

RESEARCH ARTICLE

Musculoskeletal mass and shape are correlated with competitive ability in male house mice (*Mus musculus*)

Amanda N. Cooper^{1,*}, Christopher B. Cunningham², Jeremy S. Morris³, James S. Ruff¹, Wayne K. Potts¹ and David R. Carrier¹

ABSTRACT

Intense physical competition between males for mating opportunities is widespread among mammals. In such agonistic encounters, males with combinations of morphological, physiological and behavioral characters that allow them to dominate an opponent have greater fitness. However, the specific physical traits associated with competitive ability are poorly understood. Larger body size is often correlated with fitness in mammals. Interestingly, fitness is maximized at intermediate body masses in male house mice (*Mus musculus*), a species with a polygynous mating system in which males compete physically for access to reproductive resources. Here, we used competition trials in semi-natural, mixed-sex population enclosures to directly measure competitive ability in male house mice based on control of a preferred nesting site. We tested the hypothesis that the musculoskeletal systems of male mice demonstrating high competitive ability are more specialized for competition by comparing the masses of 10 major muscle groups and eight bones as well as a set of 12 skeletal shape indices associated with anatomical specialization for fighting performance in a set of nine winners and 20 losers. Winning males possessed several traits hypothesized to enhance performance in male–male contests: relatively greater mass in several muscle groups and bones of the forelimb and hindlimb and larger scapular surface area. Unexpectedly, no measurements of the head and neck differed significantly between winners and losers. These results identify musculoskeletal traits associated with competitive ability in male house mice and suggest that our current understanding of mammalian fighting performance is incomplete and more nuanced than previously considered.

KEY WORDS: Biomechanics, Life-history traits, Morphology, Musculoskeletal system, Sexual selection

INTRODUCTION

The outcome of agonistic encounters is directly associated with reproductive fitness for males of many mammalian species (Dewsbury, 1982). Large body mass is a strong predictor of fighting performance in male–male contests (Andersson, 1994); however, other morphological, physiological and behavioral traits also influence competitive ability (e.g. Lailvaux and Irschick, 2006). House mice (*Mus musculus* Linnaeus) are an excellent model for studying the physical correlates of fighting performance in

mammals because they possess a polygynous mating system where male mice acquire reproductive resources such as territory at least in part by fighting (Crowcroft, 1955; Hayashi, 1993), and highly competitive individuals have been shown to have greater reproductive success (De Fries and McClearn, 1970; Oakeshott, 1974; Kuse and De Fries, 1976; Dewsbury, 1982; Kaufman, 1983; Wolff, 1985; Hurst, 1987; Krackow, 1993; Meagher et al., 2000; Rolland et al., 2003). Interestingly, the relationship between body mass and fighting performance in male house mice does not adhere strictly to the ‘bigger is better’ paradigm. While some studies have found a direct correlation between body mass and competitive ability in male house mice (De Fries and McClearn, 1970; Oakeshott, 1974; Cunningham et al., 2013), others have reported no effect of body size (Benton et al., 1980; Rolland et al., 2003). More recent studies have suggested an optimal body mass for competitive ability in male house mice: Ruff et al. (2017) showed that fitness, estimated by the number of offspring produced, peaks at intermediate body sizes for male mice competing in semi-natural environments. Morris et al. (2017) found in the same experimental system that, although body mass did not differ significantly with territory-holding status, non-territory-holding mice exhibited greater variance in body size than mice that were able to consistently defend a territory. These results suggest that other aspects of the musculoskeletal system may be contributing to the unexplained variation observed in competitive ability.

Previous morphological studies of male–male contests in vertebrates have focused overwhelmingly on the head, while the role of the postcranial musculoskeletal system has received much less attention. Head size morphometrics in relation to biting performance have been intensely studied (in mammals: Hanski et al., 1991; Koren et al., 2008; in lizards: Hews, 1990; Olsson, 1994; Molina-Borja et al., 1998; Alberts et al., 2002; López and Martín, 2002; Gier, 2003; Lailvaux et al., 2004; Perry et al., 2004; Huyghe et al., 2005; Lappin and Husak, 2005; Husak et al., 2006; Kohlsdorf et al., 2006; Stuart-Fox et al., 2006; Whiting et al., 2006; Stuart-Fox et al., 2009; Huyghe et al., 2012; Cameron et al., 2013; McEvoy et al., 2013; McLean and Stuart-Fox, 2015; Bush et al., 2016; Fernández et al., 2018). In several species, male-biased sexual dimorphism has been identified in muscle mass, limb length and skeletal shape indices associated with anatomical specialization for fighting performance (in primates: Gallagher et al., 1997; Zihlman and McFarland, 2000; Nindl et al., 2002; Abe et al., 2003; Lassek and Gaulin, 2009; Morris et al., 2019; in macropodids: Jarman, 1983, 1989; Warburton et al., 2013; Richards et al., 2015; in carnivores: Pasi and Carrier, 2003; Kemp et al., 2005; Morris and Brandt, 2014; Morris and Carrier, 2016), but these studies did not directly measure the correlation between these characters and the outcome of male–male contests. In such comparisons of males with high and low competitive ability, postcranial measurements have been limited to limb segment lengths in lizards (López and

¹School of Biological Sciences, University of Utah, Salt Lake City, UT 84112, USA.

²Department of Biosciences, Swansea University, Swansea SA2 8PP, UK.

³Department of Biology, Wofford College, Spartanburg, SC 29303, USA.

*Author for correspondence (amanda.cooper@utah.edu)

 A.N.C., 0000-0002-3195-9500

Martin, 2002; Huyghe et al., 2005; Kohlsdorf et al., 2006; Cameron et al., 2013).

Here, we investigated whether highly competitive male house mice are more anatomically specialized for fighting performance than less competitive males. Our first aim was to test whether muscle mass was greater in competition-winning mice than in losers. We hypothesized that sexual selection would act most strongly on the muscle groups that are most important for fighting performance in male mice. Greater muscle mass is associated with (1) larger muscle cross-sectional area, which provides an increased capacity for force production, and/or (2) longer muscle fascicles, which allow for greater shortening velocity (Biewener, 2003). Therefore, individuals with relatively larger muscle mass will be capable of producing more force and power, permitting them to more easily manipulate an opponent. Our second aim was to investigate whether winners possessed greater bone mass and other sets of skeletal shape adaptations consistent with specialization for physical competition (Morris and Brandt, 2014; Morris and Carrier, 2016; Morris et al., 2019). Overall, we expected the bones of winners to be more robust and, therefore, heavier than those of their less-competitive counterparts. Larger muscle forces require more robust bones to maintain appropriate safety factors (Alexander, 1981). Additionally, unpredictable loading directions during fighting select for a circular cross-sectional shape that makes limb bones more massive than those in animals specialized for running (Kemp et al., 2005). With respect to skeletal shape, we first predicted that winners would have relatively shorter and/or broader skulls to increase bite force by providing a greater mechanical advantage for the jaw adductors and more attachment area for the temporalis muscles, respectively (Biknevicius and Van Valkenburgh, 1996). Second, we expected winners to have broader cervical vertebrae to allow for larger cervical muscle attachment sites. Once the attacker has grasped an opponent with its jaws, larger neck muscles may facilitate jerking the head and pulling on the opponent with the teeth while resisting lateral loading of the attacker's own head, which could lead to injury (Radinsky, 1981). The cervical vertebrae also serve as attachment sites for extrinsic appendicular muscles capable of protracting the forelimb (Evans, 1993), which may be useful during upright grappling. Our third prediction was that the scapulae of winners would have more surface area for the attachment of muscles involved in transmitting force from the trunk to the forelimb (Carrier et al., 2006) and in stabilizing the shoulder joint. Finally, we expected anatomical mechanical advantage of the limbs to be greater in winners, allowing for increased force output against an opponent during grappling and/or pushing.

MATERIALS AND METHODS

Study population and experimental setup

The present study measured musculoskeletal parameters in cadavers of mice that were subjects in a previous experiment, in which naive male house mice competed in a semi-natural environment for access to a single female housed within an optimal territory (Cunningham et al., 2013). In that experiment, male and female mice were sexually mature (≥ 4 months of age), and males were age matched with their competitors to control for interactions between age and competitive ability. All mice were procured from a population of wild-derived house mice maintained at the University of Utah, School of Biological Sciences. These animals were outbred descendants of a wild-caught population initially described by Meagher et al. (2000).

Transparent acrylic semi-natural enclosures measuring 140 \times 30 \times 15 cm were constructed based on the semi-natural model

system described in Carroll and Potts (2007). Taking advantage of the natural preference of mice for seclusion from conspecifics and predators (Wolff, 1985), an 'optimal territory' of 15 \times 30 \times 15 cm with opaque walls, nesting material, a single female and its own supply of food and water was placed at one end of the enclosure. The communal (non-optimal) area provided no opportunities for hiding and had shared food and water *ad libitum* with no bedding materials, creating an incentive for competition.

Competition assessment took place over the course of two rounds, with each round lasting 3 days. This duration was deemed appropriate for assessing competitive ability because mice quickly form social hierarchies via physical competition once introduced into a semi-natural environment (De Fries and McClearn, 1970; Hayashi, 1993). A group of four males and a single female participated in the first round. The second round of competition pitted three first-round winners against each other, and three losers against other losers. In all trials, both the population density and the operational sex ratio were much greater than those seen in self-regulating natural and semi-natural populations (Lidicker, 1976; Gomez et al., 2008). We expected that both the male-biased sex ratio and the relatively small size of the enclosures would help to identify individual differences in competitive ability, as larger enclosures may result in more chases in mice (Dewsbury, 1981, 1982). These factors, combined with two rounds of competition, presumably resulted in increased importance of musculoskeletal traits that influence fighting performance.

The two rounds of competition produced nine two-time competition winners (males with high competitive ability) and 20 two-time losers (males with low competitive ability). The winner of each competitive trial was determined by assessing (1) which male most frequently occupied the optimal territory based on a series of six observations over the 3 day competition period and (2) the number of wounds on the tail and hindquarters (De Fries and McClearn, 1970; Oakeshott, 1974). The combined criteria of optimal territory occupancy and the amount of superficial wounding produced undisputed winners for all competition trials. For most trials, occupation of the preferred territory alone was sufficient to clearly identify a winner. This measure was supported by pronounced disparities in superficial wounding. Some winners consistently tolerated the presence of one or more males within the optimal territory across multiple observations; in these instances the single winning male always displayed considerably less wounding and better overall body condition than his cohabitor(s). All protocols were approved by the Institutional Animal Care and Use Committee of the University of Utah (Protocol 10-07002).

Muscle and bone mass measurements

We dissected and removed the following 10 major muscle groups from each mouse: pectoralis, ventral neck, biceps, triceps, wrist flexors and extensors, hamstrings, gluteus, quadriceps, gastrocnemius, and ankle flexors and minor extensors (Fig. 1 and Table 1). These groups were chosen based on their anticipated relevance to fighting behavior. Dissections were performed at 10 \times magnification under a stereo microscope using fine-tipped watchmaker's forceps. Muscles were kept moist at all times with a 0.9% NaCl solution. Removed muscles were placed in a gravity convection oven (Memmert, Schwabach, Germany) to dry for 24 h at 55°C. Muscles were weighed (0.0001 g, Mettler-Toledo, LLC, Columbus, OH, USA) immediately after drying to prevent rehydration. Deep fascia and minor nerves and blood vessels were not removed from their associated muscle groups prior to weighing. Very small, consistent portions of deltoid muscles were

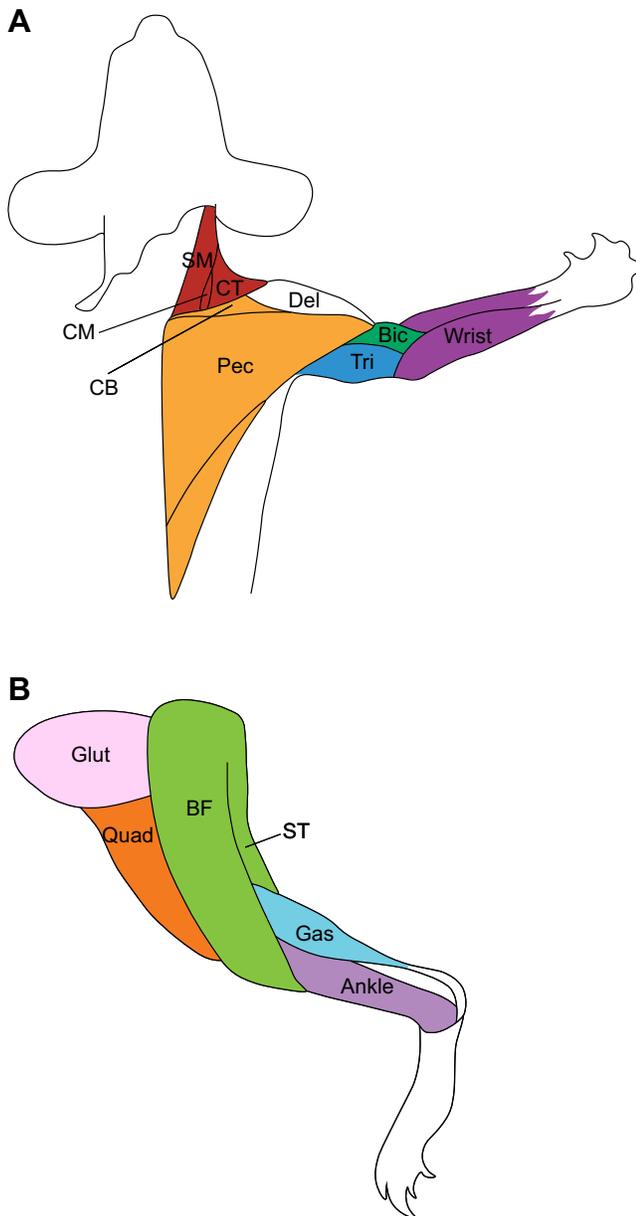


Fig. 1. Diagrams of the 10 muscle groups assessed in this study. Muscles were dissected from (A) the left forelimb, chest and ventral neck and (B) the left hindlimb. Red, ventral neck (SM, sternomastoid; CM, cleidomastoid; CT, clavotrapezius); yellow, pectoralis (Pec) and cleidobrachialis (CB); white, deltoid (Del); dark green, biceps (Bic); dark blue, triceps (Tri); purple, wrist flexors and extensors (Wrist); pink, gluteus (Glut); orange, quadriceps (Quad); light green, hamstrings (BF, biceps femoris; ST, semitendinosus); light blue, gastrocnemius (Gas); lavender, ankle flexors and minor extensors (Ankle).

inadvertently included in all pectoralis and triceps muscle group samples; fractions of both spinodeltoideus and acromiodeltoideus constituted 1.23% and 1.35% (respectively) of the total pectoralis muscle group mass, while a separate part of spinodeltoideus comprised 7.25% of the mass of the triceps muscle group.

We also collected skeletal mass data for eight bones from each mouse: skull, mandible, humerus, radius, ulna, pelvis, femur and tibiofibula. Following dissection, we placed the mouse cadavers in a dermestid beetle (*Dermestes maculatas*) colony until all soft tissue was removed. Some individual bones were excluded from further analyses after removal from the beetle colony as a result of damage

Table 1. Description of the 10 major muscle groups

Group name	Muscles
Pectoralis	Pectoralis superficialis, cranial and caudal parts of pectoralis profundus, cleidobrachialis
Ventral neck	Clavotrapezius, sternocleidomastoid
Biceps	Long and coracoid heads of biceps brachii, coracobrachialis, brachialis
Triceps	Long, lateral and medium heads of triceps brachii, anconeus, epitrochlearis
Wrist flexors and extensors	Flexor carpi radialis, flexor carpi ulnaris, radial, superficial and ulnar heads of flexor digitorum profundus, flexor digitorum superficialis, palmaris longus, pronator quadratus, pronator teres, abductor pollicis longus, long and short heads of extensor carpi radialis, extensor carpi ulnaris, extensor digitorum communis, extensor digitorum lateralis, extensor indicis proprius, supinator
Gluteus	Gluteus medius, gluteus profundus, piriformis
Hamstrings	Biceps femoris, semitendinosus
Quadriceps	Cranial and caudal parts of rectus femoris, vastus lateralis, intermedius and medialis
Gastrocnemius	Lateral and medial heads of gastrocnemius, soleus, flexor digitorum superficialis
Ankle flexors and minor extensors	Tibialis anterior, extensor digitorum longus, extensor hallucis longus, flexor hallucis longus, flexor digitorum longus, tibialis posterior, popliteus, peroneus longus, brevis, digiti IV and digiti V

that occurred during the skeletonization process, such as the loss of tiny epiphyses and/or extensive chewing damage. The remaining bones were then gently cleaned with a damp toothbrush and allowed to dry for 24 h at 55°C prior to being weighed. All dissections and mass measurements were conducted blindly with respect to which mice were competition winners/losers by a single individual (A.N.C.).

Skeletal traits and indices

The bones of each mouse were photographed. Digital imaging software (ImageJ; Rasband, 2015) was used to take 18 morphological measurements: 17 length and width measurements and the surface area of the scapula (Table 2). For postcranial measurements, we used physiological length, which is defined as the length between articular surfaces and represents the effective working length of a bone (Wilder, 1920). From this set of 18 morphometrics, we calculated 12 functional indices (Table 3) that quantify skeletal shape in the form of relative proportions, robusticity and anatomical mechanical advantage (Morris and Brandt, 2014; Morris and Carrier, 2016; Morris et al., 2019). These skeletal indices represent a set of traits hypothesized to be associated with improved fighting performance, with larger ratio values suggesting greater anatomical specialization for fighting performance. Measurements of skeletal length, breadth and surface area were made by a single individual (J.S.M.) who was blind to winning status.

Statistical analyses

All data were tested for normality (Shapiro–Wilk test) and homogeneity of variance (Bartlett's test). As measurements of ventral neck muscle group mass, ulna mass and femoral epicondyle width were found to differ from normal distributions, they were natural log transformed to improve normality. Our preliminary analyses revealed that data from the gluteus and hamstrings muscle groups and the occipital width skeletal shape index exhibited

Table 2. Description of the 18 skeletal morphological measurements taken

Metric	Definition
Skull width	Zygomatic width of skull
Skull length	Basal length of skull (basion to prosthion)
Occipital width	Greatest width at the bases of the paraoccipital processes
Atlas width	Greatest width of atlas across the wings
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 center of rotation of trochlear notch to proximal extent of olecranon process
Metacarpal length	Physiological length of 3rd metacarpal
Humerus epicondyle width	Epicondylar width of distal end of humerus
Styloid width	Combined width of distal ends of non-articulated radius and ulna
Femur length	Physiological length of femur
Tibiofibula length	Physiological length of tibiofibula
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 femur
Hindlimb malleolus width	Width of distal end of tibiofibula

Adapted from Morris and Brandt (2014), Morris and Carrier (2016) and Morris et al. (2019).

unequal variance between winners and losers ($P=0.016$, $P<0.001$ and $P=0.028$, respectively). Muscle and bone mass data were analyzed via analysis of covariance (ANCOVA) with pre-competition body mass as the covariate; this analysis assessed the

direct effects of competitive ability (competition winners versus losers) and body mass and their respective interaction. Non-significant interaction terms were removed from the final ANCOVA models for the sake of parsimony. An ANCOVA could not be performed for radius mass because it was not significantly correlated with body mass (Pearson's $r=0.21$, $P=0.348$); thus, we tested for differences in radius mass between winners and losers with a two-tailed t -test. We compared skeletal shape indices between winners and losers with analysis of variance (ANOVA). We controlled for false discovery rates in multiple comparisons by adjusting individual P -values using the Benjamini–Hochberg procedure (Benjamini and Hochberg, 1995) with a false discovery rate of 0.05. Because we were testing three distinct clusters of hypotheses regarding the respective relationships between competitive ability and muscle mass, bone mass and skeletal shape indices, we performed separate Benjamini–Hochberg procedures for these three datasets. All analyses were performed using the R statistical package (version 3.2.2; <http://www.R-project.org/>).

RESULTS

The body mass of winning male house mice ($n=9$) was 10.5% greater on average than that of their less-competitive counterparts ($n=20$) prior to the onset of competition ($t_{23}=2.64$, $P=0.015$; two-tailed t -test). For the 10 muscle groups examined post-competition with ANCOVA tests, the only competitive ability \times body mass interaction occurred in the hamstrings ($F_{2,25}=14.98$, $P<0.001$; Fig. S1), which indicated that losers, compared with winners, had a larger increase in hamstring muscle mass relative to body mass. No main effect of competitive ability was found for hamstring muscle mass ($F_{2,25}=0.25$, $P=0.688$). Five muscle groups were significantly larger in winners relative to body mass: biceps ($F_{1,26}=6.69$, $P=0.040$), triceps ($F_{1,26}=13.29$, $P=0.003$), wrist flexors and extensors ($F_{1,26}=23.90$, $P<0.001$), gluteus ($F_{1,26}=5.87$, $P=0.046$),

Table 3. Definition and functional interpretation of 12 skeletal shape indices associated with morphological specialization for fighting performance

Index	Definition and functional significance
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 a shorter skull (i.e. a 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 skull (occipital width/skull length). Indicates relative size of cervical neck musculature.
Atlas width index	Atlas width relative to length of skull (atlas width/skull length). Indicates relative surface area for attachment of cervical neck musculature.
Scapula area index	Surface area of lateral aspect of scapula relative to scapula length [$\sqrt{\text{scapula area}/\text{scapula length}}$]. Indicates relative size of muscles involved in the transfer of forces from the trunk to the forelimbs (Carrier et al., 2006) and in stabilizing the shoulder joint (Hildebrand and Goslow, 2001).
Forelimb proportions index	Length of proximal forelimb relative to length of distal forelimb [(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 muscle, 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.
Hindlimb proportions index	Length of proximal hindlimb relative to length of distal hindlimb [femur length/(tibiofibula length+metatarsal length)]. Indicates degree of morphological specialization for producing large out-forces in the hindlimb (Hildebrand, 1985).
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 ankle plantarflexor muscles (e.g. semimembranosus, gastrocnemius, extensor digitorum longus; Evans, 1993; Samuels et al., 2013).
Hindlimb malleolus index	Hindlimb malleolus width relative to tibiofibula length (hindlimb malleolus width/tibiofibula length). Indicates relative robusticity of hindlimb.
Calcaneus mechanical advantage	Length of calcaneal process relative to length of pes (calcaneus length/metatarsal length). Indicates anatomical mechanical advantage of ankle plantarflexors (e.g. gastrocnemius).

Adapted from Morris and Brandt (2014), Morris and Carrier (2016) and Morris et al. (2019). See Table 2 for description of skeletal morphometrics.

and ankle flexors and minor extensors ($F_{1,26}=13.93$, $P=0.003$; Table 4). The total mass of the 10 muscle groups was 20.7% greater on average in winners ($F_{1,26}=9.64$, $P=0.005$), with the wrist flexors and extensors, biceps and triceps groups exhibiting the greatest percentage difference in mass (34.9%, 27.5% and 25.5% larger on average in winners, respectively; Table 4). Although the gluteus muscle groups of winners and losers were found to have unequal variance, we still consider this result to be valid. Because the regression line between gluteus muscle group mass and body mass passes through the origin, we determined that the effect of body mass on gluteus muscle mass was constant throughout our observed range of body masses, thereby circumventing the major problem with analyzing ratio data containing body mass as the denominator (Curran-Everett, 2013). A two-tailed t -test performed on gluteus muscle mass to body mass ratios, which were normally distributed and had equal variance, further substantiated our finding that winners possessed relatively larger gluteus muscles ($t_{24}=2.53$, $P=0.019$).

The results from the muscle group dissections are partially corroborated by bone mass (Table 5) and skeletal shape data (Table 6). Unlike muscle mass, however, heterogeneity of linear regression slopes was more common in the bone mass data: competitive ability \times body mass interactions were found in the analyses of the pelvis ($F_{2,24}=7.17$, $P=0.013$), femur ($F_{2,25}=5.51$, $P=0.027$) and total bone mass ($F_{2,16}=6.38$, $P=0.022$; Fig. S2). All three interactions indicated that bone mass exhibited a negative relationship with respect to body mass in winners compared with losers. A significant main effect of competitive ability was found for total bone mass ($F_{2,16}=5.29$, $P=0.035$), with winners possessing 11.2% greater skeletal mass on average. The average mass of the ulna ($F_{1,26}=10.51$, $P=0.024$; ANCOVA) was greater in winners by 17.1%, with radius mass approaching significance ($t_{20}=2.59$, $P=0.068$; two-tailed t -test). ANOVA tests on skeletal shape indices indicated that winners had a larger scapula area ($F_{1,27}=15.44$, $P=0.006$).

Table 4. Descriptive statistics and ANCOVA results (with pre-competition body mass as covariate) for mass of muscle groups in competition-winning and -losing male house mice

Muscle group	Muscle mass (mg)		Average difference in means (%)	P
	Winners	Losers		
Pectoralis	31.1 \pm 8.2	26.9 \pm 6.6	15.6	0.927
Ventral neck	8.8 \pm 2.6	7.2 \pm 1.4	22.2	0.554
Biceps	11.6 \pm 2.2	9.1 \pm 1.5	27.5	0.040
Triceps	37.4 \pm 3.5	29.8 \pm 4.4	25.5	0.003
Wrist flexors and extensors	26.3 \pm 3.6	19.5 \pm 2.8	34.9	<0.001
Gluteus	43.2 \pm 2.6	35.8 \pm 6.1	20.7	0.046
Hamstrings	59.4 \pm 3.1	51.5 \pm 11.0	15.3	0.688*
Quadriceps	45.9 \pm 7.7	39.8 \pm 8.7	15.3	0.660
Gastrocnemius	40.4 \pm 4.9	34.4 \pm 5.7	17.4	0.193
Ankle flexors and minor extensors	34.7 \pm 3.0	27.9 \pm 4.1	24.4	0.003
Total	307.7 \pm 24.0	254.9 \pm 37.9	20.7	0.005

Muscle mass is given as mean \pm s.d.; total muscle mass refers to the sum of all 10 muscle group mass measurements. P -values (ANCOVA) for the 10 muscle groups have been corrected for multiple comparisons. Asterisks indicate a main effect P -value from a final model containing a significant competitive ability \times body mass interaction term; absence of an asterisk indicates P -values from final models where non-significant interaction terms were removed. Bold indicates significance.

Table 5. Descriptive statistics and ANCOVA results (with pre-competition body mass as covariate) for bone mass in competition-winning and -losing male house mice

Bone	Bone mass (mg)		Average difference in means (%)	N (W:L)	P
	Winners	Losers			
Skull	200.8 \pm 12.0	184.2 \pm 16.2	9.0	9:18	0.413
Mandible	75.9 \pm 4.0	71.9 \pm 5.7	5.6	9:19	0.413
Humerus	18.3 \pm 1.4	16.3 \pm 1.6	12.3	9:20	0.117
Radius	6.0 \pm 0.4	5.4 \pm 0.6	11.1	8:14	0.068
Ulna	8.9 \pm 1.0	7.6 \pm 0.8	17.1	9:20	0.024
Pelvis	45.4 \pm 3.2	40.2 \pm 4.2	12.9	9:19	0.132*
Femur	33.4 \pm 3.4	30.9 \pm 3.8	8.1	9:20	0.440*
Tibiofibula	31.0 \pm 2.0	28.3 \pm 2.8	9.5	9:20	0.144
Total	424.1 \pm 20.0	381.4 \pm 25.5	11.2	8:12	0.035*

Bone mass is given as mean \pm s.d.; total bone mass refers to the sum of all eight bone mass measurements. Bones that were damaged during skeletonization by the dermestid beetle colony were excluded from bone mass analyses. Sample sizes (N) for each bone are listed for winners (W) and losers (L). P -values (ANCOVA, two-tailed t -test) for the eight bones have been corrected for multiple comparisons. Asterisks indicate main effect P -values from final models containing a significant competitive ability \times body mass interaction term; absence of an asterisk indicates P -values from final models where non-significant interaction terms were removed. Bold indicates significance.

DISCUSSION

Our results are overall consistent with the hypothesis that highly competitive male house mice possess musculoskeletal traits that improve fighting performance. Winners of male–male contests possessed relatively larger muscles in five out of the 10 major muscle groups measured: biceps, triceps, wrist flexors and extensors, gluteus, and ankle flexors and minor extensors. Winning mice also had relatively more massive ulnae and exhibited a trend towards heavier radii; these bones serve as attachment sites for three of the five larger muscle groups (i.e. biceps, triceps, and wrist flexors and extensors). Data from skeletal shape indices also lend support to the hypothesis that highly competitive males are more anatomically specialized for fighting performance than less competitive males. Winners, compared with losers, had a relatively greater scapular area for housing larger muscles responsible for the transmission of forces from the trunk to the forelimb and performing work at the shoulder joint (Carrier et al., 2006).

Table 6. Skeletal shape index values and ANOVA results in competition-winning and -losing male house mice

Index	Skeletal shape index		N (W:L)	P
	Winners	Losers		
Skull shape index	0.533 \pm 0.010	0.533 \pm 0.022	7:14	0.983
Occipital width index	0.291 \pm 0.007	0.291 \pm 0.020	6:8	0.983
Atlas width index	0.246 \pm 0.007	0.247 \pm 0.009	7:13	0.932
Scapula area	4.246 \pm 0.156	3.944 \pm 0.204	9:20	0.006
Forelimb proportions index	1.432 \pm 0.034	1.419 \pm 0.029	9:18	0.732
Humerus epicondyle index	0.234 \pm 0.009	0.236 \pm 0.008	9:20	0.831
Olecranon MA	0.137 \pm 0.004	0.142 \pm 0.008	9:18	0.420
Styloid width index	0.158 \pm 0.012	0.155 \pm 0.009	9:20	0.831
Hindlimb proportions index	0.610 \pm 0.011	0.595 \pm 0.019	9:19	0.246
Femur epicondyle index	0.171 \pm 0.004	0.174 \pm 0.008	9:20	0.732
Hindlimb malleolus index	0.131 \pm 0.008	0.132 \pm 0.007	9:20	0.831
Calcaneus MA	0.201 \pm 0.012	0.204 \pm 0.010	8:15	0.831

Skeletal shape indices are mean \pm s.d. Bones that were damaged during skeletonization by the dermestid beetle colony were not used to calculate skeletal shape indices. Sample sizes (N) for each skeletal shape index are listed for winners (W) and losers (L). All P -values (ANOVA) have been corrected for multiple comparisons. Bold indicates significance. MA, mechanical advantage.

Several of these results are consistent with our current conceptualization of how mammals fight during male–male contests. Many quadrupedal mammals, including mice, often assume a bipedal stance when competing physically, allowing the powerful forelimb retractor muscles associated with locomotion to be used to strike downward at an opponent (Carrier, 2011). The increased scapular area for shoulder muscle attachment sites, as well as greater mass in the triceps, biceps, and wrist flexors and extensors muscle groups and the radius and ulna, are expected to facilitate grappling and striking performance in highly competitive male mice. Our results are also in agreement with those of studies finding male-biased sexual dimorphism in the forelimbs of mammalian species that fight at least in part by grappling. Compared with female conspecifics, western lowland gorillas (*Gorilla gorilla*: Zihlman and McFarland, 2000) and humans (Gallagher et al., 1997; Nindl et al., 2002; Abe et al., 2003; Lassek and Gaulin, 2009) have more massive forelimb muscles, and several species of anthropoid primates (Morris et al., 2019) possess a number of skeletal traits expected to facilitate force output in the forelimbs during aggressive encounters. Medium- to large-sized macropodids have also received much attention for their sexually dimorphic forelimbs. Jarman (1983, 1989) found that both forelimb musculature and limb length are greater in males than females. Warburton et al. (2013) further pursued this work, showing that male eastern grey kangaroos (*Macropus fuliginosus*) have greater forelimb muscle mass than females. In an analysis of 15 promiscuous macropodid species, Richards et al. (2015) found that sexual dimorphism in relative male humerus length increases substantially with greater body size, coinciding with the increased intensity of male fighting in the larger macropodid species. Grappling with the forelimbs appears to be an important behavior in carnivores as well. Postcranial sexual dimorphism is present in the scapular surface area of several carnivorous species, allowing for the attachment of more robust shoulder musculature (Morris and Brandt, 2014; Morris and Carrier, 2016). Finally, the distal limb muscles of dogs bred for fighting are larger than those of dogs bred for high-speed running (Pasi and Carrier, 2003). In the posterior half of the body of house mice, the larger gluteus muscle group of highly competitive males may facilitate standing upright and pushing against an opponent. Additionally, we suggest that the larger ankle flexors and minor extensors group of highly competitive mice may help to maintain a stable, upright pose during grappling.

Nevertheless, our results did not support our prediction of greater muscle mass in the neck of winning males. Dogs bred for fighting have several epaxial neck muscles that are larger than those of dogs bred for sprinting (Webster et al., 2014). We anticipated that the ventral neck muscle group of highly competitive male mice would have a phenotype similar to the epaxial neck musculature of fighting dogs. Once an opponent has been bitten, large neck muscles may allow an animal to jerk and pull on the opponent while protecting the attacker's own head from injury due to forces applied by the opponent. The muscle mass results of this study suggest, however, that the biting strategy used by mice during male–male contests may differ from that of carnivores: instead of grasping and tugging on an opponent, mice may quickly bite and release. Differences in tooth morphology provide support for this explanation. The cone-shaped canines of carnivores provide strength in multiple loading directions, such as those produced by a struggling opponent, whereas mouse incisors have relatively little cross-sectional area to resist forces applied in the fore–aft plane (Biknevicius and Van Valkenburgh, 1996).

We also found no support for predicted differences between males with high and low competitive ability in skull shape, occipital width and atlas width indices, and the mass of the skull and mandibles. This is surprising, given that several individuals in the study had wounding in the form of bite marks. In lizard species where agonistic contest outcomes are partially determined by biting, head size parameters such as length, width and depth are related to both fighting performance (e.g. Hews, 1990; Molina-Borja et al., 1998; Alberts et al., 2002; López and Martín, 2002; Gier, 2003; Perry et al., 2004) and bite force (Lailvaux et al., 2004; Huyghe et al., 2005; Lappin and Husak, 2005). However, Husak et al. (2006) found that, although bite force differed between highly competitive and less competitive male venerable collared lizards (*Crotaphytus antiquus*), there was no significant difference in any metric of head size between these two populations. If bite force is in fact correlated with competitive ability in male house mice, phenotypic variation may exist in parameters related to biting performance that were not measured here, such as masseter muscle fiber type (Eason et al., 2000).

In addition to providing information about musculoskeletal adaptations for fighting performance in male mice, our results may be consistent with a functional trade-off in evolutionary optimization for fighting and for locomotor economy (Carrier, 2002). Selection for larger muscle and bone mass, particularly in the distal limb segments (e.g. the wrist extensors and flexors muscle group and the radii and ulnae), conflicts with economical running because it increases the rotational inertia of the limbs, which increases the internal mechanical work of locomotion (Cavagna and Kaneko, 1977; Hildebrand and Hurley, 1985). Indeed, Morris et al. (2017) found in a separate experiment that territory-holding male house mice have a greater cost of transport (i.e. are less economical runners) than non-territory-holding males. This trade-off may be particularly relevant for highly competitive males, which travel regularly in order to patrol their territories for potential intruders (Crowcroft, 1955).

Finally, differences in relative musculoskeletal mass and distribution may partially explain the variable relationship between body mass and competitive ability reported by prior studies of male mice (e.g. De Fries and McClearn, 1970; Oakeshott, 1974; Benton et al., 1980; Rolland et al., 2003; Morris et al., 2017). Although we found the body mass of competition winners to be 10.5% greater on average than that of losers, the average combined mass of the 10 muscle groups and eight bones we measured was 20.7% and 11.2% greater (respectively) in winners. The prior study (Cunningham et al., 2013) that produced the mice used in the present study also examined males of intermediate competitive ability (individuals that won only one of the two competition rounds) and found that body mass only moderately predicted the outcome of competition trials: individuals displaying the highest level of competitive ability had intermediate body masses. Ruff et al. (2017) further expanded on this result by demonstrating that optimal body size for reproductive success is constrained in male house mice, a surprising discovery in a polygynous species of mammal engaging in male–male contests. In light of these findings, our results lend further support to the argument that, at least for male house mice, the ‘bigger is better’ model for the relationship between body mass and fitness appears to be an oversimplification that fails to address the role of other important musculoskeletal traits in fighting performance.

In summary, the presence of larger muscle groups, bones and scapular area in competition-winning male house mice implies that both muscle and bone mass and skeletal shape could influence

competitive ability. These traits may also be present in other mammalian species in which males fight for control of territory or access to females. The specific muscle groups and bones under selection for size or shape may vary by species and/or fighting tactics. Anatomical specialization for fighting performance appears to represent a functional trade-off with locomotor economy, suggesting that success in male–male contests may be achieved at a cost to other important life-history traits. Differences in the relative masses of muscle groups and bones between competition winners and losers may partially underlie previous findings that outcomes of physical competitions between male house mice cannot be explained entirely by body size. These results address some of the gaps in our understanding of the traits that produce variation in competitive ability, a strong correlate of fitness among mammals.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: A.N.C., C.B.C., J.S.M., D.R.C.; Methodology: A.N.C., C.B.C., J.S.M., J.S.R., W.K.P., D.R.C.; Formal analysis: A.N.C., J.S.M., J.S.R.; Investigation: A.N.C., C.B.C.; Data curation: A.N.C., C.B.C.; Writing - original draft: A.N.C.; Writing - review & editing: C.B.C., J.S.M., J.S.R., W.K.P., D.R.C.; Visualization: A.N.C.; Funding acquisition: W.K.P., D.R.C.

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Data availability

Data are available from the Dryad digital repository (Cooper et al., 2020): dryad.mw6m905t8

Supplementary information

Supplementary information available online at <http://jeb.biologists.org/lookup/doi/10.1242/jeb.213389.supplemental>

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