FUNCTIONAL SPECIALIZATION FOR AGGRESSION AND THE EVOLUTION OF SEXUAL DIMORPHISM IN VERTEBRATES

by

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A dissertation submitted to the faculty of
The University of Utah
in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

Department of Biology

The University of Utah

August 2017

The University of Utah Graduate School

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ABSTRACT

In many species, male reproductive fitness is dependent upon the ability to physically compete for access to mates. The direct link between performance in male contests and reproductive success has led to the evolution of male-biased sexual dimorphism in traits that improve fighting performance. However, species variation in social structure often leads to differences in the relative importance of intraspecific aggression and corresponding variation in the degree of sexual dimorphism. Traits such as body mass and canine size have received much attention because they have a clear impact on male fighting performance. However, additional musculoskeletal adaptations may also be under selection. Traits that improve strength, agility, and maneuverability (i.e., whole-organism performance capacities) may improve aggressive performance and this may lead to the evolution of sexual dimorphism throughout the musculoskeletal system. Because the postcranial anatomy also functions as the primary locomotor system, morphological specialization for aggression may directly conflict with locomotor performance, resulting in a functional trade-off. Given that locomotion represents a substantial proportion of total energetic expenditure in many species, compromises resulting from an aggression-locomotion trade-off may be vital to understanding the evolution of behavioral and phenotypic diversity.

In this dissertation, I first investigated the prevalence of sexual dimorphism in skeletal morphology in three subspecies of gray wolf (*Canis lupus*). I then expanded this study to 26 species of carnivores and 11 species of primates. I found male-biased sexual dimorphism in skeletal traits that are predicted to improve aggressive performance, making males better equipped for intraspecific competition. Across species, the degree of dimorphism increased with the intensity of male competition. Consistent with sexual selection theory, the evolution of this dimorphism was best explained by mating system. To test for evidence of a functional trade-off between aggressive performance and locomotion, I measured male competitive ability through social competition trials in semi-natural enclosures and locomotor economy through running trials in an enclosed treadmill and open-flow respirometry. I found evidence for an aggression-locomotion functional trade-off. Together, this work improves our understanding of the role of aggression in the evolution of vertebrates and the impact that specialization for aggression may have on locomotion.

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ACKNOWLEDGEMENTS

I thank my advisor, David Carrier, for support, guidance, and for meaningful conversations that promoted a rigorous and creative approach to studying evolutionary biology. I thank my committee, Franz Goller, Jim Martin, Ron Meyers, and Wayne Potts, for pushing me to become a better scientist through classes, advice, and critical evaluation of my ideas. Colleen Farmer provided a unique perspective and much advice. Members of the Carrier and Farmer labs, Chris Cunningham, Amanda Cooper, and Bob Cieri, were great lab mates to work with. Members of the Potts lab contributed greatly to the success of my research. In particular, Jimmy Ruff made everything I did better.

I also thank Nalini Nadkarni for being a mentor and for allowing me to get involved in a plethora of public engagement projects. I thank all of those associated with INSPIRE and Nalini's additional programs, in particular Celeste Henrickson and Emily Gaines Crockett. I also thank the current and former department chairs, Denise Dearing and Neil Vickers, for allowing me the freedom to both teach a course and to work as Project Coordinator for the INSPIRE program while pursuing my PhD. Shannon Nielsen, Terry Merritt, April Mills, and Deni Morrison made everything logistically possible.

Finally, I thank many friends for camaraderie, fun, and adventures that made the stressful ups and downs of graduate school manageable. My research was supported by NSF grant IOS-0817782 (to D. Carrier), NSF DDIG DEB-1600727 (to J. Morris), and a Grant-in-Aid from the Society for Integrative and Comparative Biology (to J. Morris).

CHAPTER 1

INTRODUCTION

Physical aggression is a central component of the life histories of many species. Aggressive performance has a strong influence on individual fitness because it is adaptive in the contexts of both naturally selected and sexually selected behaviors (Andersson 1994). While aggressive performance is often important to some degree for both sexes, sexual selection theory predicts that male mammals will be more specialized for physical aggression than females (Darwin 1871). Paternal care is limited or absent in most mammals. Because of this, male reproductive success depends predominantly on a male's ability to compete for mates and produce offspring (Trivers 1972). In many species, the mating opportunities of males, through the means of resource control, social dominance, or mate guarding, are determined by performance in male-male contests (e.g., Le Boeuf 1974; Clutton-Brock et al. 1982; Campagna and Le Boeuf 1988). Thus, aggressive performance may correlate with resource holding potential (Parker 1974), leading to greater variance in lifetime reproductive success in males than in females (Bateman 1948; Emlen and Oring 1977; Clutton-Brock 1988). This relationship between aggression and reproductive fitness has led to evolution of enhanced male weaponry (e.g., canine teeth, antlers) and fatal fighting in many species (Sherrow 2012).

In the context of aggressive performance, sexual dimorphism is thought to evolve in a two-step process (Lande 1980). First, sexual selection acts on a male trait (Darwin 1871) and the high degree of genetic correlation between the sexes causes that trait to be altered in the same way in females (Lande 1980). This sexually selected trait may incur a fitness cost in the context of natural selection (e.g., increased susceptibility to malnutrition, starvation, and predation; Darwin 1871; Owen-Smith 1993; Powell and King 1997) by driving a phenotype away from an ecological optimum (Peters 1983; Blanckenhorn 2000). Subsequent viability selection may lead to the evolution of that same trait in females to be closer to this natural selection optimum (Lande 1980). Given the maladaptive nature of some sexually selected traits in regard to natural selection, the presence of sexual dimorphism suggests that male competition for mates has played an important role in vertebrate evolution.

Body size has a strong influence on the outcome of male-male contests in many species because it confers the advantages of increasing absolute force and momentum that may be used against a competitor (Darwin 1871; Andersson 1994). This has led to the evolution of male-biased body size sexual dimorphism that is more pronounced in species with more intense male-male competition (Clutton-Brock et al. 1977; Alexander et al. 1979; Plavcan and Van Schaik 1997). However, in addition to body size, other musculoskeletal adaptations may improve male fighting performance. Traits that improve strength, agility, and maneuverability (i.e., whole-organism performance capacities) may also be under selection in males (Clutton-Brock and Harvey 1977; Carrier 2002; Lailvaux and Irschick 2006, 2007). Thus, the dynamic nature and type of male-male combat in a given species may lead to selection on specific functional traits and the evolution of sexual dimorphism in those traits.

While traits such as robust limb bones, powerful distal limb muscles, and high mechanical advantages may improve aggressive performance by increasing strength, stability, and force output for striking or manipulating opponents, these traits may have a negative impact on locomotor performance (Pasi and Carrier 2003; Kemp et al. 2005). Indeed, many traits associated with locomotor economy (e.g., elongated limbs with reduced distal mass; Gambaryan 1974; Hildebrand 1985; Steudel 1990) are in direct contrast to those associated with specialization for aggression (Carrier 2002). This may result in a functional trade-off (Lewontin 1978; Maynard Smith et al. 1985; Lauder 1991) whereby simultaneous specialization for both activities is impossible. Compromises resulting from such trade-offs may be vital to understanding the evolution of behavioral and phenotypic diversity in many vertebrate taxa (Arnold 1992).

This dissertation examines sexual dimorphism in skeletal shape associated with specialization for aggressive performance and the potential functional trade-off between aggressive performance and locomotor economy. In Chapter 2, I examined sexual dimorphism in skeletal shape in three subspecies of grey wolf (*Canis lupus*). Given that sexual dimorphism is not expected in a socially monogamous species (because of the relatively low intensity of male-male competition), the presence of skeletal sexual dimorphism in grey wolves indicated that dimorphism may be widespread in mammals. In Chapter 3, I broadened this study to include 26 species within Carnivora and used phylogenetic model selection to compare evolutionary models incorporating different selective regimes based on life history traits (diet, locomotor zone, group size, mating system, and parental care). These results showed that sexual dimorphism in skeletal shape is widespread, that it increases with the intensity of male-male competition, and that mating system best explains the evolution of this dimorphism. In Chapter 4, I extend the examination of postcranial skeletal sexual dimorphism to primates. Similar to the results found in carnivores, sexual dimorphism in skeletal shape was also found among nine species of anthropoid primates and this dimorphism was positively correlated with sexual dimorphism in body size, a common indicator of the intensity of male-male competition, even when controlling for both body mass and phylogenetic relatedness. Finally, in Chapter 5, I carried out an explicit test for a functional trade-off between locomotor economy and physical competitive ability. For this, I used 8-week social competition trials in semi-natural enclosures to directly measure male competitive ability through territorial control. I measured mass-specific oxygen consumption for each mouse using running trials in an enclosed treadmill and open-flow respirometry. My results showed that territory-holding males have higher mass-specific oxygen consumption when running (i.e., reduced locomotor economy) as compared to males that do not control territories. This relationship was significant both before and after 8-week competition trials in semi-natural enclosures.

Together, the results of this dissertation indicate that sexual selection on male aggressive performance has led to the evolution of sexual dimorphism in skeletal anatomy in multiple groups of mammals and that functional specialization for aggressive performance in male morphology represents a functional trade-off with locomotor economy. Future work will investigate morphological and physiological traits underlying the functional trade-off between aggressive performance and locomotor economy. Specifically, examination of muscle mass distribution, muscle fiber phenotype, and skeletal shape in postcranial morphology may reveal which traits are associated with this trade-off. For each of these traits, there are contrasting predictions for improving either aggressive performance (increased distal limb mass, faster muscle fiber types, and robust limbs with greater mechanical advantages) or locomotor economy (decreased distal limb mass, slower muscle fiber types, and gracile limbs with lower mechanical advantages). Another future direction from this research is to extend the examination of skeletal shape sexual dimorphism to other taxonomic groups to increase our understanding of the different manifestations of sexual dimorphism. Results from Chapters 3 and 4 suggest that constraints on the evolution of skeletal shape sexual dimorphism may differ depending on locomotor zone. In carnivores, the evolution of skeletal shape sexual dimorphism appears to be more constrained in terrestrial as compared to arboreal species. In primates, however, there is evidence for the opposite relationship. The examination of patterns of male-male competition and the degree of postcranial sexual dimorphism in other taxa will help to resolve the functional relationships and possible constraints between general locomotor performance and sexually selected performance traits.

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CHAPTER 2

SPECIALIZATION FOR AGGRESSION IN SEXUALLY DIMORPHIC SKELETAL MORPHOLOGY IN GREY WOLVES (*CANIS LUPUS*)

Morris, J. S. and E. K. Brandt. 2014. Specialization for aggression in sexually dimorphic skeletal morphology in grey wolves (*Canis lupus*). Journal of Anatomy. Volume 225, Issue 1. Reprinted with permission from John Wiley and Sons. The online version is found here: http://onlinelibrary.wiley.com/doi/10.1111/joa.12191/full.

J. Anat. (2014) **225**, pp1–11 doi: 10.1111/joa.12191

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

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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

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Accepted for publication *20 March 2014*

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 like 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 [(√scapula area)/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.

	Means (SD)			ANOVA statistics		
Index	Female	Male	Sexual dimorphism	df	*F*	*P*
Canis lupus occidentalis						
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**
Canis lupus lupus						
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 grapping 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 km^2; 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 humoral 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.

Acknowledgements

The authors thank the staff from the Idaho and Wyoming Departments of Fish and Game for the wolf carcasses used in this study. We also thank the staff from the following museums for access to their collections: American Museum of Natural History, New York (AMNH); British National History Museum, London (BMNH); Field Museum of Natural History, Chicago (FMNH); Naturhistorisches Museum, Vienna (NMW); Naturhistoriska Riksmuseet, Stockholm (NRM); Smithsonian Institution National Museum of Natural History, Washington, D.C. (USNM); Museum für Naturkunde, Berlin (ZMB). The authors thank Kira Cassidy and Daniel Stahler from the Yellowstone Wolf Project for generously providing access to unpublished data on wolf behaviour, K. Chase and F. Adler for advice on statistical analysis, and N. Schilling, C. Cunningham and D. Irschick for input on the project and manuscript. Comments by D. Stahler and an anonymous reviewer greatly improved the manuscript. This research was funded by a National Science Foundation grant to D. R. Carrier (IOS-0817782).

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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.

CHAPTER 3

SEXUAL SELECTION ON SKELETAL SHAPE IN CARNIVORA

Morris, J. S. and D. R. Carrier. 2016. Sexual selection on skeletal shape in Carnivora. Evolution. Volume 70, Issue 4. Reprinted with permission from John Wiley and Sons. The online version is found here: http://onlinelibrary.wiley.com/doi/10.1111/evo.12904/full.

Sexual selection on skeletal shape in Carnivora

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Received May 11, 2015
Accepted March 2, 2016

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 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 carnivorans 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 intensity of male–male competition in carnivorans (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 carnivoran 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 carnivorans 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 midshaft 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

[a] Calculated 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} = (mean male value/mean female value), when the male mean was greater, and

SD_{FI} = 2 – (mean female value/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 (($\sqrt{\text{Scapula area}}$)/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 ((Scapula length + Humerus length)/(Radius length + 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 (Olecranon length/(Radius length + 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 (Pisiform length/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 (Ischium length/(Femur length + Tibia length + 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 (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	Hindlimb malleolus width relative to tibia length (Hindlimb malleolus width/Tibia length). Indicates relative robusticity of distal hindlimb.
Calcaneus mechanical advantage	Length of calcaneal process relative to length of pes (Calcaneus length/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.

[a] Phylogenetic 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 ΔAICc values. A ΔAICc 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 (ΔAICc < 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	ΔAICc	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

ΔAICc 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.

			Selective optima	
Model	α	σ	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).

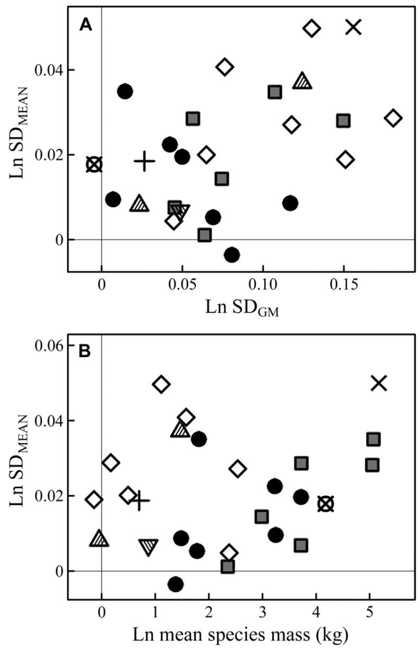

Figure 1. Mean skeletal shape dimorphism (SD_{MEAN}) plotted against (A) sexual dimorphism in body size (SD_{GM}) and (B) mean species mass for 26 Carnivora species. Spearman rank correlations indicate that SD_{MEAN} is positively correlated with SD_{GM} ($r = 0.430$, $P = 0.029$) but not with mean species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

Discussion

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

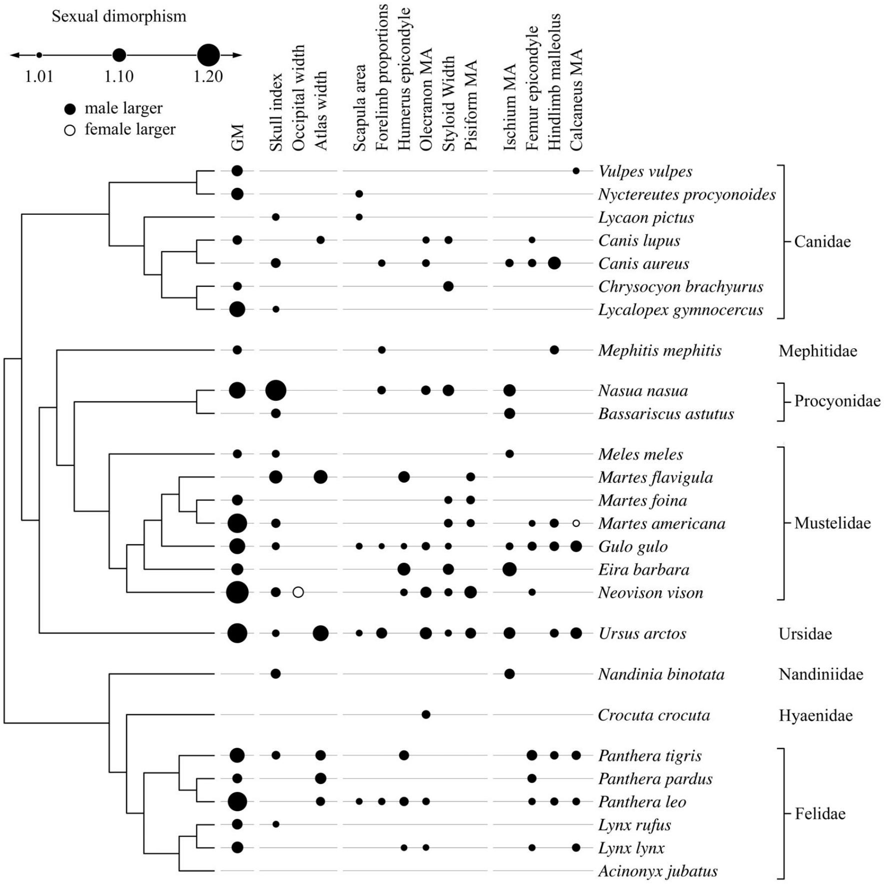

Figure 2. **Graphical summary of all data used in the analysis. Plotted SD_{FI} points indicate traits that were sexually dimorphic ($P < 0.05$; ANOVA). The size of a point indicates the degree of sexual dimorphism. Geometric mean (GM) is provided as indicator of the degree of sexual dimorphism in overall 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 correlation 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 or 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*, *Lycaon 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 constrains. 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.

ACKNOWLEDGMENTS

We thank the staff from the following museums for access to collections: American Museum of Natural History, New York; British National History Museum, London; Field Museum of Natural History, Chicago; Naturhistorisches Museum, Vienna; Naturhistoriska Riksmuseet, Stockholm; Smithsonian Institution National Museum of Natural History, Washington, D.C.; Museum für Naturkunde, Berlin. Comments from J. Ruff, F. Goller, A. Chan, and two anonymous reviewers greatly improved the manuscript. This work was funded by National Science Foundation grant IOS-0817782 (to D.R.C).

DATA ARCHIVING

The doi for our data is 10.5061/dryad.86523.

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Associate Editor: K. Sears
Handling Editor: M. Servedio

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.

CHAPTER 4

SEXUAL DIMORPHISM IN POSTCRANIAL SKELETAL SHAPE SUGGESTS MALE-BIASED SPECIALIZATION FOR PHYSICAL COMPETITION IN ANTHROPOID PRIMATES

Abstract

Sexual dimorphism often arises as a response to selection on traits that improve a male's ability to physically compete for access to mates. In primates, sexual dimorphism in body mass and canine size are more common in species with intense male-male competition. However, in addition to these traits, other musculoskeletal adaptations may improve male fighting performance. Postcranial traits that increase strength, agility, and maneuverability may also be under selection. To test the hypothesis that males, as compared to females, are more specialized for physical competition in their postcranial anatomy, we compared sex-specific skeletal shape using a set of functional indices predicted to improve fighting performance. Across species, we found significant sexual dimorphism in a subset of these indices, indicating the presence of skeletal shape sexual dimorphism in our sample of anthropoid primates. Mean skeletal shape sexual dimorphism was positively correlated with sexual dimorphism in body size, an indicator of the intensity of male-male competition, even when controlling for both body mass and

phylogenetic relatedness. These results suggest that selection on male fighting ability has played a role in the evolution of postcranial morphology in primates.

Introduction

Male-biased sexual dimorphism is generally attributed to sexual selection acting on traits that improve a male's ability to compete for mates and produce offspring (Darwin 1871; Andersson 1994). In many species, the mating opportunities of males, through the means of resource control, social dominance, or mate guarding, are determined by male performance in agonistic contests (e.g., Le Boeuf 1974; Clutton-Brock et al. 1982; Campagna and Le Boeuf 1988). This has led to the evolution of male-biased sexual dimorphism in traits that improve fighting performance (Darwin 1871; Crook 1972; Leutenegger and Kelly 1977; Clutton-Brock 1985; Kay et al. 1988; Kappeler 1990, 1991; Plavcan and van Schaik 1992; Ford 1994; Martin et al. 1994; Plavcan and Van Schaik 1997; Lindenfors and Tullberg 1998; Plavcan 2001). For example, body mass has a strong influence on the outcome of male-male contests in many species because it confers the advantages of increasing absolute force and momentum that may be used against a competitor (Darwin 1871; Andersson 1994). Because of this, male body mass is positively correlated with reproductive success within many species (Clutton-Brock et al. 1988; Fisher and Lara 1999; Kruuk et al. 1999; Clinchy et al. 2004; Zedrosser et al. 2007). Likewise, body mass dimorphism is more pronounced in species with more intense male-male competition (Clutton-Brock et al. 1977; Alexander et al. 1979; Gaulin and Sailer 1984; Mitani et al. 1996; Plavcan and Van Schaik 1997; Plavcan 1999, 2004; Puts 2010, 2016). Similarly, canine teeth are primary weapons in male-male contests in many mammal species. As with body mass, canine size dimorphism increases with levels of male-male competition in some primate taxa (Leutenegger and Kelly 1977; Kay et al. 1988; Plavcan and van Schaik 1992), though not when analyzed using phylogenetic comparative methods (Plavcan 2004; but see Thorén et al. 2006).

In addition to body mass and canine teeth, other musculoskeletal adaptations may improve male fighting performance. Traits that improve strength, agility, and maneuverability (i.e., whole-organism performance capacities) may also be under selection in males (Clutton-Brock and Harvey 1977; Leutenegger and Kelly 1977; Kappeler 1990, 1991, 1996; Carrier 2002; Lindenfors 2002; Pasi and Carrier 2003; Kemp et al. 2005; Lawler et al. 2005; Lailvaux and Irschick 2006; Carrier 2007; Lailvaux and Irschick 2007; Lawler 2009). In several lizard species, for example, winning in male contests is predicted by sprint speed (Garland et al. 1990; Robson and Miles 2000) or jumping ability (Lailvaux et al. 2004). The dynamic nature of male fighting has led to the evolution of sexual dimorphism in functional traits underlying fighting performance. In kangaroo species in which males compete for access to females, male-biased dimorphism is found in forearm length and muscle mass (in shoulder adductors, arm retractors, and elbow flexors) that functions to improve performance in grappling actions that occur during fights (Jarman 1983, 1989; Warburton et al. 2013; Richards et al. 2015). Similar patterns of male-biased dimorphism are found in other species that use their forelimbs when fighting, including 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). Recently, we found widespread sexual dimorphism in the postcranial skeleton in a sample of 26 Carnivora species (Morris and Brandt 2014; Morris and Carrier 2016). Phylogenetic model selection incorporating a variety of life history traits indicated that the evolution of this dimorphism was most strongly associated with sexual selection on male fighting performance (Morris and Carrier 2016).

Anthropoid primates are a useful group to examine postcranial specialization for male-male competition because of the variation of competition intensity across this taxon in addition to a well-resolved phylogeny. In addition to biting, fighting between males typically involves dynamic actions of the postcranial musculoskeletal system, such as striking with hands, kicking, grappling, lunging, and chasing (Southwick 1970; Goodall 1986; Huntingford and Turner 1987; Lawler et al. 2005). These actions can result in skull or limb bone fractures (Fossey 1983; Goodall 1986; Jurmain 1997) and may even be fatal (Southwick 1970; Goodall 1986; Huntingford and Turner 1987; Enquist and Leimar 1990; Drews 1996; Wrangham and Peterson 1996; Sherrow 2012; Daly 2016), resulting in female-biased adult sex ratios in some species (from higher rates of male mortality; Clutton-Brock et al. 1977; Clutton-Brock 1991; Kappeler 1999). Sexual dimorphism in postcranial anatomy received much attention prior to the arrival of modern phylogenetic-informed comparative methods. Those early studies showed that postcranial dimorphism was present but typically interpreted these patterns as a correlated response to increases in male body mass (“size-required” allometry; Wood 1976; Leutenegger and Larson 1985). However, more recent studies have shown that phylogenetic-informed analyses are crucial to the study of primate postcranial anatomy. For example, long bones metrics show significant phylogenetic signal both before and after adjusting for body mass (O'Neill and Dobson 2008). Similarly, the intermembral index, a measurement of relative forelimb to hindlimb length commonly associated with primate locomotor mode, was previously shown to be positively correlated with body mass across species (Jungers 1984; Martin 1990). When performing the same analysis using phylogenetic independent contrasts, however, this association is nearly absent ($R^2 = 0.04$; Nunn 2011). Thus, there is a need to examine patterns of sexual dimorphism in the postcranial skeleton of primates while incorporating phylogenic relatedness.

Here, we evaluate the postcranial skeletal anatomy of 11 anthropoid primate species using a set of functional indices that reflect specialization for improved performance in physical competition (Morris and Brandt 2014; Morris and Carrier 2016). Greater values in these functional indices are associated with the following traits: (1) broader distal ends of limbs that increase surface area for muscle attachment (Swindler and Wood 1973) and increase safety factors (Alexander 1981); (2) greater mechanical advantages across limb joints to increase force output (Maynard Smith and Savage 1956); and (3) relatively broader scapulae to house larger muscles associated with stabilizing the shoulder joint (Larson 1993) when using the forelimbs (e.g., for striking or grappling with a competitor). Together, these traits function to increase forces that may be applied to a competitor, increase stability and acceleration capacity, and increase safety factors to resist high limb loading in variable directions that may occur when fighting (Pasi and Carrier 2003; Morris and Brandt 2014; Morris and Carrier 2016). We predicted that males, as compared to females, would have greater values in these functional indices. We test this by examining functional index values for sex-based differences among species. We also predicted that mean skeletal shape sexual dimorphism (calculated as the mean sexual dimorphism of all functional indices) would increase with both sexual dimorphism in body mass (size sexual dimorphism; SSD) and canine height (canine sexual dimorphism; CSD). We examine these relationships using both standard and phylogenetic-informed methods. Because both SSD and CSD are correlated with body mass (Leutenegger 1982; Smith and Cheverud 2002), we use data adjusted for body mass using residual analysis. However, we also evaluate uncorrected data because of the suggestion by Plavcan (2004) that adjusting sexual dimorphism values for body mass also removes variation in the causal variable (sexual selection).

Materials and Methods

We measured male (n = 74) and female (n = 63) skeletons from specimens housed at the Smithsonian Institution National Museum of Natural History (Washington, D.C.), the British Natural History Museum (London), and the American Museum of Natural History (New York). All specimens were osteologically mature, as determined by fusion of epiphyses of the long bones. From physiological length (distance between articular surfaces) and width measurements, we calculated nine functional indices that are associated with increased specialization for physical competition (Table 4.1; Morris and Brandt 2014; Morris and Carrier 2016).

To test for sexual dimorphism across the species in our data set, we compared ln-transformed male and female functional index values using both standard paired *t*-tests as well as phylogenetic paired *t*-tests (Lindenfors et al. 2010). We calculated sexual dimorphism in each functional index (SD_{FI}) as male mean/female mean when the male mean was greater and 2 – female mean/male mean when the female mean was greater (Lovich and Gibbons 1992; Smith 1999). SD_{FI} values for each species were calculated separately and then ln-transformed.

To test the prediction that skeletal shape sexual dimorphism increases with the intensity of male-male competition, we examined the relationships between mean skeletal shape sexual dimorphism (SD_{SHAPE}; calculated separately for each species by taking the mean of all nine SD_{FI} values) and SSD and CSD. We obtained SSD and CSD values from the literature (SSD data: Smith and Jungers 1997; Kingdon et al. 2013; CSD data: Plavcan 2004). We took four approaches to evaluate the relationships between SD_{SHAPE}, SSD, and CSD. First, ln-transformed species values of SD_{SHAPE} were regressed against ln-transformed SSD or CSD. Second, we corrected data for body mass by calculating least-squares residuals of SD_{SHAPE}, SSD, and CSD on mean species body mass. Following this, body mass residuals of SD_{SHAPE} were regressed against body mass residuals of SSD and CSD. Third, we adjusted data for phylogenetic relatedness by calculating phylogenetic independent contrasts (PIC; Felsenstein 1985) for SD_{SHAPE}, SSD, and CSD. PIC values for SD_{SHAPE} were then regressed against PIC values for SSD and CSD. Fourth, to adjust for both phylogenetic relatedness and body mass simultaneously, we calculated body mass residuals of PIC values of SD_{SHAPE}, SSD, and CSD. For this, we regressed PIC values of SD_{SHAPE}, SSD, and CSD against PIC values of mean species body mass using least-squares regression with the intercept restricted to zero (Garland et al. 1992). We then regressed body mass residuals of SD_{SHAPE} PIC values against body mass residuals of SSD and CSD PIC values. For all phylogenetic-informed analyses, we used a recent species-level Primates supertree (Perelman et al. 2011). PIC values were calculated using the pic function in the *ape* package (Paradis et al. 2004). All analyses were carried out in the R statistical programming environment (R Development

Core Team 2016).

To graphically summarize the data, we plotted SD_{FI} values for each species onto the phylogeny used in the analysis. We plotted a given SD_{FI} value only when a univariate analysis of variance (ANOVA) indicated sexual dimorphism was present ($p < 0.05$).

Results

Among the 11 species of anthropoid primates in the analysis, sexual dimorphism was found in 4 of 9 functional indices (Table 4.2). Results from the non-phylogenetic and phylogenetic paired *t*-tests differed slightly, with 3 of 4 significant differences ($p < 0.05$) being in the same functional indices (humerus epicondyle index, olecranon mechanical advantage, and ischium mechanical advantage). The styloid width index was significant in the non-phylogenetic test and was marginally significant in the phylogenetic test ($p = 0.052$). Conversely, the femur epicondyle index was significant in the phylogenetic test and trended the same way in the non-phylogenetic test ($p = 0.089$). The hindlimb malleolus index trended toward dimorphism in both the non-phylogenetic ($p = 0.074$) and phylogenetic tests ($p = 0.093$). In all significant and trending results, males had greater functional index values.

Across species, SD_{SHAPE} was positively correlated with SSD when using species values, PIC values, and body mass residuals of PIC values, but not when using body mass residuals of species values (Table 4.3; Figure 4.1). SD_{SHAPE} was positively correlated with CSD only when using PIC values (Table 4.3; Figure 4.1). A graphical summary of the data set showing the presence ($p < 0.05$; ANOVA) and degree of dimorphism in SD_{FI} values for each species is presented in Figure 4.2.

Discussion

In our sample of 11 anthropoid primate species, we found sexual dimorphism in a subset of postcranial functional indices associated with morphological specialization for physical competition. Consistent with our predictions, sexual dimorphism was male-biased in all significant and trending results. Mean sexual dimorphism in skeletal shape (SD_{SHAPE}) was positively correlated with SSD. When controlling for species relatedness using phylogenetic independent contrasts, evolutionary change in SD_{SHAPE} is strongly associated with evolutionary change in SSD ($R^2 = 0.659$); when adjusting contrasts for body mass, this relationship remains moderately strong ($R^2 = 0.485$). SD_{SHAPE} was correlated with CSD only when using phylogenetic independent contrasts and resulted in a weaker but significant correlation ($R^2 = 0.334$). Together, these results indicate the presence of sexual dimorphism in skeletal shape within the anthropoid lineage and that this dimorphism increases with the intensity of male-male competition (using SSD as a proxy; Mitani et al. 1996; Plavcan and Van Schaik 1997; Plavcan 1999, 2004).

Sexually dimorphic traits in the forelimb identified in our analysis include a relatively broader humeral epicondyle, broader styloid, and greater mechanical advantage associated with the triceps muscle (olecranon mechanical advantage) in males. These traits increase surface area for muscle attachment of forelimb muscles, increase forelimb bone safety factors that resist high loading in variable directions that may occur during aggressive interactions, and increase force output during forearm extension. Functionally, these traits allow for greater force delivery for striking or manipulating opponents and greater safety factors for bones used in these dynamic actions. In the hindlimbs, males had a greater ischium mechanical advantage, which increases force output during hindlimb retraction, and a broader hindlimb malleolus. These traits increase forces available for accelerating the body, increase stability, and increase limb robusticity.

Our results are similar to previous studies investigating the relationship between sexual selection and sexual dimorphism in anthropoid primates. Numerous studies have shown a strong association between SSD or CSD and the degree of sexual selection as measured by mating system, the frequency and intensity of male-male competition, or the operational sex ratio (Clutton-Brock et al. 1977; Leutenegger and Kelly 1977; Harvey et al. 1978; Leutenegger 1982; Gaulin and Sailer 1984; Kay et al. 1988; Plavcan and van Schaik 1992; Ford 1994; Mitani et al. 1996; Plavcan and Van Schaik 1997; Lindenfors and Tullberg 1998; Plavcan 1999, 2004). The results of the present study extend these by showing that sexual selection may be acting on specific components of the musculoskeletal system in addition to body and canine size. Our results are also in agreement with other studies examining adaptations for male fighting ability and dimorphism in functional traits of the postcranial skeleton. Male-biased sexual dimorphism in forelimb morphology has been identified in several anthropoid primates in which males use their forelimbs when fighting (Wrangham and Peterson 1996), including greater forelimb mass and larger deltoids (both relative to body mass) in western lowland gorillas (*Gorilla gorilla*; Zihlman and McFarland 2000), greater skeletal robusticity of the forelimb in australopiths (McHenry 1986, 1991, 1996), and greater muscle mass in the arms of humans (Fuller et al. 1992; Nindl et al. 2002; Abe et al. 2003; Lassek and Gaulin 2009). Similarly, male kangaroos fight by grappling and striking with their forelimbs (Ganslosser 1989) and they also exhibit male-biased sexual dimorphism in forearm bone length and muscle mass (Jarman 1983, 1989; Warburton et al. 2013; Richards et al.

2015). Recently, we have shown widespread sexual dimorphism in the postcranial skeleton (forelimbs and hindlimbs) in a sample of 26 species of carnivorans (Morris and Brandt 2014; Morris and Carrier 2016). Using a similar set of functional indices as in the present study, we found male-biased skeletal shape sexual dimorphism that was positively correlated with body size dimorphism (used as a proxy for the intensity of male-male competition). Furthermore, phylogenetic model selection analyses indicated that the evolution of sexual dimorphism in skeletal shape was best explained by sexual selection (polygynous versus nonpolygynous species) and not by models based on diet, locomotor zone, social or foraging group sizes, or parental care (Morris and Carrier 2016). Specialization for aggressive behavior may also have played a role in the evolution of short hindlimbs and the derived plantigrade foot posture of Hominoidea (Carrier 2007; Carrier and Cunningham 2017).

The different manifestations of sexual dimorphism within and among groups of primates are likely a function of disparate selective pressures on morphological traits (Kappeler 1990; Plavcan 2004; Carrier 2007). In the context of postcranial sexual dimorphism, the relative importance of specific functional morphological traits may depend upon the dynamics of male-male combat (Lailvaux and Irschick 2006; Lassek and Gaulin 2009; Morgan and Carrier 2013; Carrier and Morgan 2015). For example, Kappeler (1996) suggested that the lack of sexual dimorphism in body mass or canine size in strepsirrhine primates, despite high levels of male-male aggression, may be due to the lack of importance of these traits during fights (in contrast to haplorrhine primates). Instead, agility and maneuverability may be more important for male fighting performance (Clutton-Brock and Harvey 1977; Leutenegger and Kelly 1977; Kappeler

1990, 1996; Lindenfors 2002; Lawler et al. 2005; Lawler 2009) or they may simply add to the arsenal of morphological traits that improve competitive ability.

The environmental substrate where male-male contests occur may also influence which traits improve performance (Kappeler 1990, 1991; Lawler et al. 2005; Lawler 2009). This may be especially salient in primarily arboreal species such as most primates. The Lawler et al. (2005) study of Verreaux's sifaka (*Propithecus verreauxi*) provides a relevant example. This species is sexually monomorphic in both body and canine size yet males compete in sustained, violent contests involving chasing, lunging, grabbing, and biting, all of which occurs arboreally (Richard 1978, 1992). In this case, the importance of arboreal agility may be greater than that of body size. Analysis showing that males of intermediate body size have the greatest reproductive fitness supports this assertion (Lawler et al. 2005). This may also explain the combination of high intensity male-male competition and low level of sexual dimorphism found in other lemur species (Kappeler 1990, 1991; Richard 1992; Kappeler 1996; Lindenfors 2002; Lawler et al. 2005) as well as monomorphism in body size of avian species in which males physically compete with each other (Székely et al. 2000; Raihani et al. 2006).

Locomotor demands may also constrain phenotypic divergence between males and females. In primates, arboreal locomotion may constrain the evolution of body size sexual dimorphism more strongly than terrestrial locomotion (Clutton-Brock et al. 1977; Leutenegger and Kelly 1977; Harvey et al. 1978; Plavcan and Van Schaik 1997; Lindenfors and Tullberg 1998; Lawler et al. 2005). This pattern contrasts with that found in carnivores, for which the evolution of skeletal shape sexual dimorphism appears to be more constrained in primarily terrestrial species as compared to primarily arboreal species (Morris and Carrier 2016). This difference may be due to a variety of ecological factors. In primates, body size evolution may be constrained by limits imposed by small braches used during arboreal foraging (Harvey et al. 1987). In carnivores, a group characterized by high daily travel distances (Garland 1983), the importance of locomotor economy may limit postcranial trait evolution (Morris and Carrier 2016). Functional trade-offs between locomotor performance and aggressive performance at the level of bone and muscle morphology may underlie these constraints (Carrier 2002; Pasi and Carrier 2003; Kemp et al. 2005). The examination of patterns of male-male competition and the degree of postcranial sexual dimorphism in other taxa will help to resolve the functional relationships and possible constraints between general locomotor performance and sexually selected performance traits. Particularly, phylogenetic-informed examination of skeletal shape sexual dimorphism in strepsirrhines would be informative, given the low degree of size sexual dimorphism despite intense male-male competition in this group.

In summary, we found evidence of sexual dimorphism in postcranial skeletal shape among a sample of 11 anthropoid primate species. A subset of functional morphological traits that are predicted to improve physical competition performance are sexually dimorphic in our sample, allowing males to have greater surface areas for attachment of limb muscles, greater safety factors in the limb bones, and greater force output. Though the dimorphism identified in our analysis was restricted to a subset of functional indices, overall mean sexual dimorphism (all indices included) was significantly positively correlated with dimorphism in body size, a common proxy for the intensity of male-male competition. In conclusion, our results suggest that selection on male fighting ability has played a role in the evolution of postcranial morphology in primates.

Acknowledgements

We thank the staff from the following museums for access to collections: American Museum of Natural History, New York; British National History Museum, London; Smithsonian Institution National Museum of Natural History, Washington, D.C. This work was funded by National Science Foundation grant IOS-0817782 (to DRC).

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Table 4.1. Postcranial morphological indices, definitions, and functional interpretations associated with morphological specialization for aggression.

Index	Definition
Scapula width index	Width of scapula along medial border relative to length of scapula along spine. Indicates relative size of surface area for attachment of muscles involved in stabilizing the shoulder joint during arm movements (supraspinatus, infraspinatus, subscapularis; Larson 1993).
Forelimb proportions index	Length of humerus relative to length of radius. Indicates degree of morphological specialization for producing large out-forces in the forelimb (Maynard Smith and Savage 1956). Note: this is the inverse of the "brachial index" (Mivart 1867; Napier and Napier 1967).
Humerus epicondyle index	Humerus epicondyle width relative to humerus length. Indicates relative surface area for attachment of wrist and digit flexor, extensor, pronator, and supinator muscles (Swindler and Wood 1973; Williams et al. 1995).
Olecranon mechanical advantage	Length of olecranon process relative to length of radius. Indicates anatomical mechanical advantage of triceps brachii, the main extensor of the elbow (Maynard Smith and Savage 1956; Rose 1993).
Styloid width index	Width of distal end of articulated radius/ulna relative to radius length. Indicates relative robusticity of distal forelimb.
Ischium mechanical advantage	Length of ischium relative to length of hindlimb (femur length + tibia length). Indicates anatomical mechanical advantage of main hindlimb retractor muscles (biceps femoris, semimembranosus, semitendinosus; Swindler and Wood 1973; Emerson 1985; Williams et al. 1995).
Hindlimb proportions index	Length of femur relative to length of tibia. Indicates degree of morphological specialization for producing large out-forces in the hindlimb (Maynard Smith and Savage 1956). Note: this is the inverse of the "crural index" (Mivart 1867; Napier and Napier 1967).
Femur epicondyle index	Femur epicondyle width relative to femur length. Indicates relative surface area for attachment of knee flexor and foot plantarflexor muscles (e.g., gastrocnemius; Swindler and Wood 1973; Williams et al. 1995).
Hindlimb malleolus index	Width of distal end of articulated tibia/fibula relative to tibia. Indicates relative robusticity of distal hindlimb.

Table 4.2. Mean sexual dimorphism in functional indices (SD_{FI}) and T-test results for 11 anthropoid primate species. Statistics for both non-phylogenetic and phylogenetic two-tailed paired *t*-tests are given.

Index	Mean SD_{FI} (std. dev.)	Paired *t*-test		Phylogenetic paired *t*-test	
		t	*p*-value	*t*	*p*-value
Scapula width index	1.010 (0.020)	-1.67	0.125	-1.26	0.241
Forelimb proportions index	0.992 (0.025)	1.03	0.329	0.64	0.542
Humerus epicondyle index	1.067 (0.035)	-6.54	**< 0.001***	14.00	**< 0.001***
Olecranon MA	1.075 (0.056)	-4.58	**0.001***	-3.13	0.014*
Styloid width index	1.035 (0.040)	-2.86	0.017*	-2.23	0.057
Ischium MA	1.047 (0.070)	-2.27	0.047*	-2.33	0.048*
Hindlimb proportions index	1.000 (0.016)	0.01	0.989	-0.09	0.929
Femur epicondyle index	1.025 (0.044)	-1.88	0.089	-2.73	0.034*
Hindlimb malleolus index	1.027 (0.045)	-2.02	0.071	-1.80	0.115

MA, mechanical advantage

* $p < 0.05$; bold type *p*-values indicate variables that remained significant after correction for multiple comparisons using the false discovery rate procedure (Benjamini and Hochberg 1995).

Table 4.3. Analyses of the relationships between mean sexual dimorphism in skeletal shape (SD_{SHAPE}) and sexual dimorphism in body mass (SSD) or canine height (CSD) for 11 anthropoid primate species.

	Species values		Body mass residuals		PIC		Body mass residuals of PIC	
	R^2	*p*-value	R^2	*p*-value	R^2	*p*-value	R^2	*p*-value
SD_{SHAPE} versus SSD	0.388	0.024*	0.067	0.157	0.659	0.003*	0.485	0.015*
SD_{SHAPE} versus CSD	0.076	0.210	0.012	0.734	0.334	0.047*	0.131	0.164

*Slope of regression significant ($p < 0.05$)
PIC: phylogenetic independent contrasts

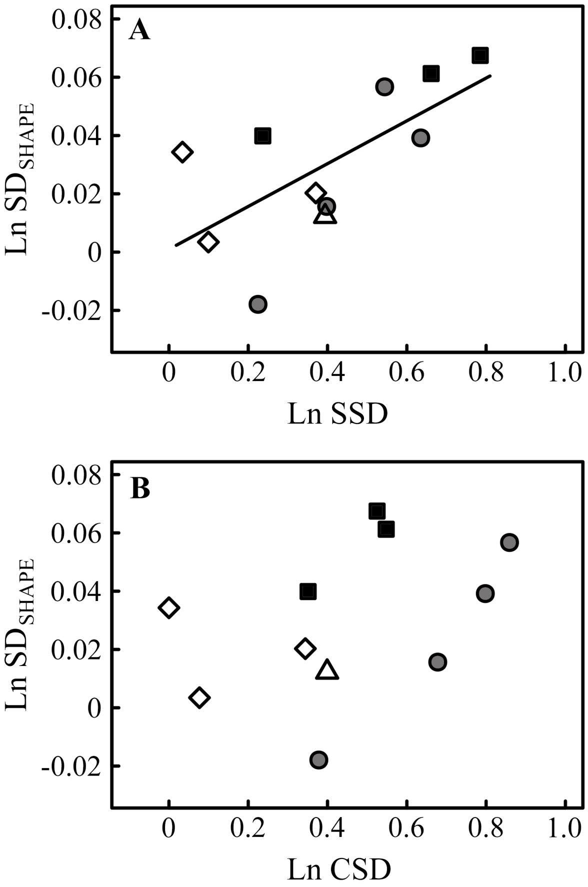

Figure 4.1. Regressions of mean sexual dimorphism in skeletal shape (SD_{SHAPE}) on (A) sexual dimorphism in body mass (SD_{MASS}) and (B) sexual dimorphism in canine height (SD_{CANINE}) for 11 anthropoid primate species. Unique symbols represent families: Cebidae (diamonds), Cercopithecidae (circles), Hominidae (squares), Atelidae (triangle). A regression line is shown for a significant linear regression equation ($p < 0.05$).

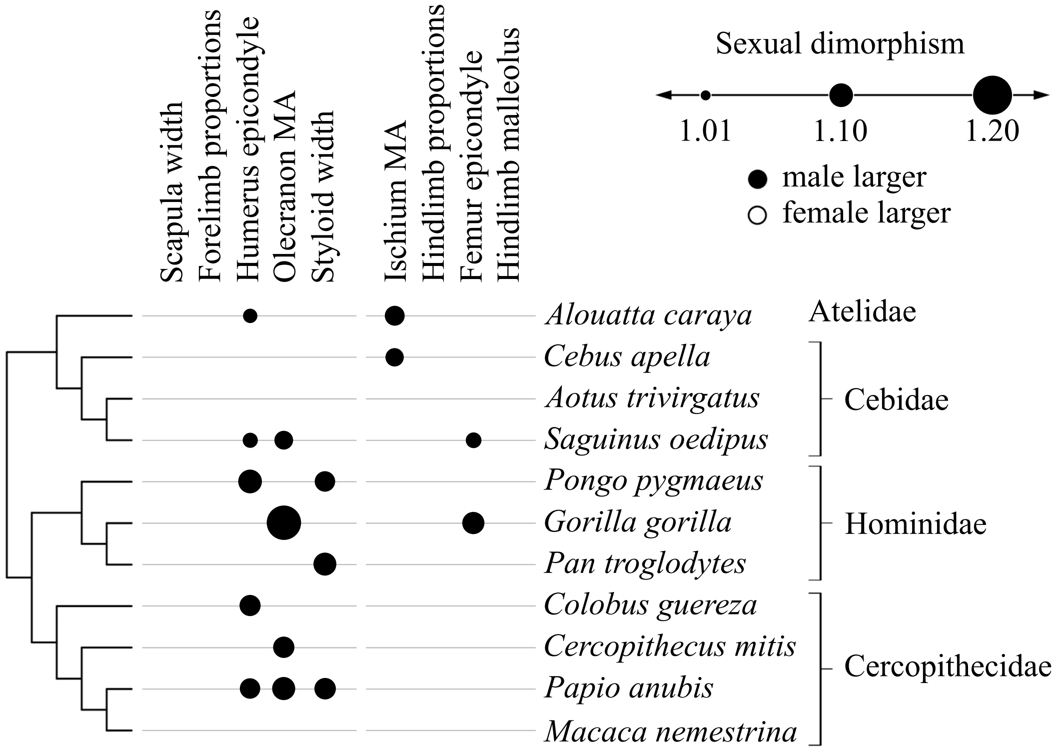

Figure 4.2. Graphical summary of data from 11 anthropoid primate species used in the analysis. Plotted points indicate SD_{FI} values that were sexually dimorphic ($p < 0.05$; ANOVA). The size of a point indicates the degree of sexual dimorphism (see scale). The phylogeny was pruned from a recent Primates supertree (Perelman et al. 2011).

CHAPTER 5

A DISPARITY BETWEEN LOCOMOTOR ECONOMY AND TERRITORY-HOLDING ABILITY IN MALE HOUSE MICE

Abstract

Both economical locomotion and physical fighting are important performance traits to many species because of their direct influence on components of Darwinian fitness. Locomotion represents a substantial portion of the total daily energy budget of many animals. Fighting performance often determines individual reproductive fitness through the means of resource control, social dominance, and access to mates. However, phenotypic traits that improve either locomotor economy or fighting ability may diminish performance in the other. Here we test for a disparity between locomotor economy and competitive ability in wild-derived house mice (*Mus musculus*). We used 8-week social competition trials in semi-natural enclosures to directly measure male competitive ability through territorial control and female occupancy within territories. We also measured oxygen consumption for each mouse using running trials in an enclosed treadmill and open-flow respirometry. Our results show that territory-holding males have higher absolute and mass-specific oxygen consumption when running (i.e., reduced locomotor economy) as compared to males that do not control territories. This relationship was

present both before and after 8-week competition trials in semi-natural enclosures. This disparity between physical competitive ability and economical locomotion may impose viability costs on males in species for which competition over mates is common and may constrain the evolution of behavioral and phenotypic diversity, particularly in natural settings with environmental and resource variability.

Introduction

Whole-organism performance is dependent upon a variety of integrated physiological traits. Because performance often directly determines aspects of Darwinian fitness, functional constraints on performance may limit phenotypic and life history evolution. Many phenotypic traits may be under conflicting selective pressures because of incompatible performance demands. For example, both economical locomotion and physical fighting play key roles in many aspects of the life history and ecology of animals. However, phenotypic traits that improve either locomotor economy or fighting ability may conflict with performance in the other (Carrier 2002; Oufiero and Garland 2007), resulting in a functional trade-off (Lewontin 1978; Maynard Smith et al. 1985; Lauder 1991; Vanhooydonck et al. 2001; Van Damme et al. 2002) whereby simultaneous specialization for both activities is impossible. Compromises resulting from such trade-offs may be vital to understanding the evolution of behavioral and phenotypic diversity in many species (Arnold 1992).

Locomotion represents a substantial portion of the total daily energy budget of many animals (Altmann 1987; Kenagy and Hoyt 1989; Karasov 1992; Chappell and Dlugosz 2009; Rezende et al. 2009). Locomotor economy is an important performance trait because of its direct influence on energetics. For example, reduced locomotor economy and the resulting higher energetic demand may impose viability costs in the manner of increased foraging time, increased exposure to predation, and decreased free energy for growth, maintenance, reproduction, or other behaviors (Blanckenhorn 2000). Likewise, fighting has profound effects on individual fitness because it often determines control of resources and access to mates (Andersson 1994). Male reproductive success is frequently linked to traits that improve fighting ability and social dominance, such as larger body mass (Clutton-Brock et al. 1982; Le Boeuf and Reiter 1988), larger weapon size (Preston et al. 2001; Coltman et al. 2002; Kruuk et al. 2002), greater bite force (Huyghe et al. 2005; Husak et al. 2009), and greater agility (Lailvaux et al. 2004).

Functional trade-offs between locomotor economy and fighting ability are likely to exist for a variety of physiological and biomechanical reasons (Carrier 2002). Specialization for economical locomotion is often associated with elongation of the limbs, which decreases the number of locomotor cycles to travel a given distance as well as the required rate and amplitude of muscle force generation (Gambaryan 1974; Hildebrand 1985; Kram and Taylor 1990), and reduced distal limb mass, which decreases the energy required to cycle the limbs (Hildebrand and Hurley 1985; Steudel 1990). In direct contrast to these traits, specialization for fighting appears to result in stout body plans, greater muscle mass in the distal limbs (Pasi and Carrier 2003), high mechanical advantages about the limb joints (Morris and Brandt 2014; Morris and Carrier 2016), and increased safety factors (Alexander 1981) in the limb bones to resist high loading in variable directions that may occur during aggressive interactions (Kemp et al. 2005). These contrasting phenotypes may lead to a performance disparity between economical locomotion and fighting ability.

Previous studies examining relationships between locomotor performance and sexually selected performance traits have provided mixed results. Studies on lizards have shown both increased (Garland et al. 1990; Robson and Miles 2000; Perry et al. 2004; Husak et al. 2006) and decreased (López and Martín 2002) locomotor performance (sprint speed and/or stamina) with social dominance or reproductive success and with characters improving competitive ability (e.g., bite force and head size; Cameron et al. 2013). In fact, many studies have found that certain individuals outperform others in all tasks, a phenomenon that has invoked a recent surge in research on the concept of "individual quality" (Van Damme et al. 2002; Wilson and Nussey 2010; Lailvaux and Kasumovic 2011; Wilson et al. 2014). However, few studies have been carried out examining similar performance traits in mammals and no study to our knowledge has examined the relationship between resource holding potential (e.g., individual fighting ability; Parker 1974) and locomotor economy. In combination with previous work on ectothermic species, the inclusion of studies on mammals will lead to a broader understanding of whole-organism performance and the importance of specific performance traits. Additionally, given the central role of energetics in physiological ecology (McNab 2002), there is a need for the incorporation of potential energetic trade-offs into performance studies (Lailvaux and Husak 2014).

In house mice (*Mus musculus*), the importance of fighting ability for increasing reproductive fitness as well as the high daily costs of locomotion are expected to generate selection on these two potentially conflicting performance traits. House mice have a polygynous mating system in which territory control among males is determined by frequent and intense fighting, resulting in a high incidence of injury and even death (Brown 1953; DeVries et al. 1997; Demas et al. 1999). Though biting is the major mode of inflicting damage, fighting between mice also involves grappling, rolling, and pushing, as well as lunging toward (aggressively) or jumping away from (defensively) an opponent (Miczek et al. 2001). Together, these data indicate that fighting in house mice involves dynamic actions and is dependent upon multiple aspects of morphology and physiology (i.e., whole-organism performance; Lailvaux and Irschick 2006). Likewise, house mice are dependent on locomotor performance for frequent travel in order to forage, to patrol and scent-mark territories, as well as when dispersing to new areas (Latham and Mason 2004). Home ranges of feral house mice range from 235 m^2 in open fields (Quadagno 1968) to 6000 m^2 in forests (Fitzgerald et al. 1981). Typical foraging behavior includes an average of 200 small meals per night, spread out between 20-30 food sites (Meehan 1984), in order to meet a daily food intake of up to 20% of body mass (Berry 1970; Meehan 1984). Additionally, mice may cover large distances (> 1.5 km) when dispersing (Berry 1968). Though data are not currently available for daily travel distance in wild house mice, laboratory mice furnished with a voluntary running wheel cover an average of 4.4 km per day (up to 11.6 km per day with artificial selection; Koteja et al. 1999) and expend 26-28% of total daily energetic output on locomotion (Rezende et al. 2009).

Based on the functional anatomy and physiological arguments above, we expect territory-holding (TH) male mice to have reduced locomotor economy as compared to non-territory-holding (non-TH) males. To test this, we used three separate populations of 10 male and 16 female unrelated age-matched adult mice in 8-week semi-natural enclosure trials to directly measure male territory control and female occupancy within territories. Genetic parentage analyses of mice populations in the experimental system used in this study have shown that territory control is a proxy of male reproductive fitness, with TH males siring approximately 80% of all offspring (Carroll et al. 2004). In addition, for each mouse, we measured oxygen consumption at intermediate running speeds and used both $\dot{V}_{O2}$ (ml O_2 min^{-1}) and mean mass-specific oxygen consumption (ml O_2 g^{-1} hr^{-1}; Taylor et al. 1970, 1982) as measures of locomotor economy. For these running trials, we used open-flow respirometry in an enclosed treadmill across a small range of speeds centered around the preferred voluntary running speeds of house mice (15 – 25 m min^{-1}; Rezende et al. 2006). Oxygen consumption at the mid-range of running speeds has been shown to be highly correlated with the overall cost of transport (general equation across all aerobic speeds; Taylor et al. 1982). We conducted running trials both before and after semi-natural enclosure trials. These methods allowed us to determine (i) whether there is a difference in locomotor economy between TH and non-TH male house mice; and (ii) whether or not this difference is a result of being in a competitive environment (i.e., from a decrease in performance associated with stress, injury, exhaustion, or temporary hormonal surges that may occur during semi-natural enclosure trials).

Materials and Methods

Study population and design

Mice used in our study were from an established wild-derived colony (Meagher et al. 2000) that has been managed to maintain genetic diversity similar to that of wild populations (Cunningham et al. 2013). A major advantage of using wild-derived mice is that they retain wild behaviors that are often lost in both inbred and outbred laboratory-bred strains (Koide et al. 2000; Nelson et al. 2013b). Three separate populations of 10 male and 16 female unrelated age-matched (55 ± 3.7 weeks old) adult mice were communally housed in 30 m^2 (similar to wild population densities; Sage 1981) semi-natural enclosures (Fig. 5.1). These enclosures simulate natural habitat complexity and provide easily-defended abundant resources. This is consistent with natural settings in which territorial strategies are common (Sage 1981; Latham and Mason 2004) and have been found to induce normal behaviors in wild mice (e.g., Potts et al. 1991; Manning et al. 1992; Meagher et al. 2000; Ilmonen et al. 2008). All enclosures were located within the same facility, with controlled ambient temperature (16-20 °C) and photoperiod (12 hours light: 12 hours dark). Mice were kept in this facility for the duration of the experiment. Prior to entering into the experimental protocol, all mice were individually housed for at least 2 weeks and were socially naïve (had not previously lived in a socially competitive environment). All protocols were approved by the Institutional Animal Care and Use Committee of the University of Utah (Protocol 14-05010).

Social competition trials

Passive integrated transponder (PIT) tags (TX1400ST, BioMark, Boise, ID, USA) implanted in each mouse and PIT tag readers (FS2001F-ISO, BioMark, Boise, ID, USA) at each feeder allowed real-time monitoring of social structure (individual occupancy and territorial control). Enclosure trials lasted 8 weeks with minimal human disturbance. At the conclusion of enclosure trials, PIT tag reader data were analyzed. Males were designated as “territory-holding” (TH) if they successfully controlled a territory with a minimum of 2 females (i.e., a polygynous territory) for at least 3 continuous weeks. Territory control was defined as a given male excluding all other males from a territory, such that > 80% of all male PIT tag reads were for that given male. Males that never reached this degree of territory control were designated as “non-territory-holding” (non-TH; adapted from Nelson et al. 2013a; Ruff et al. 2013).

Locomotor trials

Running trials were conducted both before and after competition trials. During running trials and for 2 weeks (pre-enclosure) or 24 hours (post-enclosure) prior, mice were individually housed (food and water *ad libitum*) to control for any previously existing differences in food or water consumption, injury, exhaustion, or temporary hormone surges. Mice were not handled when being transferred between cages and the treadmill in order to minimize any stress from human contact. Day 1 was for treadmill training and consisted of the following 5-minute intervals: acclimation (0 m min^{-1}), 8 m min^{-1}, 12 m min^{-1}, recovery (0 m min^{-1}), 16 m min^{-1}, and 20 m min^{-1}. Day 2 was a rest day. On day 3, oxygen consumption data were collected using the following protocol: 5-minute acclimation, 10-minute warm-up at 12 m min^{-1}, 5-minute recovery, 10-minute trial at 16 m min^{-1}, 5-minute recovery, 10-minute trial at 20 m min^{-1}. Day 4 was a rest day. On day 5, data were collected using the following protocol: 5-minute acclimation, 10-minute warm-up at 12 m min^{-1}, 5-minute recovery, 10-minute trial at 24 m min^{-1}.

Trials were carried out on a fully-enclosed airtight AccuPacer Mouse Treadmill (volume 2,300 ml; Omnitech Electronics, Inc., Columbus, OH, USA) with a clear top panel. Rates of oxygen consumption ($\dot{V}_{O2}$) were measured via open-flow respirometry. Flow rate through the running chamber was maintained at 750 ml min^{-1} using mass flow meters (Model M-10; Sierra Instruments, Monterey, CA, USA), which ensured that oxygen concentrations within the chamber remained above 20.5%. Subsamples were drawn (at 100 ml min^{-1}) from the excurrent air flow, scrubbed of CO_2 (soda lime), dried of water vapor (Drierite), and analyzed for O_2 concentration using O_2 analyzers (Model S-3A**,** AEI Technologies, Pittsburgh, PA, USA; FoxBox Respirometry System, Sable Systems International, Las Vegas, NV, USA). Because these O_2 analyzers have different response times, we used different lag times for analysis. Otherwise, the respirometry setup for each analyzer was identical. We verified that each analyzer obtained equivalent results for O_2 response using controlled flows of nitrogen gas. Analyzers were used simultaneously and randomly with respect to individuals and running speeds. Data were collected at 5 Hz using a Biopac MP100 (Biopac Systems, Inc., Goleta, CA, USA) and analyzed using LabAnalyst software (Warthog Systems, www.warthog.ucr.edu). All trials were conducted during the first half of dark cycle, corresponding to the highest activity period of mice (Rhodes et al. 2003). Body mass was measured after each running trial.

$\dot{V}_{O2}$ for each running speed was calculated as:

$$\dot{V}_{O2} = \dot{V} \times (FI_{O2} - FE_{O2}) / (1 - FE_{O2})\ ,$$

where $\dot{V}$ is flow rate (ml min^{-1} at standard temperature and pressure) and FI_{O2} and FE_{O2} are incurrent and excurrent fractional O_2 concentrations. We used the lowest 1-minute average within the last 5 minutes of a running interval to ensure that steady-state metabolism was reached. The coefficient of variation of $\dot{V}_{O2}$ data within the minimum

1-minute periods did not differ between territory-holding and non-territory-holding groups, for either pre-enclosure or post-enclosure running trials (two-tailed T-tests; *p* = 0.302 and 0.243, respectively). Mean mass-specific oxygen consumption (ml O_2 g^{-1} hr^{-1}) was calculated from these $\dot{V}_{O2}$ data as the mean of $\dot{V}_{O2}$ values from each of the 16, 20, and 24 m min^{-1} running intervals divided by body mass. Trial quality was assessed using a subjective scale (Swallow et al. 1998): "poor" trials when mice failed to run, "fair" trials when mice changed running direction or jumped around treadmill, or "good" trials when mice ran steadily and continuously in the same position on the treadmill. Only mice scoring "good" at all running speeds for all of the pre-enclosure running trials were included in the study. Because of this, 6 male mice were excluded and replaced. For post-enclosure trials, all individuals obtained "good" scores for running trials. All treadmill measurements and analyses were blind with respect to territory-holding status and were completed by one individual (J. S. Morris).

Statistical analysis

To assess the influence of territory-holding status, running speed, and body mass on oxygen consumption ($\dot{V}_{O2}$), a series of linear mixed-effects models (LMMs) were conducted. First, a "full model' was constructed predicting $\dot{V}_{O2}$ based on the fixed effects of territory-holding status, body mass, running speed, time point (pre- *versus* post-enclosure), and all possible interactions; additionally, this model included the random effects of individual (as a slope with running speed) and population. Then a "best model" was selected based on AICc scores from all possible candidates constructed by removing interaction terms and the fixed effect of time point: ΔAICc between the best model and the next leading candidate was 2.31. All candidate models included territory-holding status (to directly test our hypothesis) and both body mass and running speed (as both have been strongly linked to oxygen consumption; Taylor et al. 1970, 1982). These models were based on 180 observations (three running speeds each, for both pre- and post-enclosure running trials) from 30 mice that form the three study populations. The model intercept for these models was set at non-TH males, mean mass (23.59 g), mean speed (20 m min^{-1}), and pre-enclosure. Models were remarkably consistent indicating that no interaction was significant in any given candidate.

An additional series of LMMs was used to predict the mean mass-specific oxygen consumption (mean of $\dot{V}_{O2}$ values from each of the three running speeds, divided by mass; units of ml O_2 g^{-1} hr^{-1} from Taylor et al. 1970, 1982). First, a “full model” was constructed predicting mean mass-specific oxygen consumption based on the fixed effects of territory-holding status, body mass, time point, and all possible interactions; additionally, this model included the random effects of individual and population. Then a “best model” was selected based on AICc scores from all possible candidates constructed by removing interaction terms and the fixed effect of time point: ΔAICc between the best model and the next leading candidate was 4.78. All candidate models included territory-holding status and body mass. These models were based on 60 observations (one each for both pre- and post-enclosure running trials) from 30 individuals and the intercept was set at non-TH males, mean mass (23.59 g), and pre-enclosure. Models were consistent in indicating that no interaction term was significant in any candidate.

Finally, to explicitly test for a difference in body mass between TH and non-TH males, we ran a LMM in which body mass was predicted by the fixed effects of territory-holding status, time point, and a territory-holding-status-by-time-point interaction. Individual and population were modeled as random effects. The model was based on 60 observations (one each for both pre- and post-enclosure mass measurements) from 30 individuals and the intercept was set for non-TH males and pre-enclosure. All LMMs were performed using the lmer function of the lme4 package (Bates et al. 2016) in R (R Development Core Team, 2016). Degrees of freedom and resulting *p*-values were calculated with a Satterthwaite approximation using the lmerTest package (Kuznetsova et al. 2016). AICc scores were calculated using the AICcmodavg package (Mazerolle 2016).

Results

Out of 30 male mice in the study, 11 held exclusive territories with a minimum of 2 females for at least 3 continuous weeks (TH; n = 3, 4, and 4 for populations 1, 2, and 3, respectively). TH males successfully controlled exclusive territories for an average of 48 days out of 56 total days in the enclosures (the first week in enclosures is highly variable; following this, social patterns stabilize). The remaining 19 males were those that never successfully controlled a territory (non-TH).

Both the full and best models assessing the influence of territory-holding status on $\dot{V}_{O2}$ indicate that TH males have higher $\dot{V}_{O2}$ than non-TH males (Table 5.1). Specifically, according to the full model, TH males have $\dot{V}_{O2}$ levels 0.159 ± 0.067 (s.e.) ml O_2 min^{-1} higher than non-TH males (LMM; $t = 2.38$, df = 35.4, $p = 0.023$). $\dot{V}_{O2}$ was also found to have a positive relationship with body mass, increasing by 0.059 ± 0.015 ml O_2 min^{-1} per gram (LMM; $t = 4.06$, df = 108.8, $p < 0.001$). Interactions between territory-holding status and body mass or running speed did not significantly influence $\dot{V}_{O2}$ (LMM; $p =$

0.871 and 0.483, respectively). Likewise, no significant interaction between territory-holding status and time point was detected, indicating that the elevated $\dot{V}_{O2}$ of TH males did not change across the study (LMM; $p = 0.712$). Similarly, the best model indicates that TH males have higher $\dot{V}_{O2}$ than non-TH males. TH males have $\dot{V}_{O2}$ levels 0.136 ± 0.057 ml O_2 min^{-1} higher than do non-TH males (LMM; $t = 2.40$, df = 35.1, $p = 0.022$). $\dot{V}_{O2}$ was again found to have a positive relationship with body mass, increasing by 0.066 ± 0.008 ml O_2 min^{-1} per gram (LMM; $t = 8.16$, df = 118.8, $p < 0.001$). Additionally, running speed positively influenced $\dot{V}_{O2}$, with levels increasing by 0.015 ± 0.004 ml O_2 min^{-1} per m min^{-1} (LMM; $t = 3.76$, df = 172.9, $p < 0.001$). No interactions were included in this model nor was the fixed effect of time point.

Territory-holding status was also found to influence mean mass-specific oxygen consumption according to both the full and best models (Table 5.2). Specifically, the full model indicates that TH males consumed 0.408 ± 0.195 ml O_2 g^{-1} hr^{-1} more than did non-TH males (LMM; $t = 2.09$, df = 46.8, $p = 0.042$; Fig. 5.1) and that there is a marginally statistically significant negative correlation with body mass (-0.094 ± 0.049 ml O_2 g^{-1} hr^{-1} per g; LMM; $t = -1.90$, df = 52.0, $p = 0.062$); there was no interaction between territory-holding status and body mass ($p = 0.778$). Moreover, mean mass-specific oxygen consumption was not influenced by time point (LMM; $p = 0.596$) nor was there a significant interaction between time point and territory-holding status (LMM; $p = 0.943$) or time point and body mass (LMM; $p = 0.920$). The simplified best model indicates that TH males consumed 0.398 ± 0.155 ml O_2 g^{-1} hr^{-1} more than did non-TH males (LMM; $t = 2.58$, df = 26.1, $p = 0.016$) and that there is a statistically significant negative correlation with body mass (-0.097 ± 0.027 ml O_2 g^{-1} hr^{-1} per g; LMM; $t = -3.65$, df = 47.8, $p =$

0.001). No interactions were included in this model nor was the fixed effect of time point.

Territory-holding status did not influence body mass (Table 5.1). No significant difference in the body mass of TH and non-TH males was detected (LMM; $p = 0.810$; Fig. 5.2). Body mass did not change between time points (LMM; $p = 0.902$) nor was there a significant interaction with territory-holding status (LMM; $p = 0.717$).

Discussion

Our results show that territory-holding (TH) male house mice have higher absolute oxygen consumption ($\dot{V}_{O2}$) as well as higher mean mass-specific oxygen consumption (ml O_2 g^{-1} hr^{-1}) when running at intermediate speeds (i.e., reduced locomotor economy) as compared to non-territory-holding (non-TH) males. This difference was present both before and after 8-week competition trials in semi-natural enclosures. Prior to beginning the experimental protocol, all mice were individually housed in cages, indicating that this disparity is not a result of the experience of being in the competition enclosures (e.g., from stress, unequal access to food or water, injury, exhaustion, or temporary hormone surges).

Analysis of $\dot{V}_{O2}$ data indicated that, consistent with previous studies, oxygen consumption increases with both running speed and body mass (Taylor et al. 1970, 1982; Rezende et al. 2006, 2009). According to the model based on $\dot{V}_{O2}$, the added energetic cost of running in TH males is equivalent to being 2.1 g heavier or running 9.1 m min^{-1} faster. The model based on mean mass-specific oxygen consumption indicated that TH males have 6.1% higher rates of energy expenditure across a range intermediate running speeds. This equates to a difference in the distance-specific energetic cost of running of

0.340 ml O_2 g^{-1} km^{-1}. Assuming a resting metabolic rate of 0.557 ml O_2 min^{-1} (based on mean mass of 23.59 g from this study and the equation for resting metabolic rate from Rezende et al. 2009), this difference would result in a daily energetic savings substantial enough to sustain an individual at resting metabolic rate for about 37 minutes (for 1 km traveled per day). If extrapolated to the average voluntary running distance of male lab mice furnished with a running wheel (4.4 km per day; Koteja et al. 1999), this would result in a difference of 1.496 ml O_2 g^{-1}, enough to sustain resting metabolism for more than two and a half hours. Thus, while the percentage difference between oxygen consumption rates is relatively small, this difference may have a notable impact on daily energetic expenditure.

A caveat of the present study is that we do not have data on the resting or basal metabolic rates of individual mice. While we cannot exclude the possibility that systematic differences in non-active metabolic rates between TH and non-TH males may contribute to the differences in locomotor economy identified in our study, this scenario seems unlikely for several reasons. First, the difference in mean mass-specific oxygen consumption between TH and non-TH males was 0.429 ml O_2 g^{-1} hr^{-1} (effect of territory status in LMM). This represents 30% of the calculated mass-specific resting metabolic rate (1.418 ml O_2 g^{-1} hr^{-1}, based on the equation of Rezende et al. 2009) and is close to or greater than two standard deviations in mean basal metabolic rate from previous studies of lab mice (2 s.d. = 0.332 and 0.458; Konarzewski and Diamond 1995; Wone et al. 2009). Thus, a difference of this magnitude in non-active metabolic rate between TH and non-TH males seems unlikely. Second, a previous study on another rodent species (bank voles, *Myodes glareolus*) found no association between male social dominance in competitive arenas and basal metabolic rate (Radwan et al. 2004).

Interestingly, body mass was not correlated with territory control in our study, either before or after competition trials. Variance in post-enclosure body mass was greater among non-TH as compared to TH males (Bartlett test; $p = 0.031$). These data suggest that an intermediate body mass may be optimal for securing and maintaining exclusive territories, possibly because of the importance of agility and maneuverability in the dynamic actions of physical fighting (sensu Székely et al. 2000; Lailvaux et al. 2004; Lawler et al. 2005; Lailvaux and Irschick 2006; Raihani et al. 2006; Lawler 2009). Indeed, recent evidence from the same experimental system used in the present study indicates that males of intermediate body mass have greater reproductive fitness than larger or smaller males (Ruff et al. 2017).

While territory control equates to greater reproductive fitness in this study system (based on genetic parentage analysis; Carroll et al. 2004) and others (Andersson 1994), higher locomotor costs in TH males may impose viability costs in the manner of increased foraging time to meet their higher energetic demands. This would effectively decrease free energy and time for other activities and may increase mortality risk by exposing individuals to greater threat of predation (Blanckenhorn 2000). Sexually selected behaviors (i.e., fighting for territory and mates, and scent-marking) are also energetically costly (Karasov 1992; Briffa and Sneddon 2007). When combined with the high energetic costs of locomotion (26-28% of total daily energetic expenditure in laboratory mice; Rezende et al. 2009), this may lead to phenotypic or behavioral constraints, and ultimately fitness costs, via resource allocation trade-offs (Zera and Harshman 2001; Lailvaux and Husak 2014). Alternatively, TH males may avoid these potential viability costs through decreased foraging time/distance allowed by living in high quality resource-rich territories. However, males that are not capable of controlling high quality territories likely spend more time foraging because they are often in lower quality habitat and may spend more time dispersing and traveling while seeking out available territory. The lower locomotor costs that we found in non-TH males may be beneficial in these circumstances and may also be advantageous in variable resource environments, particularly when food is ephemeral and abundance is low. In natural environments (as compared to our semi-natural settings with food *ad libitum*), resource acquisition limitations may exacerbate performance constraints underlying trade-offs (Blanckenhorn 2000; Lailvaux and Husak 2014).

The performance differences identified in this study are likely caused by conflicting functional demands within the musculoskeletal system. Fighting between mice involves biting, pushing, grappling, and lunging (Miczek et al. 2001). Mice in the present study exhibit these behaviors during frequent fighting and as indicated by characteristic wounding (J. S. Morris, personal observation). Many of these actions are accomplished using the same anatomical structures that compose the primary locomotor system (i.e., limb bones and muscles). This creates a conflict because the demands imposed by economical locomotion and fighting predict optimization in opposing directions (i.e., long, gracile limbs *versus* stout, muscular limbs). Comparisons of closely-related species, such as cheetahs and lions or gibbons and gorillas, exemplify these disparate phenotypes as well as the corresponding social behaviors (i.e., low to high levels of male-male competition) and mating systems (i.e., non-polygynous to highly polygynous) associated with each (Carrier 2002). Within a species or sex, however, simultaneous specialization for both aggression and economical locomotion is not possible without the evolution of novel structures, behaviors, or other mechanisms of compensation (Oufiero and Garland 2007; Husak and Lailvaux 2014). For example, the evolution of horns in bovids, antlers in cervids, and bipedal hopping in kangaroos (by freeing the forelimbs) have allowed both a high degree of cursoriality *and* polygynous mating systems with intense male-male competition (Carrier 2002). In these taxa, the constraints imposed by locomotion-aggression trade-offs have been circumvented by decoupling anatomical weapons from the primary locomotor system. The apparent lack of novel solutions in mice and other mammals may limit performance in functionally conflicting tasks.

In summary, we found that TH male house mice have reduced locomotor economy as compared to non-TH males. These results are likely caused by a functional trade-off between economical locomotion and physical fighting (Carrier 2002). Locomotor economy is an important performance trait because it is a major determinant of total daily energetic expenditure, and because of this, is relevant to many vertebrate species. Additionally, we directly measured territory control that is, in our study system, a proxy for reproductive success. These methods allowed direct comparison of two whole-organism performance traits that are important components of Darwinian fitness. We suggest that future studies on performance disparities may be improved by incorporating an energetics-based approach to the examination of locomotor traits that may be in functional conflict with sexually selected performance traits.

Acknowledgements

We thank L. Morrison for colony management and data collection; D. Cornwall for assistance with animal processing; C. Farmer for respirometry equipment and instruction; and M. Chappell, B. Cieri, and A. Cooper for useful discussions. P. Koteja and one anonymous reviewer provided feedback that greatly improved the manuscript.

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Table 5.1. Linear mixed model results for the influence of territory-holding (TH) status, body mass, running speed, and time point on oxygen consumption ($\dot{V}_{O_2}$)

$\dot{V}_{O_2}$ full model — Linear mixed model with 180 observations of 30 individuals in 3 populations. Intercept set at non-TH, mean mass (23.59 g), mean speed (20 m min^{-1}), and pre-enclosure levels.

Random effects	*Variance*	*Std. Dev.*			
Individual × speed (slope)	0.0000	0.0007			
Population	0.0040	0.0632			
Fixed effects	*Estimate*	*Std. Err.*	*df*	*t value*	*Pr(>|t|)*
Intercept	2.624	0.054	3.6	48.22	< 0.001 ***
TH status	0.159	0.067	35.4	2.38	0.023 *
Mass	0.059	0.015	108.8	4.06	< 0.001 ***
Speed	0.009	0.007	151.7	1.21	0.228
Time	0.018	0.032	134.8	0.56	0.578
TH status × mass	-0.006	0.036	159.7	-0.16	0.871
TH status × speed	0.008	0.012	151.7	0.70	0.483
Mass × speed	-0.001	0.003	142.0	-0.24	0.807
TH status × time	-0.001	0.053	135.5	-0.01	0.991
Mass × time	0.004	0.012	152.9	0.33	0.741
Speed × time	0.006	0.010	134.5	0.63	0.530
TH status × mass × speed	0.002	0.008	137.5	0.19	0.849
TH status × mass × time	0.025	0.037	158.2	0.67	0.505
TH status × speed × time	0.006	0.016	134.5	0.37	0.712
Mass × speed × time	-0.001	0.004	135.8	-0.18	0.857
TH status × mass × speed × time	0.006	0.009	136.6	0.64	0.524

$\dot{V}_{O_2}$ best model — Linear mixed model with 180 observations of 30 individuals in 3 populations. Intercept set at non-TH, mean mass (23.59 g), and mean speed (20 m min^{-1}).

Random effects	*Variance*	*Std. Dev.*			
Individual × speed (slope)	0.0000	0.0007			
Population	0.0040	0.0596			
Fixed effects	*Estimate*	*Std. Err.*	*df*	*t value*	*Pr(>|t|)*
Intercept	2.639	0.049	3.0	53.53	< 0.001 ***
TH status	0.136	0.057	35.1	2.40	0.022 *
Mass	0.066	0.008	118.8	8.16	< 0.001 ***
Speed	0.015	0.004	172.9	3.76	< 0.001 ***

* $p < 0.05$, *** $p < 0.001$

Table 5.2. Linear mixed model results for the influence of territory-holding (TH) status, body mass, and time point on mean mass-specific oxygen consumption (ml O_2 g^{-1} hr^{-1})

Mean mass-specific oxygen consumption (ml O_2 g^{-1} hr^{-1}) full model — Linear mixed model with 60 observations of 30 individuals in 3 populations. Intercept set at non-TH, mean mass (23.59 g), and pre-enclosure levels.

Random effects	*Variance*	*Std. Dev.*			
Individual	0.0720	0.2683			
Population	0.0010	0.0322			
Fixed effects	*Estimate*	*Std. Err.*	*df*	*t value*	*Pr(>|t|)*
Intercept	6.682	0.120	9.7	55.80	< 0.001 ***
TH status	0.408	0.195	46.8	2.09	0.042 *
Mass	-0.094	0.049	52.0	-1.91	0.062
Time	0.077	0.143	24.5	0.54	0.596
TH status × mass	0.039	0.136	48.4	0.28	0.778
TH status × time	-0.017	0.237	24.8	-0.07	0.943
Mass × time	-0.005	0.054	30.8	-0.10	0.920
TH status × mass × time	-0.036	0.151	41.1	-0.24	0.813

Mean mass-specific oxygen consumption (ml O_2 g^{-1} hr^{-1}) best model — Linear mixed model with 60 observations of 30 individuals in 3 populations. Intercept set at non-TH and mean mass (23.59 g) levels.

Random effects	*Variance*	*Std. Dev.*			
Individual	0.0828	0.2878			
Population	0.0013	0.0369			
Fixed effects	*Estimate*	*Std. Err.*	*df*	*t value*	*Pr(>|t|)*
Intercept	6.721	0.096	4.49	70.1	< 0.001 ***
TH status	0.398	0.155	26.14	2.58	0.016 *
Mass	-0.097	0.027	47.84	-3.65	< 0.001 ***

* $p < 0.05$, *** $p < 0.001$

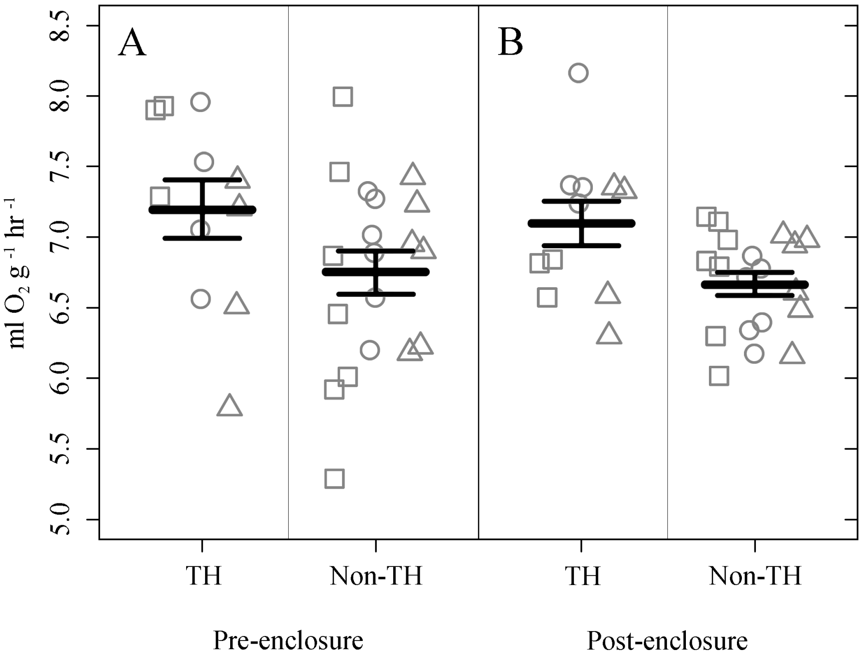

Figure 5.1. Mean mass-specific oxygen consumption across intermediate running speeds for territory-holding (TH) and non-territory-holding (non-TH) male house mice. Populations are represented by unique symbols. Scatter was added to horizontal values to aid visualization. Means ± s.e. are shown by bars. TH males had greater mean mass-specific oxygen consumption rates than non-TH males (LMM; $p < 0.05$). Mean mass-specific oxygen consumption for TH males was 6.4% greater than non-TH males.

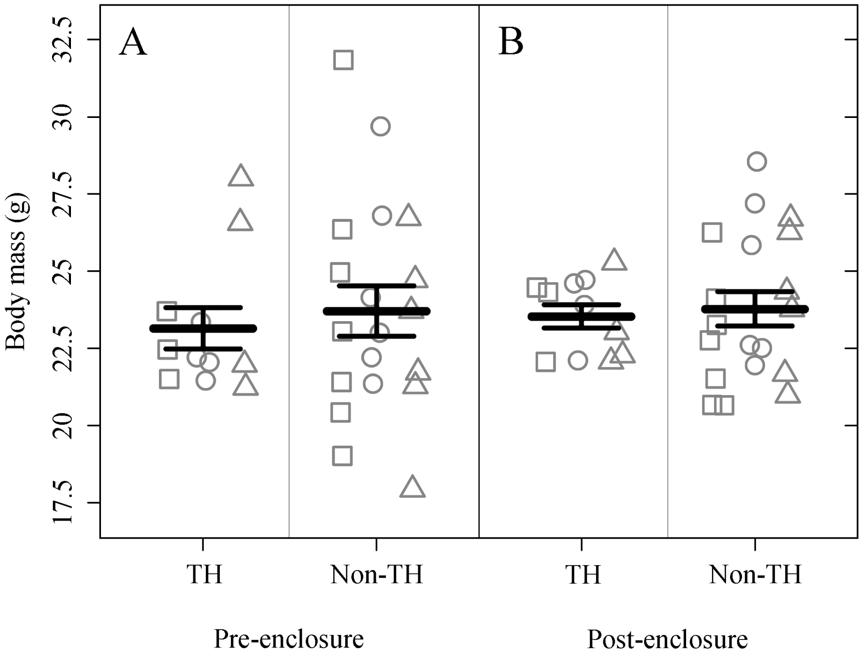

Figure 5.2. Body mass for TH and non-TH male house mice. Populations are represented by unique symbols. Scatter was added to horizontal values to aid visualization. Means ± s.e. are shown by bars. Body mass before (A) and after (B) competition trials in semi-natural enclosures did not differ between TH and non-TH males (LMM; $p > 0.05$).