **4**, 243–250.
- Girman DJ, Mills M, Geffen E, et al. (1997) A molecular genetic analysis of social structure, dispersal, and interpack relationships of the African wild dog (*Lycaon pictus*). *Behav Ecol Sociobiol* **40**, 187–198.
- Gittleman J, Van Valkenburgh B (1997) Sexual dimorphism in the canines and skulls of carnivores: effects of size, phylogeny, and behavioural ecology. *J Zool* **242**, 97–117.
- Godfrey L, Sutherland M, Boy D, et al. (1991) Scaling of limb joint surface areas in anthropoid primates and other mammals. *J Zool* **223**, 603–625.
- Hildebrand M (1985a) Digging of quadrupeds. In: *Functional Vertebrate Morphology*. (eds Hildebrand M, Bramble DM, Liem KF, Wake DB), pp. 89–109. Cambridge: Harvard University Press.
- Hildebrand M (1985b) Walking and running. In: *Functional Vertebrate Morphology*. (eds Hildebrand M, Bramble DM, Liem KF, Wake DB), pp. 38–57. Cambridge: Harvard University Press.
- Husak JF, Lappin AK, Van Den Bussche RA (2009) The fitness advantage of a high-performance weapon. *Biol J Linn Soc* **96**, 840–845.
- Huyghe K, Vanhooydonck B, Scheers H, et al. (2005) Morphology, performance and fighting capacity in male lizards, *Gallotia galloti*. *Funct Ecol* **19**, 800–807.
- Jennions MD, Petrie M (2000) Why do females mate multiply? A review of the genetic benefits. *Biol Rev* **75**, 21–64.
- Jungers WL, Falsetti AB, Wall CE (1995) Shape, relative size, and size-adjustments in morphometrics. *Am J Phys Anthropol* **38**, 137–161.
- Kemp T, Bachus K, Nairn J, et al. (2005) Functional trade-offs in the limb bones of dogs selected for running versus fighting. *J Exp Biol* **208**, 3475–3482.
- Kiesewalter L (1888) *Skelettmessungen am Pferde als Beitrag zur theoretischen Grundlage der Beurteilungslehre des Pferdes*. Leipzig: Universität Leipzig.
- Kitchen AM, Gese EM, Waits LP, et al. (2006) Multiple breeding strategies in the swift fox, *Vulpes velox*. *Anim Behav* **71**, 1029–1038.
- Lailvaux SP, Irschick DJ (2006) A functional perspective on sexual selection: insights and future prospects. *Anim Behav* **72**, 263–273.
- Lailvaux SP, Herrel A, VanHooydonck B, et al. (2004) Performance capacity, fighting tactics and the evolution of life-stage male morphs in the green anole lizard (*Anolis carolinensis*). *Proc Biol Sci* **271**, 2501–2508.
- Lande R (1980) Sexual dimorphism, sexual selection, and adaptation in polygenic characters. *Evolution* **34**, 292–305.
- Landis B (2010) *The Rise of Black Wolf [DVD]*. Washington, DC: National Geographic Television.
- Lappin AK, Husak JF (2005) Weapon performance, not size, determines mating success and potential reproductive output in the collared lizard (*Crotaphytus collaris*). *Am Nat* **166**, 426–436.
- Lauder G (1991) An evolutionary perspective on the concept of efficiency: how does function evolve. In: *Efficiency and Economy in Animal Physiology*. (ed. Blake R), pp. 169–184. Cambridge: Cambridge University Press.
- Lawler RR, Richard AF, Riley MA (2005) Intrasexual selection in Verreaux's sifaka (*Propithecus verreauxi verreauxi*). *J Hum Evol* **48**, 259–277.
- Le Boeuf BJ (1974) Male–male competition and reproductive success in elephant seals. *Am Zool* **14**, 163–176.
- López P, Martín J (2002) Locomotor capacity and dominance in male lizards *Lacerta monticola*: a trade-off between survival and reproductive success? *Biol J Linn Soc* **77**, 201–209.
- Lovich J, Gibbons JW (1992) A review of techniques for quantifying sexual size dimorphism. *Growth Dev Aging* **56**, 269–281.
- MacNulty DR (2002) The predatory sequence and the influence of injury risk on hunting behavior in the wolf. MS thesis. University of Minnesota.
- MacNulty DR, Smith DW, Mech LD, et al. (2009) Body size and predatory performance in wolves: is bigger better? *J Anim Ecol* **78**, 532–539.
- Maynard Smith J, Savage RJ (1956) Some locomotory adaptations in mammals. *Zool J Linn Soc Lond* **42**, 603–622.
- Maynard Smith J, Burian R, Kauffman S, et al. (1985) Developmental constraints and evolution: a perspective from the Mountain Lake conference on development and evolution. *Q Rev Biol* **60**, 265–287.
- Meachen-Samuels J, Van Valkenburgh B (2009a) Craniodental indicators of prey size preference in the Felidae. *Biol J Linn Soc* **96**, 784–799.

- Meachen-Samuels J, Van Valkenburgh B (2009b) Forelimb indicators of prey-size preference in the Felidae. *J Morphol* **270**, 729–744.
- Mech LD (1970) *The Wolf: The Ecology and Behavior of an Endangered Species*. Garden City: Natural History Press.
- Mech LD (1993) Details of a confrontation between two wild wolves. *Can J Zool* **71**, 1900–1903.
- Mech LD (1994) Buffer zones of territories of gray wolves as regions of intraspecific strife. *J Mammal* **75**, 199–202.
- Mech LD (1999) Alpha status, dominance, and division of labor in wolf packs. *Can J Zool* **77**, 1196–1203.
- Mech LD (2000) Leadership in wolf, *Canis lupus*, packs. *Can Field-Nat* **114**, 259–263.
- Mech LD, Boitani L (2003) *Wolves: Behavior, Ecology, and Conservation*. Chicago: University of Chicago Press.
- Mech LD, Adams LG, Meier TJ, et al. (1998) *The Wolves of Denali*. Minneapolis: University of Minnesota Press.
- Mech LD, Wolf PC, Packard JM (1999) Regurgitative food transfer among wild wolves. *Can J Zool* **77**, 1192–1195.
- Metz MC, Smith DW, Vucetich JA, et al. (2012) Seasonal patterns of predation for gray wolves in the multi-prey system of Yellowstone National Park. *J Anim Ecol* **81**, 553–563.
- Moehlman PD (1989) Intraspecific variation in canid social systems. In: *Carnivore Behavior, Ecology, and Evolution*. (ed. Gittleman JL), pp. 143–163. Ithaca: Cornell University Press.
- Moran MD (2003) Arguments for rejecting the sequential Bonferroni in ecological studies. *Oikos* **100**, 403–405.
- Murie A (1944) *The Wolves of Mount McKinley*. Washington, DC: US Government Printing Office.
- Pasi BM, Carrier DR (2003) Functional trade-offs in the limb muscles of dogs selected for running vs. fighting. *J Evol Biol* **16**, 324–332.
- Plavcan JM (2001) Sexual dimorphism in primate evolution. *Am J Phys Anthropol* **116**, 25–53.
- R Development Core Team (2013) *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.
- Radinsky LB (1981) Evolution of skull shape in carnivores: 1. Representative modern carnivores. *Biol J Linn Soc* **15**, 369–388.
- Raihani G, Székely T, Serrano-Meneses MA, et al. (2006) The influence of sexual selection and male agility on sexual size dimorphism in bustards (Otididae). *Anim Behav* **71**, 833–838.
- Randall DA, Pollinger JP, Wayne RK, et al. (2007) Inbreeding is reduced by female-biased dispersal and mating behavior in Ethiopian wolves. *Behav Ecol* **18**, 579–589.
- Rasband WS (2013) *ImageJ*. Bethesda: US National Institutes of Health.
- Robson M, Miles D (2000) Locomotor performance and dominance in male tree lizards, *Urosaurus ornatus*. *Funct Ecol* **14**, 338–344.
- Roemer GW, Smith DA, Garcelon DK, et al. (2001) The behavioural ecology of the island fox (*Urocyon littoralis*). *J Zool* **255**, 1–14.
- Samuels JX, Van Valkenburgh B (2008) Skeletal indicators of locomotor adaptations in living and extinct rodents. *J Morphol* **269**, 1387–1411.
- Samuels JX, Meachen JA, Sakai SA (2013) Postcranial morphology and the locomotor habits of living and extinct carnivores. *J Morphol* **274**, 121–146.
- Sand H, Wikenros C, Wabakken P, et al. (2006) Effects of hunting group size, snow depth and age on the success of wolves hunting moose. *Anim Behav* **72**, 781–789.
- Sand H, Wabakken P, Zimmermann B, et al. (2008) Summer kill rates and predation pattern in a wolf–moose system: can we rely on winter estimates? *Oecologia* **156**, 53–64.
- Scantlebury M, Butterwick R, Speakman JR (2000) Energetics of lactation in domestic dog (*Canis familiaris*) breeds of two sizes. *Comp Biochem Physiol A Mol Integr Physiol* **125**, 197–210.
- Sherrow HM (2012) Violence across animals and within early Hominins. In: *The Oxford Handbook of Evolutionary Perspectives on Violence, Homicide, and War*. (eds Shackelford TK, Weekes-Shackelford VA), pp. 23–40. New York: Oxford University Press.
- Smale L, Nunes S, Holekamp K (1997) Sexually dimorphic dispersal in mammals: patterns, causes, and consequences. In: *Advances in the Study of Behavior*. (eds Slater P, Rosenblatt J, Snowdon C, Milinski M), pp. 181–250. San Diego: Academic Press.
- Smith RJ (1999) Statistics of sexual size dimorphism. *J Hum Evol* **36**, 423–459.
- Stahler DR (2011) Life history, social dynamics, and molecular ecology of Yellowstone wolves. PhD dissertation. University of California, Los Angeles.
- Stuedel K (1990) The work and energetic cost of locomotion. I. The effects of limb mass distribution in quadrupeds. *J Exp Biol* **154**, 273–285.
- Székely T, Reynolds JD, Figuerola J (2000) Sexual size dimorphism in shorebirds, gulls, and alcid: the influence of sexual and natural selection. *Evolution* **54**, 1404–1413.
- Theberge JB, Theberge MT (2004) *The Wolves of Algonquin Park: a 12 Year Ecological Study*. Waterloo: University of Waterloo.
- Trivers R (1972) Parental investment and sexual selection. In: *Sexual Selection and the Descent of Man*. (ed. Campbell B), pp. 136–179. Chicago: Aldine Press.
- Van Damme R, Wilson RS, Vanhooydonck B, et al. (2002) Performance constraints in decathletes. *Nature* **415**, 755–756.
- Van Valkenburgh B (1987) Skeletal indicators of locomotor behavior in living and extinct carnivores. *J Vert Paleontol* **7**, 162–182.
- Van Valkenburgh B, Koenig K (1993) Cranial and dental adaptations to predation in canids. In: *Mammals as Predators: Symposia of the Zoological Society of London*. (eds Dunstone N, Gorman ML), pp. 15–37. Oxford: Oxford University Press.
- Vanhooydonck B, Van Damme R, Aerts P (2001) Speed and stamina trade-off in Lacertid lizards. *Evolution* **55**, 1040–1048.
- VonHoldt BM, Stahler DR, Smith DW, et al. (2008) The genealogy and genetic viability of reintroduced Yellowstone grey wolves. *Mol Ecol* **17**, 252–274.
- VonHoldt BM, Pollinger JP, Earl DA, et al. (2011) A genome-wide perspective on the evolutionary history of enigmatic wolf-like canids. *Genome Res* **21**, 1294–1305.
- Walter RM, Carrier DR (2007) Ground forces applied by galloping dogs. *J Exp Biol* **210**, 208–216.
- Walter RM, Carrier DR (2009) Rapid acceleration in dogs: ground forces and body posture dynamics. *J Exp Biol* **212**, 1930–1939.
- Warburton NM, Bateman PW, Fleming PA (2013) Sexual selection on forelimb muscles of western grey kangaroos (Skippy was clearly a female). *Biol J Linn Soc* **109**, 923–931.
- Waser P (1996) Patterns and consequences of dispersal in gregarious carnivores. In: *Carnivore Behavior, Ecology and Evolution*. (ed. Gittleman JL), pp. 267–295. Ithaca: Cornell University Press.

- Wayne RK** (1986) Limb morphology of domestic and wild canids: the influence of development on morphologic change. *J Morphol* **187**, 301–319.
- Weckerly FW** (1998) Sexual-size dimorphism: influence of mass and mating systems in the most dimorphic mammals. *J Mammal* **79**, 33–52.
- Weston Glenn JL, Civitello DJ, Lance SL** (2009) Multiple paternity and kinship in the gray fox (*Urocyon cinereoargenteus*). *Mammalian Biology-Zeitschrift für Säugetierkunde* **74**, 394–402.
- Wilder HH** (1920) *A Laboratory Manual of Anthropometry*. Philadelphia: P. Blakiston's Son & Co.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

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

Table S2. Means and standard deviations (SD) in cm for skeletal morphometrics taken for *Canis lupus* specimens.

Table S3. Means and standard deviations (SD) for morphological indices for *Canis lupus* specimens.