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

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KEYWORDS

Biomechanics, life-history traits, morphology, musculoskeletal system, sexual selection

SUMMARY STATEMENT

Male house mice demonstrating high competitive ability possess several musculoskeletal traits hypothesized to improve fighting performance in male-male contests.

32 **ABSTRACT**

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

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59 INTRODUCTION

60 The outcome of agonistic encounters is directly associated with reproductive fitness for males of
61 many mammalian species (Dewsbury, 1982). Large body mass is a strong predictor of fighting
62 performance in male-male contests (Andersson, 1994); however, other morphological,
63 physiological, and behavioral traits also influence competitive ability (e.g., Lailvaux and
64 Irschick, 2006). House mice (*Mus musculus*; Linnaeus) are an excellent model for studying the
65 physical correlates of fighting performance in mammals because they possess a polygynous
66 mating system where male mice acquire reproductive resources such as territory at least in part
67 by fighting (Crowcroft, 1955; Hayashi, 1993), and highly competitive individuals have been
68 shown to possess greater reproductive success (De Fries and McClearn, 1970; Oakeshott, 1974;
69 Kuse and De Fries, 1976; Dewsbury, 1982; Kaufman, 1983; Wolff, 1985; Hurst, 1987; Krackow,
70 1993; Meagher et al., 2000; Rolland et al., 2003). Interestingly, the relationship between body
71 mass and fighting performance in male house mice does not adhere strictly to the “bigger is
72 better” paradigm. While some studies have found a direct correlation between body mass and
73 competitive ability in male house mice (De Fries and McClearn, 1970; Oakeshott, 1974;
74 Cunningham et al., 2013), others have reported no effect of body size (Benton et al., 1980;
75 Rolland et al., 2003). More recent studies have suggested an optimal body mass for competitive
76 ability in male house mice: Ruff et al. (2017) showed that fitness, estimated by the number of
77 offspring produced, peaks at intermediate body sizes for male mice competing in semi-natural
78 environments. Morris et al. (2017) found in the same experimental system that, although body
79 mass did not differ significantly with territory-holding status, non-territory-holding mice
80 exhibited greater variance in body size than mice that were able to consistently defend a territory.
81 These results suggest that other aspects of the musculoskeletal system may be contributing to the
82 unexplained variation observed in competitive ability.

83 Previous morphological studies of male-male contests in vertebrates have focused
84 overwhelmingly on the head, while the role of the postcranial musculoskeletal system has
85 received much less attention. Head size morphometrics in relation to biting performance have
86 been intensely studied (in mammals: Hanski et al., 1991; Koren et al., 2008; in lizards: Hews,
87 1990; Olsson, 1994; Molina-Borja et al., 1998; Alberts et al., 2002; López and Martín, 2002;
88 Gier, 2003; Lailvaux et al., 2004; Perry et al., 2004; Huyghe et al., 2005; Lappin and Husak,
89 2005; Husak et al., 2006; Kohlsdorf et al., 2006; Stuart-Fox et al., 2006; Whiting et al., 2006;

90 Stuart-Fox et al., 2009; Huyghe et al., 2012; Cameron et al., 2013; McEvoy et al., 2013; McLean
91 and Stuart-Fox, 2015; Bush et al., 2016; Fernández et al., 2018). In several species, male-biased
92 sexual dimorphism has been identified in muscle mass, limb length, and skeletal shape indices
93 associated with anatomical specialization for fighting performance (in primates: Gallagher et al.,
94 1997; Zihlman and McFarland, 2000; Nindl et al., 2002, Abe et al., 2003; Lassek and Gaulin,
95 2009; Morris et al., 2019; in macropodids: Jarman, 1983, 1989; Warburton et al., 2013; Richards
96 et al., 2015; in carnivores: Pasi and Carrier, 2003; Kemp et al., 2005; Morris and Brandt, 2014;
97 Morris and Carrier, 2016), but these studies did not directly measure the correlations between
98 these characters and the outcome of male-male contests. In such comparisons of males with high
99 and low competitive ability, postcranial measurements have been limited to limb segment
100 lengths in lizards (López and Martín, 2002; Huyghe et al., 2005; Kohlsdorf et al., 2006; Cameron
101 et al., 2013).

102 Here, we investigated whether highly competitive male house mice are more
103 anatomically specialized for fighting performance than less competitive males. Our first aim was
104 to test whether muscle mass was greater in competition-winning mice compared to losers. We
105 hypothesized that sexual selection would act most strongly on the muscle groups that are most
106 important for fighting performance in male mice. Greater muscle mass is associated with (1)
107 larger muscle cross-sectional area, which provides an increased capacity for force production,
108 and/or (2) longer muscle fascicles, which allow for greater shortening velocity (Biewener, 2003).
109 Therefore, individuals with relatively larger muscle mass will be capable of producing more
110 force and power, permitting them to more easily manipulate an opponent. Our second aim was to
111 investigate whether winners possessed greater bone mass and other sets of skeletal shape
112 adaptations consistent with specialization for physical competition (Morris and Brandt, 2014;
113 Morris and Carrier, 2016; Morris et al., 2019). Overall, we expected the bones of winners to be
114 more robust and, therefore, heavier than those of their less-competitive counterparts. Larger
115 muscle forces require more robust bones to maintain appropriate safety factors (Alexander,
116 1981). Additionally, unpredictable loading directions during fighting select for a circular cross-
117 sectional shape that makes limb bones more massive than those in animals specialized for
118 running (Kemp et al., 2005). With respect to skeletal shape, we first predicted that winners
119 would have relatively shorter and/or broader skulls to increase bite force by providing a greater
120 mechanical advantage for the jaw adductors and more attachment area for the temporalis

121 muscles, respectively (Biknevičius and Van Valkenburgh, 1996). Second, we expected winners
122 to have broader cervical vertebrae to allow for larger cervical muscle attachment sites. Once the
123 attacker has grasped an opponent with its jaws, larger neck muscles may facilitate jerking the
124 head and pulling on the opponent with the teeth while resisting lateral loading of the attacker's
125 own head which could lead to injury (Radinsky, 1981). The cervical vertebrae also serve as
126 attachment sites for extrinsic appendicular muscles capable of protracting the forelimb (Evans,
127 1993), which may be useful during upright grappling. Our third prediction was that the scapulae
128 of winners would have more surface area for the attachment of muscles involved in transmitting
129 force from the trunk to the forelimb (Carrier et al., 2006) and in stabilizing the shoulder joint.
130 Finally, we expected anatomical mechanical advantages of the limbs to be greater in winners,
131 allowing for increased force output against an opponent during grappling and/or pushing.

132

133 **METHODS**

134 **Study Population and Experimental Setup**

135 The present study measured musculoskeletal parameters in cadavers of mice that were subjects
136 in a previous experiment, in which naïve male house mice competed in a semi-natural
137 environment for access to a single female housed within an optimal territory (Cunningham et al.,
138 2013). Male and female mice were sexually mature (≥ 4 months of age), and males were age-
139 matched with their competitors to control for interactions between age and competitive ability.
140 All mice were procured from a population of wild-derived house mice maintained at the
141 University of Utah, School of Biological Sciences. These animals were outbred descendants of a
142 wild-caught population initially described by Meagher et al. (2000).

143 Transparent acrylic semi-natural enclosures measuring 140 x 30 x 15 cm were constructed
144 based on the semi-natural model system as described in Carroll and Potts (2007). Taking
145 advantage of the natural preference of mice for seclusion from conspecifics and predators
146 (Wolff, 1985), an “optimal territory” of 15 x 30 x 15 cm with opaque walls, nesting material, a
147 single female, and its own supply of food and water was placed at one end of the enclosure. The
148 communal (non-optimal) area provided no opportunities for hiding and had shared food and
149 water *ad libitum* with no bedding materials, creating an incentive for competition.

150 Competition assessment took place over the course of two rounds, with each round
151 lasting three days. This duration was deemed appropriate for assessing competitive ability

152 because mice quickly form social hierarchies via physical competition once introduced to a semi-
153 natural environment (De Fries and McClearn, 1970; Hayashi, 1993). A group of four males and a
154 single female participated in the first round. The second round of competition pitted three first-
155 round winners against each other, and three losers against other losers. In all trials, both the
156 population density and the operational sex ratio were much greater than those seen in self-
157 regulating natural and semi-natural populations (Lidicker, 1976; Gomez et al., 2008). We
158 expected that both the male-biased sex ratio and the relatively small size of the enclosures would
159 help to identify individual differences in competitive ability, since larger enclosures may result in
160 more chases in mice (Dewsbury, 1981; Dewsbury, 1982). These factors, combined with two
161 rounds of competition, presumably resulted in increased importance of musculoskeletal traits that
162 influence fighting performance.

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

177

178 **Muscle and Bone Mass Measurements**

179 We dissected and removed the following 10 major muscle groups from each mouse: pectoralis,
180 ventral neck, biceps, triceps, wrist flexors and extensors, hamstrings, gluteus, quadriceps,
181 gastrocnemius, and ankle flexors and minor extensors (Fig. 1 and Table 1). These groups were
182 chosen based on their anticipated relevance to fighting behavior. Dissections were performed at

183 10x magnification under a stereo microscope using fine-tipped watchmaker's forceps. Muscles
184 were kept moist at all times with a 0.9% NaCl solution. Removed muscles were placed in a
185 gravity convection oven (Memmert, Schwabach, Germany) to dry for 24 hours at 55°C. Muscles
186 were weighed (± 0.0001 g, Mettler-Toledo, LLC, Columbus, OH, USA) immediately after
187 drying to prevent rehydration. Deep fascia and minor nerves and blood vessels were not removed
188 from their associated muscle groups prior to weighing. Very small, consistent portions of deltoid
189 muscles were inadvertently included in all pectoralis and triceps muscle group samples; fractions
190 of both spinodeltoideus and acromiodeltoideus constituted 1.23 and 1.35% (respectively) of the
191 total pectoralis muscle group mass, while a separate part of spinodeltoideus comprised 7.25% of
192 the mass of the triceps muscle group.

193 We also collected skeletal mass data for eight bones from each mouse: skull, mandible, humerus,
194 radius, ulna, pelvis, femur, and tibiofibula. Following dissection, we placed the mouse cadavers
195 in a dermestid beetle (*Dermestes maculatas*) colony until all soft tissue was removed. Some
196 individual bones were excluded from further analyses after removal from the beetle colony due
197 to damage that occurred during the skeletonization process, such as the loss of tiny epiphyses
198 and/or extensive chewing damage. The remaining bones were then gently cleaned with a damp
199 toothbrush and allowed to dry for 24 hours at 55°C prior to being weighed. All dissections and
200 mass measurements were conducted blindly with respect to which mice were competition
201 winners/losers by a single individual (A. N. Cooper).

202

203 **Skeletal Traits and Indices**

204 The bones of each mouse were photographed. Digital imaging software (ImageJ; Rasband, 2015)
205 was used to take 18 morphological measurements: 17 length and width measurements and the
206 surface area of the scapula (Table 2). For postcranial measurements, we used physiological
207 length, which is defined as the length between articular surfaces and represents the effective
208 working length of a bone (Wilder, 1920). From this set of 18 morphometrics, we calculated 12
209 functional indices (Table 3) that quantify skeletal shape in the form of relative proportions,
210 robusticity, and anatomical mechanical advantages (Morris and Brandt, 2014; Morris and
211 Carrier, 2016; Morris et al., 2019). These skeletal indices represent a set of traits hypothesized to
212 be associated with improved fighting performance, with larger ratio values suggesting greater

213 anatomical specialization for fighting performance. Measurements of skeletal length, breadth,
214 and surface area were made by a single individual (J. S. Morris) who was blind to winning status.

215

216 **Statistical Analyses**

217 All data were tested for normality (Shapiro-Wilk test) and homogeneity of variance (Bartlett's
218 test). As measurements of ventral neck muscle group mass, ulna mass, and femoral epicondyle
219 width were found to differ from normal distributions, they were natural log-transformed to
220 improve normality. Our preliminary analyses revealed that data from the gluteus and hamstrings
221 muscle groups and the occipital width skeletal shape index exhibited unequal variance between
222 winners and losers ($P=0.016$, $P<0.001$, and $P=0.028$, respectively). Muscle and bone mass data
223 were analyzed via analysis of covariance (ANCOVA) with pre-competition body mass as the
224 covariate; this analysis assessed the direct effects of competitive ability (competition winners vs
225 losers) and body mass and their respective interaction. Non-significant interaction terms were
226 removed from the final ANCOVA models for the sake of parsimony. An ANCOVA could not be
227 performed for radius mass because it was not significantly correlated with body mass (Pearson's
228 $r=0.21$; $P=0.348$); thus, we tested for differences in radius mass between winners and losers with
229 a two-tailed t -test. We compared skeletal shape indices between winners and losers with analysis
230 of variance (ANOVA). We controlled for false discovery rates in multiple comparisons by
231 adjusting individual P -values using the Benjamini-Hochberg procedure (Benjamini and
232 Hochberg, 1995) with a false discovery rate of 0.05. Because we are testing three distinct clusters
233 of hypotheses regarding the respective relationships between competitive ability and muscle
234 mass, bone mass, and skeletal shape indices, we performed separate Benjamini-Hochberg
235 procedures for these three datasets. All analyses were performed using the R statistical package
236 (Version 3.2.2; R Development Core Team, 2013).

237

238 **RESULTS**

239 The body mass of winning male house mice ($n=9$) was 10.5% greater on average than their less-
240 competitive counterparts ($n=20$) prior to the onset of competition ($t_{23}=2.64$, $P=0.015$; two-tailed
241 t -test). For the 10 muscle groups examined post-competition with ANCOVA tests, the only
242 competitive ability \times body mass interaction occurred in the hamstrings ($F_{2,25}=14.98$, $P<0.001$;
243 Fig. S1), which indicated that losers, compared to winners, had a larger increase in hamstrings

244 muscle mass relative to body mass. No main effect of competitive ability was found for
245 hamstrings muscle mass ($F_{2,25}=0.25$, $P=0.688$). Five muscle groups were significantly larger in
246 winners relative to body mass: biceps ($F_{1,26}=6.69$, $P=0.040$), triceps ($F_{1,26}=13.29$, $P=0.003$),
247 wrist flexors and extensors ($F_{1,26}=23.90$, $P<0.001$), gluteus ($F_{1,26}=5.87$, $P=0.046$), and ankle
248 flexors and minor extensors ($F_{1,26}=13.93$, $P=0.003$; Table 4). The total mass of the 10 muscle
249 groups was 20.7% greater on average in winners ($F_{1,26}=9.64$, $P=0.005$), with the wrist flexors
250 and extensors, biceps, and triceps groups exhibiting the greatest percentage differences in mass
251 (34.9%, 27.5%, and 25.5% larger on average in winners, respectively; Table 4). Although the
252 gluteus muscle groups of winners and losers were found to have unequal variance, we still
253 consider this result to be valid. Because the regression line between gluteus muscle group mass
254 and body mass passes through the origin, we determined that the effect of body mass on gluteus
255 muscle mass was constant throughout our observed range of body masses, thereby circumventing
256 the major problem with analyzing ratio data containing body mass as the denominator (Curran-
257 Everett, 2013). A two-tailed t -test performed on gluteus muscle mass:body mass ratios, which
258 were normally distributed and had equal variance, further substantiated our finding that winners
259 possessed relatively larger gluteus muscles ($t_{24}=2.53$, $P=0.019$).

260 The results from the muscle group dissections are partially corroborated by bone mass
261 (Table 5) and skeletal shape data (Table 6). Unlike muscle mass, however, heterogeneity of
262 linear regression slopes was more common in the bone mass data: competitive ability \times body
263 mass interactions were found in the analyses of the pelvis ($F_{2,24}=7.17$, $P=0.013$), femur
264 ($F_{2,25}=5.51$, $P=0.027$), and total bone mass ($F_{2,16}=6.38$, $P=0.022$; Fig. S2). All three interactions
265 indicated that bone mass exhibited a negative relationship with respect to body mass in winners
266 compared to losers. A significant main effect of competitive ability was found for total bone
267 mass ($F_{2,16}=5.29$, $P=0.035$), with winners possessing 11.2% greater skeletal mass on average.
268 The average mass of the ulna ($F_{1,26}=10.51$, $P=0.024$; ANCOVA) was greater in winners by
269 17.1%, with radius mass approaching significance ($t_{20}=2.59$, $P=0.068$; two-tailed t -test).
270 ANOVA tests on skeletal shape indices indicated that winners had a larger scapula area
271 ($F_{1,27}=15.44$, $P=0.006$).

272

273 **DISCUSSION**

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

285 Several of these results are consistent with our current conceptualization of how
286 mammals fight during male-male contests. Many quadrupedal mammals, including mice, often
287 assume a bipedal stance when competing physically, allowing the powerful forelimb retractor
288 muscles associated with locomotion to be used to strike downward at an opponent (Carrier,
289 2011). The increased scapular area for shoulder muscle attachment sites, as well as greater mass
290 in the triceps, biceps, and wrist flexors and extensors muscle groups and the radius and ulna, are
291 expected to facilitate grappling and striking performance in highly competitive male mice. Our
292 results are also in agreement with those of studies finding male-biased sexual dimorphism in the
293 forelimbs of mammalian species that fight at least in part by grappling. Compared to female
294 conspecifics, western lowland gorillas (*Gorilla gorilla*: Zihlman and McFarland, 2000) and
295 humans (Gallagher et al., 1997; Nindl et al., 2002, Abe et al., 2003; Lassek and Gaulin, 2009)
296 have more massive forelimb muscles, and several species of anthropoid primates (Morris et al.,
297 2019) possess a number of skeletal traits expected to facilitate force output in the forelimbs
298 during aggressive encounters. Medium- to large-sized macropodids have also received much
299 attention for their sexually dimorphic forelimbs. Jarman (1983; 1989) found that both forelimb
300 musculature and limb length are greater in males than females. Warburton et al. (2013) further
301 pursued this work, showing that male eastern grey kangaroos (*Macropus fuliginosus*) have
302 greater forelimb muscle mass than females. In an analysis of 15 promiscuous macropodid
303 species, Richards et al. (2015) found that sexual dimorphism in relative male humerus length
304 increases substantially with greater body size, coinciding with the increased intensity of male

305 fighting in the larger macropodid species. Grappling with the forelimbs appears to be an
306 important behavior in carnivores as well. Postcranial sexual dimorphism is present in the
307 scapular surface area of several carnivoran species, allowing for the attachment of more robust
308 shoulder musculature (Morris and Brandt, 2014; Morris and Carrier, 2016). Finally, the distal
309 limb muscles of dogs bred for fighting are larger than those of dogs bred for high-speed running
310 (Pasi and Carrier, 2003). In the posterior half of the body of house mice, highly competitive
311 males' larger gluteus muscle group may facilitate standing upright and pushing against an
312 opponent. Additionally, we suggest that the larger ankle flexors and minor extensors group of
313 highly competitive mice may help to maintain a stable, upright pose during grappling.

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

327 We also found no support for predicted differences between males with high and low
328 competitive ability in skull shape, occipital width and atlas width indices, and the masses of the
329 skulls and mandibles. This is surprising, given that several individuals in the study had wounding
330 in the form of bite marks. In lizard species where agonistic contest outcomes are partially
331 determined by biting, head size parameters such as length, width, and depth are related to both
332 fighting performance (e.g., Hews, 1990; Molina-Borja et al., 1998; Alberts et al. 2002; López
333 and Martín, 2002; Gier, 2003; Perry et al., 2004) and bite force (Lailvaux et al., 2004; Huyghe et
334 al., 2005; Lappin and Husak, 2005). However, Husak et al. (2006) found that, although bite force
335 differed between highly competitive and less competitive male venerable collared lizards

336 (*Crotaphytus antiquus*), there was no significant difference in any metric of head size between
337 these two populations. If bite force is in fact correlated with competitive ability in male house
338 mice, phenotypic variations may exist in parameters related to biting performance that were not
339 measured here, such as masseter muscle fiber type (Eason et al., 2000).

340 In addition to providing information about musculoskeletal adaptations for fighting
341 performance in male mice, our results may be consistent with a functional trade-off between
342 evolutionary optimization for fighting and for locomotor economy (Carrier, 2002). Selection for
343 larger muscle and bone mass, particularly in the distal limb segments (e.g., the wrist extensors
344 and flexors muscle group and the radii and ulnae), conflicts with economical running because it
345 increases the rotational inertia of the limbs, which increases the internal mechanical work of
346 locomotion (Cavagna and Kaneko, 1977; Hildebrand and Hurley, 1985). Indeed, Morris et al.
347 (2017) found in a separate experiment that territory-holding male house mice have a greater cost
348 of transport (i.e., are less economical runners) than non-territory-holding males. This trade-off
349 may be particularly relevant for highly competitive males, who travel regularly in order to patrol
350 their territories for potential intruders (Crowcroft, 1955).

351 Finally, differences in relative musculoskeletal mass and distribution may partially
352 explain the variable relationship between body mass and competitive ability reported by prior
353 studies of male mice (e.g., De Fries and McClearn, 1970; Oakeshott, 1974; Benton et al., 1980;
354 Rolland et al., 2003; Morris et al., 2017). Although we found the body mass of competition
355 winners to be 10.5% greater on average than that of losers, the average combined masses of the
356 10 muscle groups and eight bones we measured were 20.7% and 11.2% greater (respectively) in
357 winners. The prior study (Cunningham et al., 2013) that produced the mice used in the present
358 study also examined males of intermediate competitive ability (individuals who won only one of
359 the two competition rounds) and found that body mass only moderately predicted the outcome of
360 competition trials: individuals displaying the highest level of competitive ability had
361 intermediate body masses. Ruff et al. (2017) further expanded on this result by demonstrating
362 that optimal body size for reproductive success is constrained in male house mice, a surprising
363 discovery in a polygynous species of mammal engaging in male-male contests. In light of these
364 findings, our results lend further support to the argument that, at least for male house mice, the
365 “bigger is better” model for the relationship between body mass and fitness appears to be an

366 oversimplification that fails to address the role of other important musculoskeletal traits in
367 fighting performance.

368 In summary, the presence of larger muscle groups, bones, and scapular area in
369 competition-winning male house mice implies that both muscle and bone mass and skeletal
370 shape could influence competitive ability. These traits may also be present in other mammalian
371 species in which males fight for control of territory or access to females. The specific muscle
372 groups and bones under selection for size or shape may vary by species and/or fighting tactics.
373 Anatomical specialization for fighting performance appears to represent a functional trade-off
374 with locomotor economy, suggesting that success in male-male contests may be achieved at a
375 cost to other important life history traits. Differences in the relative masses of muscle groups and
376 bones between competition winners and losers may partially underlie previous findings that
377 outcomes of physical competitions between male house mice cannot be explained entirely by
378 body size. These results address some of the gaps in our understanding of the traits that produce
379 variation in competitive ability, a strong correlate of fitness among mammals.

380

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386

387 **COMPETING INTERESTS**

388 We have no competing interests to declare.

389

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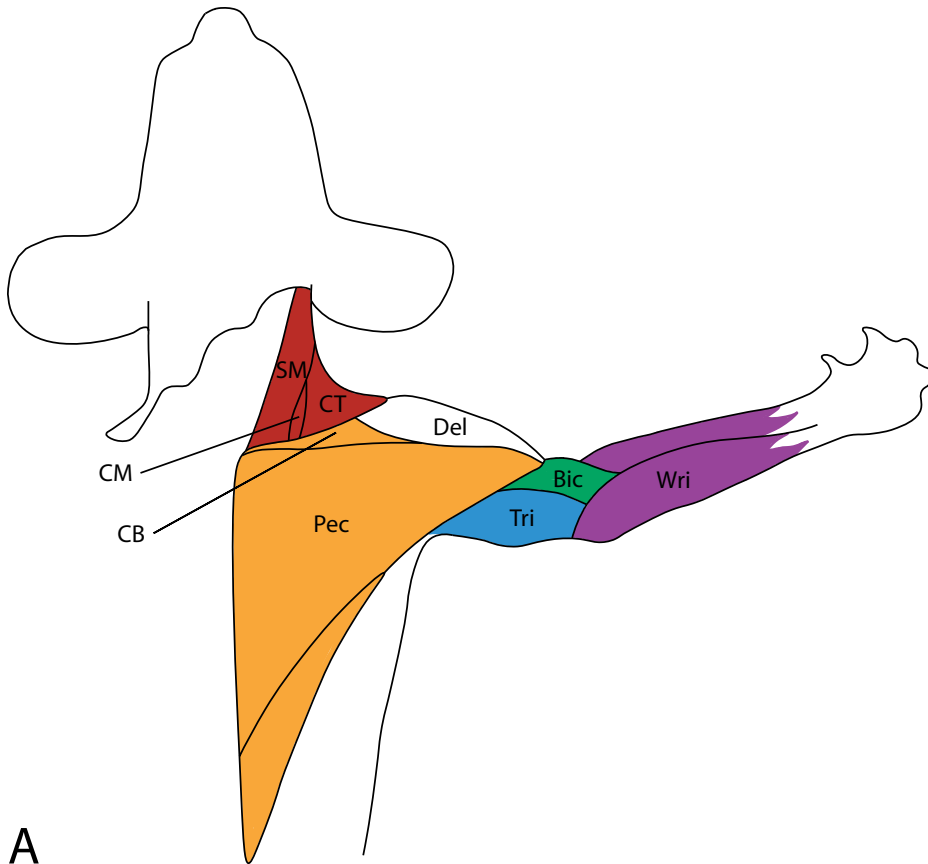
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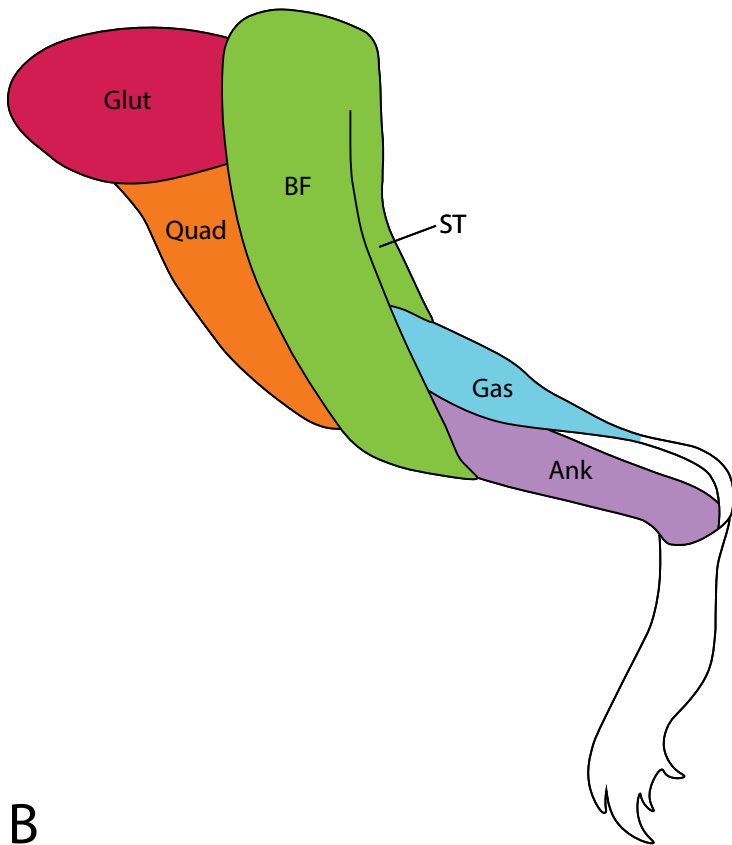
608 **FIGURES AND TABLES**

609

610 **Fig. 1. Diagrams of the 10 muscle groups dissected from A) the left forelimb, chest, and**
611 **ventral neck and B) the left hindlimb.** Red – ventral neck; yellow – pectoralis; green – biceps;
612 blue – triceps; purple – wrist flexors and extensors; magenta – gluteus; orange – quadriceps; light
613 green – hamstrings; light blue – gastrocnemius; lavender – ankle flexors and minor extensors.
614 Abbreviations: SM – sternomastoid; CM – cleidomastoid; CT – clavotrapezius; pec – pectoralis;
615 del – deltoid; bic – biceps; tri – triceps; wri – wrist flexors and extensors; glut – gluteus; quad –
616 quadriceps; BF – biceps femoris; ST – semitendinosus; gas – gastrocnemius; ank – ankle flexors
617 and minor extensors.



618 **A**



619 **B**

620 **Table 1. Description of 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 & 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 & 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

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632 **Table 2. Description of 18 skeletal morphometrics.**

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 3 rd 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 3 rd metatarsal
Femur epicondyle width	Epicondylar width of distal femur
Hindlimb malleolus width	Width of distal end of tibiofibula

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

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643 **Table 3. Definitions and functional interpretations of 12 skeletal shape indices associated**
 644 **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 (Biknevičius 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).

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

647 See Table 2 for descriptions of skeletal morphometrics.

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

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

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674 Total muscle mass refers to the sum of all 10 muscle group mass measurements. *P*-values for the
675 10 muscle groups have been corrected for multiple comparisons. Dagger indicates main effect *P*-
676 value from a final model containing a significant competitive ability × body mass interaction
677 term; no dagger indicates *P*-values from final models where non-significant interaction terms
678 were removed.

679 **P*<0.05.

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

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

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 687 Bones that were damaged during skeletonization by the dermestid beetle colony were excluded
 688 from bone mass analyses. Sample sizes (N) for each bone are listed for winners (W) and losers
 689 (L). Total bone mass refers to the sum of all eight bone mass measurements. *P*-values for the
 690 eight bones have been corrected for multiple comparisons. Dagger indicates main effect *P*-values
 691 from final models containing a significant competitive ability × body mass interaction term; no
 692 dagger indicates *P*-values from final models where non-significant interaction terms were
 693 removed.

694 **P*<0.05.

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704 **Table 6. Skeletal shape index values in competition-winning and competition-losing male**
 705 **house mice.**

Index	Means (SD)		N (W:L)	<i>P</i> ANOVA
	Winners	Losers		
Skull shape index	0.533 (0.010)	0.533 (0.022)	7:14	0.960
Occipital width index	0.291 (0.007)	0.291 (0.020)	6:8	0.983
Atlas width index	0.246 (0.007)	0.247 (0.009)	7:13	0.777
Scapula area	4.246 (0.156)	3.944 (0.204)	9:20	<0.001*
Forelimb proportions index	1.432 (0.034)	1.419 (0.029)	9:18	0.291
Humerus epicondyle index	0.234 (0.009)	0.236 (0.008)	9:20	0.575
Olecranon MA	0.137 (0.004)	0.142 (0.008)	9:18	0.105
Styloid width index	0.158 (0.012)	0.155 (0.009)	9:20	0.547
Hindlimb proportions index	0.610 (0.011)	0.595 (0.019)	9:19	0.041
Femur epicondyle index	0.171 (0.004)	0.174 (0.008)	9:20	0.305
Hindlimb malleolus index	0.131 (0.008)	0.132 (0.007)	9:20	0.623
Calcaneus MA	0.201 (0.012)	0.204 (0.010)	8:15	0.511

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 707 Bones that were damaged during skeletonization by the dermestid beetle colony were not used to
 708 calculate skeletal shape indices. Sample sizes (N) for each skeletal shape index are listed for
 709 winners (W) and losers (L). All *P*-values have been corrected for multiple comparisons.

710 MA – mechanical advantage.

711 **P*<0.05.

712

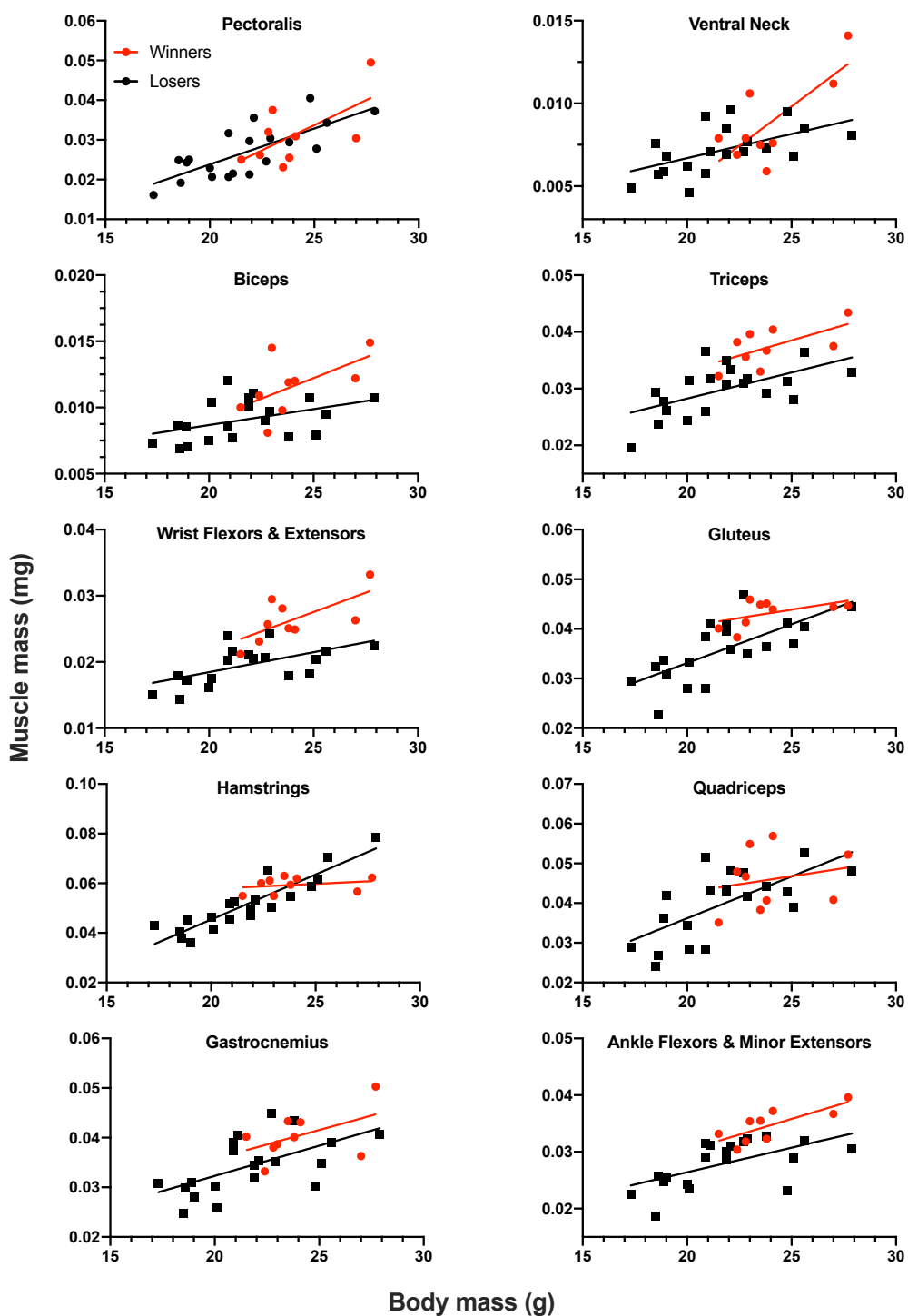


Fig. S1. Muscle mass plotted against pre-competition body mass for winning and losing male house mice. A significant interaction between competitive ability and body mass was detected in the ANCOVA analysis of the hamstrings muscle group.