



Sexual selection on forelimb muscles of western grey kangaroos (Skippy was clearly a female)

NATALIE M. WARBURTON^{1*}, PHILIP W. BATEMAN^{2,3*} and
PATRICIA ANNE FLEMING^{1*}

¹Veterinary and Biomedical Sciences, Murdoch University, Murdoch, WA 6150, Australia

²Department of Environment and Agriculture, Curtin University, Perth, WA 6102, Australia

³Department of Zoology and Entomology, University of Pretoria, Pretoria 0002, South Africa

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Studies of sexual selection have tended to concentrate on obvious morphological dimorphisms such as crests, horns, antlers, and other physical displays or weapons; however, traits that show no obvious sexual dimorphism may nevertheless still be under sexual selection. Sexual selection theory generally predicts positive allometry for sexually selected traits. When fighting, male kangaroos use their forelimbs to clasp and hold their opponent and, standing on their tail, bring up their hind legs to kick their opponent. This action requires substantial strength and balance. We examined allometry of forelimb musculature in male and female western grey kangaroos (*Macropus fuliginosus*) to determine whether selection through male–male competition is associated with sex differences in muscle development. Forelimbs of males are more exaggerated than in females, with relatively greater muscle mass in males than the equivalent muscles in females. Furthermore, while muscles generally showed isometric growth in female forelimbs, every muscle demonstrated positive allometry in males. The significant positive allometry in male forelimb musculature, particularly those muscles most likely involved in male–male combat (a group of muscles involved in grasping: shoulder adduction, elbow flexion; and pulling: arm retraction, elbow flexion), clearly suggests that this musculature is subject to sexual selection. In addition to contributing to locomotion, the forelimbs of male kangaroos can also act as a signal, a weapon, and help in clasping, features that would contribute towards their importance as a sexually selected trait. Males would therefore benefit from well-developed musculature of the arms and upper body during competition for mates. © 2013 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2013, 109, 923–931.

ADDITIONAL KEYWORDS: allometry – body shape – body size – intra-sexual competition.

INTRODUCTION

Darwin (1871) recognized that physical differences, other than genitalia, between the sexes are a result of sexual selection. Males either compete among themselves for access to females (male–male competition), persuade females to favour them above other males (female choice), or harass and force females to mate with them (sexual coercion, Clutton-Brock & Parker, 1995). None of these forms of sexual selection is mutually exclusive, although it often appears intuitively

which is the major selective pressure, e.g. display plumage of male birds (female choice), antlers or horns of male ungulates (male–male competition), or gonopodia of male poeciliid fish (male coercion, e.g. Bisazza, Vaccari & Pilastro, 2001). Studies of sexual selection have tended to concentrate on obvious morphological dimorphisms such as crests, horns, antlers, or weapons (Bonduriansky, 2007). However, many traits that show no obvious sexual dimorphism might nevertheless still be under sexual selection, although it can be difficult to tease apart the different potential selective pressures, e.g. the elongated necks of male and female giraffes (*Giraffa camelopardalis*) (Simmons & Scheepers, 1996; Mitchell, Van Sittert & Skinner, 2009).

*Corresponding author.

E-mail: n.warburton@murdoch.edu.au;

pwbateman@zoology.up.ac.za; t.fleming@murdoch.edu.au

Both sexes of the larger kangaroos and wallabies (Macropodidae) have similar morphology but males often have extremely well-developed musculature of the arms and upper body. Can this difference in degree of development be explained in terms of sexual selection? The larger kangaroos and wallabies are generally gregarious and form groups of mixed sexes and ages that vary in size and lability, depending on season and available forage (Jarman & Coulson, 1989; Jarman, 1991). They are usually polygynous (Johnson, 1983; Arnold, Steven & Grassia, 1990) and correspondingly tend to have extremely high sexual dimorphism (male to female mass average 1.6:1, calculated from maximum masses for 19 species presented by Jarman, 1991). Consistent with Rensch's rule (demonstrated in a wide range of taxa, Fairbairn, 1997), this sexual dimorphism increases with larger body size (Jarman, 1989b), such that the largest macropods have the highest degree of body size dimorphism – male to female body mass (m_b) in red kangaroo *Macropus rufus* is 2.5:1, eastern grey kangaroo *M. giganteus* 1.9:1, and western grey kangaroo *M. fuliginosus* 1.8:1 (Jarman, 1991).

As a mating system, the large macropod species display hierarchical promiscuity, with males of high rank having disproportionately higher mating success (Croft, 1989; Glanslosser, 1989; Jarman, 1989b). There is a clear link between body size and reproductive advantage for males. In the eastern grey kangaroo, males of all sizes and ranks intermingle in a mob, but it is the larger males that gain an exclusive consort relationship with oestrous females (Croft, 1989), and position in the hierarchy partly determines a male's probability of gaining undisputed access to oestrous females (Jarman, 1989b). Males may also maximize their chances of contacting and inspecting females by spending time at resources frequented by females (e.g. waterholes, food patches) and the largest males tend to have larger home-ranges (Croft, 1989). Finally, genetic studies of captive groups have also linked body size to biased paternity, where alpha males may be able to outcompete and exclude smaller males from access to females (Miller *et al.*, 2010).

Males appear to establish or maintain the dominance hierarchy through sparring contests that are usually undamaging (Croft, 1989). Male–male contests are generally ritualized, although the dominance relationships may become weaker in the presence of oestrous females (particularly when group structure is disturbed), leading to more frequent active displacements or brief, unritualized fights (Glanslosser, 1989). A wide repertoire of actions is involved in agonistic behaviour of large macropods, culminating with animals grappling with their arms and clawed hands, wrestling, and kicking with their

back legs (Glanslosser, 1989); the belly, shoulders, and throat of males have the additional protection of thickened skin (Jarman, 1989a).

Examining the allometry of a trait can help identify if sexual selection has a role in the development of that trait (Eberhard, Rodriguez & Polihronakis, 2009). When the slope of a trait size against body size is 'isometric', the relative trait size is constant across a range of body sizes. Where the trait size decreases with body size, the slope shows 'negative allometry' and where the trait size increases with body size the slope shows 'positive allometry'. A trait that is positively allometric is therefore relatively larger, in proportion to body size, in larger individuals (Bonduriansky, 2007). If this relationship differs between the sexes, then it can be interpreted that there is differential selective pressure acting on males and females as they grow larger. We predicted that the musculature of the arms and shoulders of male western grey kangaroos would show a growth pattern that was indicative of sexual selection (positive allometry), while the musculature of female kangaroos would not show this pattern (isometry).

MATERIALS AND METHODS

Whole carcass specimens of western grey kangaroo were purchased for dissection from NFC Products, Mandurah and Westate Pet Meats, Medina. Additional partial specimens comprising thorax, forelimbs, and associated femurs were purchased from King River Processing, Canningvale and Westate Pet Meats, Medina. We did not know the age of the animals, but all were adults and we selected a wide range of body size for each sex ($N = 13$ males, $N = 15$ females).

Specimens were dissected fresh or stored frozen until being thawed for dissection. Specimens were skinned and excess connective tissue removed immediately before dissection to avoid dehydration of tissues. In partial specimens, the extrinsic muscles of the neck were damaged due to prior removal of the head; thus data for these muscles were not collected. Dissection proceeded as follows (muscles are shown in Fig. 1): removal of cutaneous muscles and extrinsic m. trapezius cervicis, m. atlantoscapularis, and sternocleidomastoid complex; isolation, removal, and weighing of m. trapezius thoracis, m. latissimus dorsi, m. rhomboideus thoracis, pectoralis muscle group, and m. serratus ventralis; separation of the forelimb from the thorax by dislocation of sternoclavicular joint; isolation, removal, and weighing of deltoid muscle group, m. teres major, m. teres minor, m. infraspinatus, m. coracobrachialis, m. subscapularis, and m. supraspinatus; isolation, removal, and weighing of the muscles of the antebrachium comprising dorsal extensor (hereafter 'extensors') and

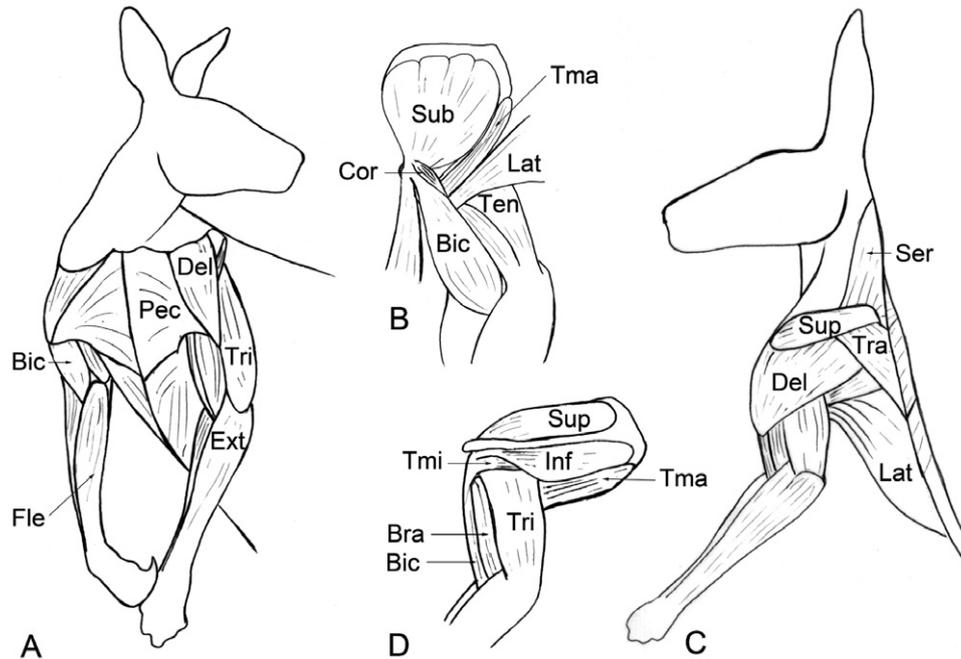


Figure 1. Forelimb muscles of the western grey kangaroo (*Macropus fuliginosus*) dissected for the study. A, superficial anterior view; B, deep medial view of right arm; C, superficial dorsolateral view (after removal of panniculus and cranial trapezius muscles); D, deep lateral view of left brachium (after removal of m. deltoideus and m. trapezius). Abbreviations: Bic, m. biceps brachialis; Bra, m. brachialis; Cor, coracobrachialis; Del, m. deltoideus; Ext, extensor group of the antebrachium; Fle, flexor group of the antebrachium; Inf, m. infraspinatus; Lat, m. latissimus dorsi; Pec, mm. pectorales; Ser, m. serratus anterior; Sub, m. subscapularis; Sup, m. supraspinatus; Ten, m. tensor fascia antebrachii; Tma, m. teres major; Tmi, m. teres minor; Tra, m. trapezius thoracis; Tri, m. triceps.

ventral flexor (hereafter 'flexors') groups; isolation, removal, and weighing of m. brachialis, m. biceps brachii, and combined m. tensor fascia antebrachii and m. triceps brachii. In each case muscles were weighed (± 0.01 g; Mettler BasBal digital scale) immediately upon removal from the carcass to avoid dehydration.

Body mass (kg) was calculated from measurement of the circumference (mm) of the femur of each individual; this bone is not expected to be under sexual selection (see Kinahan *et al.*, 2007; Tasikas *et al.*, 2009; Lemaître *et al.*, 2012). Following removal of the muscles, the femur of each specimen was cleaned of soft tissue and further cleaned via bacterial maceration, rinsed, and air dried. Femur circumference was measured by tape-measure at the narrowest point (approximately mid-shaft), immediately below the posterior tubercle (insertion of the m. quadratus femoris). Circumference measures have low variability (coefficient of variation of three repeated measures on each bone averaged $0.61 \pm 0.40\%$). Body mass for each individual was calculated following Helgen *et al.* (2006):

$$\text{Log-}m_b = 2.5932 \cdot \text{log}-(\text{femur shaft circumference}) - 3.2842.$$

The relationship between the mass of each muscle (m_m , log-transformed) and $\text{log-}m_b$ was estimated by simple linear regression (Microsoft Excel; Table 1). The slopes of these lines (β) were tested against the null hypothesis that $\beta = 1$ by calculating the t ratio = $(\beta - 1)/\text{standard error of the slope}$ (Wikipedia, 2013). Where the t coefficient was not significant, there was no evidence to suggest that $\beta \neq 1$ and the muscle was assumed to demonstrate isometric growth. A significant regression (t significant) indicated an allometric relationship (either positive or negative, as indicated by the β coefficient).

To test for differences in slopes between muscles (in males only), the slopes of each pair of muscles (each plotted as $\text{log-}m_m$ against $\text{log-}m_b$) were compared using Statistix 1.8 using the comparison of slopes function.

RESULTS

Forelimb muscle mass in males were heavier than the equivalent muscles in females (Fig. 2), although much of this difference was due to differences in body mass between the sexes (Fig. 3). Males averaged m_b 41.9 ± 13.5 kg ($N = 13$, range 23–61 kg) and females m_b 28.4 ± 4.4 kg ($N = 15$, range 21–38 kg). When the

Table 1. Regression analyses for forelimb muscle mass compared against body mass for male and female western grey kangaroos. ‘-’ indicates the slope of the relationship could not be tested since the regression line was not significant

| Muscle(s) | Males (<i>N</i> = 13) | | | | | | Females (<i>N</i> = 15) | | | | | | | |
|---|------------------------|------|----------|-------------|---------|-----------------|--------------------------|-----------------------|------|--------------|-------|---------|-----------------|----------|
| | Regression statistics | | | Coefficient | | | Regression statistics | | | Coefficient | | | | |
| | <i>R</i> ² | SE | <i>P</i> | β | SE of β | <i>t</i> -ratio | β ≠ 1 | <i>R</i> ² | SE | <i>P</i> | β | SE of β | <i>t</i> -ratio | <i>P</i> |
| <i>M. deltoideus</i> | 0.96 | 0.08 | < 0.001 | 2.32 | 0.15 | 9.04 | < 0.001 | 0.56 | 0.10 | 0.001 | 1.51 | 0.37 | 1.39 | 0.188 |
| <i>M. supraspinatus</i> | 0.95 | 0.08 | < 0.001 | 2.17 | 0.15 | 8.04 | < 0.001 | 0.77 | 0.05 | < 0.001 | 1.31 | 0.20 | 1.56 | 0.143 |
| <i>M. infraspinatus</i> & <i>M. teres minor</i> | 0.94 | 0.10 | < 0.001 | 2.33 | 0.18 | 7.40 | < 0.001 | 0.81 | 0.05 | < 0.001 | 1.24 | 0.16 | 1.48 | 0.163 |
| <i>M. teres major</i> | 0.92 | 0.12 | < 0.001 | 2.56 | 0.23 | 6.89 | < 0.001 | 0.73 | 0.06 | < 0.001 | 1.22 | 0.20 | 1.07 | 0.303 |
| <i>M. subscapularis</i> | 0.94 | 0.10 | < 0.001 | 2.33 | 0.18 | 7.45 | < 0.001 | 0.78 | 0.05 | < 0.001 | 1.21 | 0.18 | 1.16 | 0.267 |
| <i>M. coracobrachialis</i> | 0.93 | 0.11 | < 0.001 | 2.44 | 0.20 | 7.32 | < 0.001 | 0.05 | 0.15 | 0.413 | 0.46 | 0.55 | - | - |
| <i>M. biceps brachii</i> | 0.95 | 0.09 | < 0.001 | 2.43 | 0.17 | 8.46 | < 0.001 | 0.77 | 0.05 | < 0.001 | 1.12 | 0.17 | 0.70 | 0.499 |
| <i>M. brachialis</i> | 0.94 | 0.09 | < 0.001 | 2.15 | 0.16 | 7.18 | < 0.001 | 0.55 | 0.07 | 0.002 | 1.06 | 0.27 | 0.22 | 0.828 |
| <i>M. triceps brachii</i> & <i>M. tensor fasciae</i> <i>antebrachii</i> | 0.97 | 0.06 | < 0.001 | 2.04 | 0.11 | 9.76 | < 0.001 | 0.45 | 0.08 | 0.006 | 0.99 | 0.30 | -0.05 | 0.965 |
| Extensor | 0.79 | 0.16 | < 0.001 | 1.99 | 0.30 | 3.25 | 0.008 | 0.58 | 0.07 | 0.001 | 1.05 | 0.25 | 0.19 | 0.856 |
| Flexor | 0.81 | 0.17 | < 0.001 | 2.17 | 0.32 | 3.69 | 0.004 | 0.59 | 0.07 | 0.001 | 1.06 | 0.25 | 0.26 | 0.801 |
| <i>M. trapezius pars</i> <i>thoracica</i> | 0.93 | 0.09 | < 0.001 | 1.93 | 0.16 | 5.63 | < 0.001 | 0.67 | 0.09 | < 0.001 | 1.77 | 0.34 | 2.25 | 0.042 |
| <i>M. latissimus dorsi</i> | 0.94 | 0.09 | < 0.001 | 2.14 | 0.16 | 7.17 | < 0.001 | 0.64 | 0.05 | < 0.001 | 0.84 | 0.18 | -0.89 | 0.390 |
| Pectoral muscles | 0.86 | 0.14 | < 0.001 | 2.12 | 0.25 | 4.40 | 0.001 | 0.00 | 0.31 | 0.991 | -0.01 | 1.13 | - | - |
| <i>M. serratus ventralis</i> <i>thoracis</i> | 0.96 | 0.07 | < 0.001 | 1.98 | 0.12 | 7.92 | < 0.001 | 0.01 | 0.11 | 0.775 | 0.12 | 0.40 | - | - |

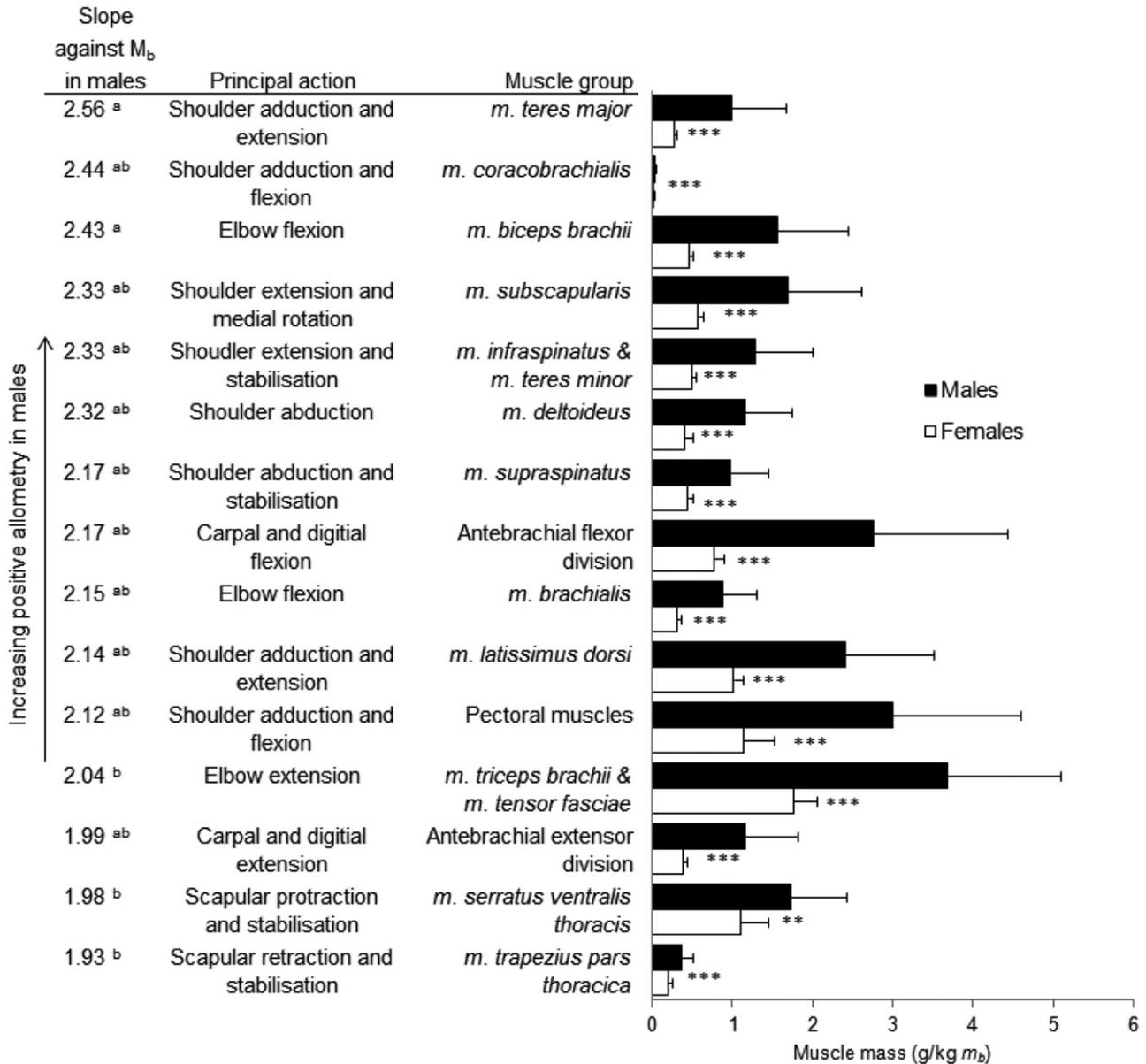


Figure 2. Mean (± 1 SD) mass of each forearm muscle in male and female grey kangaroos (*Macropus fuliginosus*), standardized for body mass. Muscles are ordered in decreasing value of the slope of the regression between muscle mass and body mass in males; letters (first column) link linear regressions where the slopes of this relationship for males were not significantly different. Asterisks indicate sex differences in the body mass-specific muscle masses (** $P < 0.02$, *** $P < 0.001$).

muscle mass values were corrected for individual body mass (Fig. 2), the coefficient of variation averaged across all muscles was $18.4 \pm 8.6\%$ for females, but $51.0 \pm 7.9\%$ for males.

With few exceptions (there were no significant relationships in females for *m. serratus ventralis thoracis*, pectoral muscles, and *m. coracobrachialis*), there was a significant linear relationship between $\log-m_m$ and $\log-m_b$ for each muscle measured (tested in males $P < 0.001$ and females $P < 0.01$ separately). In females

the slope of these regression lines was generally not significantly different from 1; the only exception was *m. trapezius thoracica* ($\beta = 1.8$, $P = 0.042$). By contrast, in males every muscle demonstrated positive allometry ($\beta > 1$, $P < 0.001$ or $P < 0.01$ for extensors and flexors; Table 1). The slopes of these relationships varied between muscles, ranging from $\beta = 1.9$ to $\beta = 2.6$. The slopes for three muscles/muscle groups showing shallow slopes (1, *m. trapezius thoracis*; 2, *m. serratus ventralis*; 3, *m. triceps brachii* and

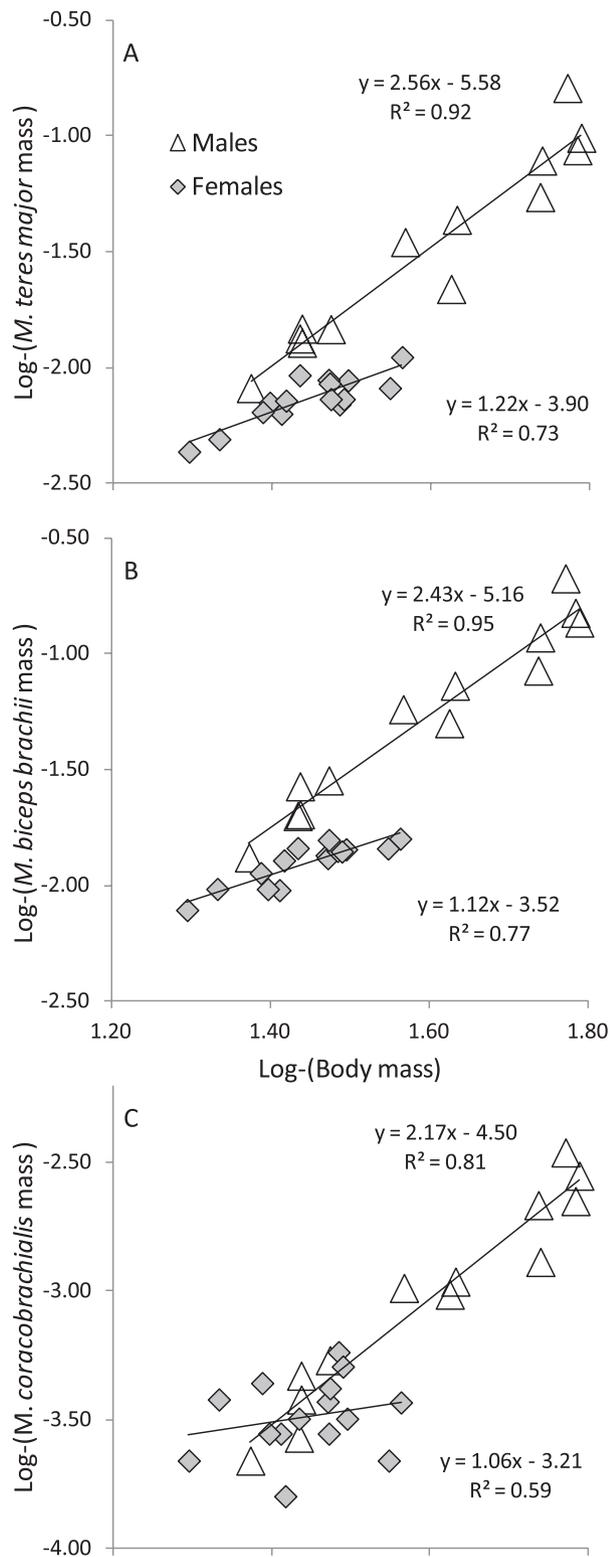


Figure 3. Three muscle groups demonstrating the strongest positive allometry in male kangaroos. While there was positive allometry shown for males, the relationships for females were generally not different from $\beta = 1$ (i.e. isometric growth).

m. tensor fascia antebrachii) (Fig. 3) were significantly different from those for two muscles showing strong positive relationship (*m. teres major* and *m. biceps brachii*) (Fig. 2). The relationships with the *m. coracobrachialis* did not reach statistical significance due to high variability in the data for this small muscle (1, $P = 0.056$; 2, $P = 0.058$; 3, $P = 0.082$ for comparison with each of the three shallow-slope muscles, respectively) (Fig. 3).

DISCUSSION

Many studies have indicated sex differences in overall muscle mass for various taxa, e.g. dragonflies (Marden, 1989), primates (Gaulin & Sailer, 1984), and brushtail possum (*Trichosurus vulpecula*) (Isaac, 2006). However, few have found differential allometric relationships between the sexes that would signify that the development of the trait is subject to different selective pressures between the sexes. Several criteria identify the likelihood for a role for sexual selection acting on a trait, including:

- 1 the exaggeration of the trait in one sex than in the other (Simmons & Scheepers, 1996)
- 2 more phenotypic variability in the trait (Eberhard *et al.*, 2009; but see Pomiankowski & Moller, 1995; Eberhard *et al.*, 1998)
- 3 a role for the trait in dominance contests or courtship displays (Zahavi, 1975; Grafen, 1990; Simmons & Scheepers, 1996)
- 4 no immediate survival benefit from the trait – unlike traits under natural selection (Darwin, 1871; Simmons & Scheepers, 1996)
- 5 a survival cost may be incurred from the trait (Zahavi, 1975; Grafen, 1990)
- 6 some authors have also argued that the trait should demonstrate positive allometry (but see Bonduriansky, 2007).

In this discussion, we address how the musculature of the kangaroo forelimb meets these requirements for a sexually selected trait.

The forelimb musculature of grey kangaroos clearly fits the first two criteria: data from the present study shows that forelimbs of males are more exaggerated than in females and that there is a greater amount of variability in relative muscle masses in males than females. Under the third criterion, there is also evidence that forelimb strength may play a role in determining male reproductive advantage. The structure of male kangaroo boxing fights suggests that 'the main goal is to push or wrestle the opponent off balance and down to the ground rather than inflict potentially injurious kicks as seen in resource conflicts' (Croft & Snaith, 1991: p. 221). Strength of the forelimbs plays an important part in the success of these fights. Also,

smaller males appear to engage in fights less often than size-matched males (Croft & Snaith, 1991), while larger males may use their additional force to overpower opponents and secure matings (Jarman, 2000). Musculature may also be an important aspect of visual signalling (presumably of potential fighting ability) and dominant males will frequently adopt poses which best display their muscularity and size (Jarman, 1983, 1991). As an aside, we note that muscles as a visual signal (i.e. as part of female choice) have been speculated on for humans (Grammer *et al.*, 2003) but have not been explored in any other taxon.

The fourth criterion is more difficult to identify for kangaroo forelimbs, as these limbs have a clear primary role in locomotion and feeding, where male and female macropods use their arms similarly, i.e. support on the ground during pentapedal movement, manipulating browse, grooming, etc. It can be argued that robust forelimbs would contribute to survival through these actions alone.

In terms of the fifth criterion, potential costs of increased musculature (e.g. energetic costs) may be difficult to isolate. However, under conditions of extreme environmental stress (e.g. drought) there is evidence of male-biased mortality (Robertson, 1986; Norbury, Coulson & Walters, 1988; Coulson, 2006). This differential mortality may be the result of the disparate energy costs imposed by sex differences in body size/mass/musculature (Norbury *et al.*, 1988).

In this study we present data which clearly support the sixth criterion for a sexually selected trait: while these muscles grow proportionally to body size in females (isometric growth), there is significant positive allometry in the forelimb muscles of males. While Jarman (1989b) describes positive allometry of overall forearm girth/length, or the overall mass of arm muscle/bone in three species of macropod, the present study highlights individual muscles of the entire forelimb. The significant positive allometry in male forelimb musculature clearly suggests that this musculature is subject to sexual selection. The strongest allometric relationship was demonstrated for a functional group of muscles involved in shoulder adduction, retraction of the arms, and flexion of the elbow. Together with the actions of the flexor muscles, these comprise the principal actions involved in grasping (elbow and digital flexion, arm adduction) and pulling (arm retraction, elbow flexion). These actions are important in male–male competition where combatants use their forelimbs to grapple and grasp one another. In descriptions of agonistic behaviour in macropods (Glanslosser, 1989; Croft & Snaith, 1991) these actions would be advantageous for ‘embracing’ an opponent or ‘locking forearms’ during wrestling, where two animals try to make each other fall by

pulling and vigorously pushing and pressing with their forelimbs or to maintain balance when kicking with their hind limbs. Development of these muscle groups in male kangaroo forelimbs may reflect increased use during fighting. By contrast, the two muscles that are responsible for scapular protraction and stabilization (m. trapezius thoracis and m. serratus ventralis) demonstrated the shallowest slopes (the m. trapezius thoracis also showed allometric growth in females), suggesting the least sexual selection acting on these muscles.

Bonduriansky (2007) argues that where growth is determinate (i.e. ends at a certain point, usually maturity), and the pool of available resources is finite, this will result in a trade-off between the final size of the secondary sexual trait and the size of the body in the adult. However, in kangaroos both sexes continue to grow after physiological reproductive maturity, and both sexes of the larger species (> 20 kg body mass) may continue to grow throughout life (indeterminate body growth) (Jarman, 1989b, 1991). Upon emergence from the pouch, the growth trajectories of the sexes diverge markedly (e.g. Poole, Carpenter & Wood, 1982a, b; Jarman, 1989b). For example, female eastern grey kangaroos have largely reached mature size by ~2 years of age but males grow substantially larger than females and, even though they grow faster than females, males attain their full size considerably later or continue to grow (Poole *et al.*, 1982a; Norbury *et al.*, 1988; Jarman, 1989b); consequently, there is marked heteromorphism in male body size (Jarman, 1989b). Male eastern grey kangaroos that sire offspring have significantly higher testosterone concentrations than non-sires (Miller *et al.*, 2010), and elevated testosterone and participation in ritualized fighting as animals develop (Jarman, 1991) would contribute towards muscle development in dominant males. These factors would favour continual increase in forelimb length (Poole *et al.*, 1982b; Jarman, 1989b) and musculature (this study).

Three main forms of sexual selection have been identified: female choice, male–male competition and female coercion. In kangaroos, we have identified a likely role of sexual selection on male–male competition through muscular investment (Jarman, 1989b). It is possible that increased muscularity in this species can also signal good genes (Kirkpatrick, 1996) (female choice or to warn off other males) (Jarman, 1991). Muscularity may also play a role in restraining females for copulations; although there appears to be little evidence of coerced copulations in macropods (Glanslosser, 1989), the size differential between males and primiparous females in particular may preclude the females rejecting importunate males (Jarman, 1989b).

In conclusion, this study emphasizes the significant role of intrasexual selection on dimorphism in otherwise undifferentiated body parts that are intrinsically useful and fulfil many similar functions in both sexes. In addition to contributing to locomotion, the forelimbs of male kangaroos might also act as a signal, weapon, and contribute towards clasping, features that would contribute towards their importance as a sexually selected trait.

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SUPPORTING INFORMATION

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

Table S1. Regression analyses for forelimb muscle mass compared against body mass for male and female western grey kangaroos.