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Source: Zoological Science, 32(5) : 438-446

Published By: Zoological Society of Japan

URL: https://doi.org/10.2108/zs150027

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ZOOLOGICAL SCIENCE **32**: 438–446 (2015)
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Sexual Dimorphisms of Appendicular Musculoskeletal Morphology Related to Social Display in Cuban *Anolis* Lizards

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In *Anolis* lizards, sexual dimorphism has been reported in morphological and ecological traits. Males show larger body size and longer limbs related to territorial combat and courtship display with the dewlap. Although functional-anatomical traits are closely related to locomotor behaviors, differences between sexes in musculoskeletal traits on limbs remain unclear. We explored the relationships among sexual dimorphisms in musculoskeletal morphology, habitat, and locomotor traits in *Anolis* lizards. Specifically, we examined appendicular musculoskeletal morphology in three species of Cuban *Anolis* by measuring muscle mass and lengths of moment arms. Through comparisons of crossing locomotion, we found that the runner species possessed larger extensors in hindlimbs, which are advantageous for running, whereas the masses of the humeral and femoral retractors were larger in climber species, allowing these lizards to hold up their bodies and occupy tree substrates. Comparisons between the sexes showed different trends among the three species. Males of *A. porcatus*, which inhabit narrow branches or leaves, had stronger elbow extensors that maintain the display posture. In contrast, males of *A. sagrei*, which occupy broad surfaces, did not show sexual differences that affected social display. Moreover, *A. bartschi* indicated sexual differences despite the absence of dewlapping behavior. Our findings suggest that both sexes show fundamentally similar relationships between muscular morphology and locomotor habits to adapt arboreal or terrestrial substrates, and yet sexual dimorphism in forelimb muscles may additionally affected by male specific display with the dewlap.

Key words: adaptation, *Anolis*, musculature, sexual dimorphisms, social behavior

INTRODUCTION

Sexual dimorphism may arise because of sexual selection, in which reproductive strategies are different between male and female. In *Anolis* lizards, a model organism for the study of adaptive radiation and convergent evolution (Losos, 2009), sexual dimorphisms in body size, body shape, and social behavior have been reported in various species (Schoener, 1967; Fitch, 1976; Butler et al., 2000, 2007). Males tend to possess larger bodies and heads and longer limbs than females in most species (Butler et al., 2000, 2007). It has been suggested that these traits relate to territory defense by male animals against other males. Higher bite-force produced by a larger body and head is advantageous for male–male combat, while long limbs enable lizards to move in wider home-range (Herrel et al., 2007; Lailvaux and Irschick, 2007; Vanhooydonck et al., 2009). *Anolis* lizards are characterized by an extensible structure located on the throat, the dewlap. The dewlap is extended in social behaviors, such as ramping to male or courtship to female (Jenssen, 1977; Losos and Chu, 1998; Nicholson et al., 2007). During male displaying, lizards raise the head and anterior body by pushing up (head-bobbing) with repeated extension and contraction of the dewlap (Jenssen, 1977). Extension of the dewlap is produced by contracting the ceratohyoideus muscle, and accordingly this muscle is better developed in males than females (Font and Rome, 1990; O'Bryant and Wade, 1999; Johnson and Wade, 2010). This suggests that a behavior specific to males may produce sexual differences in the musculoskeletal system. However, whether the locomotive behavior is reflected by intersexual differences in limb muscles is unclear. Additionally, according to our observation, the forelimb posture for creating space to extend the dewlap during displaying is apparently different between terrestrial and arboreal species. Since musculoskeletal morphology of limbs are intimately related to locomotion or habitat use (Herrel et al., 2008; Anzai et al., 2014), behavioral divergence between male and female may be reflected by sexual dimorphism of appendicular muscles.

Here, we explore whether the sexual differences in appendicular musculoskeletal morphology are correlated with habitat use or locomotor style in three species of *Anolis*

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Supplemental material for this article is available online.
doi:10.2108/zs150027

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lizards. The three species are known to occur in different habitats and to show sexual dimorphisms in body size (Schettino, 1999). *Anolis sagrei* tends to be a terrestrial runner and can be found mainly on the ground or broad tree trunks (Collete, 1961; Schettino, 1999). This species shows a high frequency of rapid running with relatively long hindlimbs (Losos, 1990; Schettino, 1999). *Anolis porcatus* is a wide-ranging arboreal species whose habitats range from tree trunks to the narrow twigs near the top of canopy (Collette, 1961; Schettino, 1999). In these two species, the male has a larger body size and a larger dewlap than the female, as in most other species of *Anolis* lizards (Schoener, 1969; Schettino, 1999). *Anolis bartschi* is a runner species, which only occurs in caves or rocky substrates of limestone in western Cuba (Schettino, 1999). This species never displays with the dewlap, as this structure is exceptionally absent in both sexes (Schettino, 1999; Poe, 2004). Although males of *A. sagrei* and *A. porcatus* show different musculoskeletal morphologies, which are thought to represent adaptations to different locomotor styles or habitat uses (Anzai et al., 2014), whether females show similar adaptations remains unknown. In this study, we compare the musculoskeletal morphology of limbs among these three *Anolis* lizards with different habitats, locomotor styles, and dewlapping displays to test 1) whether there are intersexual differences in the appendicular musculature, and 2) whether sexual dimorphism of limb muscles is related to sexual dimorphism of social behaviors using the dewlap.

Table 1. Details of *Anolis* lizards examined in this study. SVL is the length from snout to vent. Mass is individual weight just before dissection. The mean value and standard deviation of each measurement are indicated for each species. Habitat and locomotor classification follows Schettino (1999).

species	Habitat	Locomotion	Sex	n	SVL (mm)	mass (g)
A. sagrei	ground, tree trunk	runner	male	5	55.5 ± 3.38	3.60 ± 0.55
			female	3	41.2 ± 1.70	1.48 ± 1.05
A. porcatus	tree trunk, crown	climber	male	4	67.7 ± 6.24	5.89 ± 1.91
			female	3	51.7 ± 3.80	2.11 ± 0.62
A. bartschi	cave, rocky area	runner	male	3	70.2 ± 1.58	6.92 ± 1.21
			female	4	57.4 ± 3.12	3.33 ± 0.59

MATERIALS AND METHODS

Specimens

In September 2010 and September 2011, we captured a total of 22 adult specimens of three species of *Anolis* lizards by hand or noose in Cuba (Table 1). All animals were anesthetized and fixed in 100% ethanol, and stored in 70% ethanol. Since dry muscles are easily frayed and difficult to isolate, the samples were soaked in 30% ethanol overnight before dissection. The fore- and hindlimbs were dissected, and each muscle was isolated under a microscope (S240; Olympus, Tokyo, Japan). Nineteen muscles from forelimbs related to rotation of

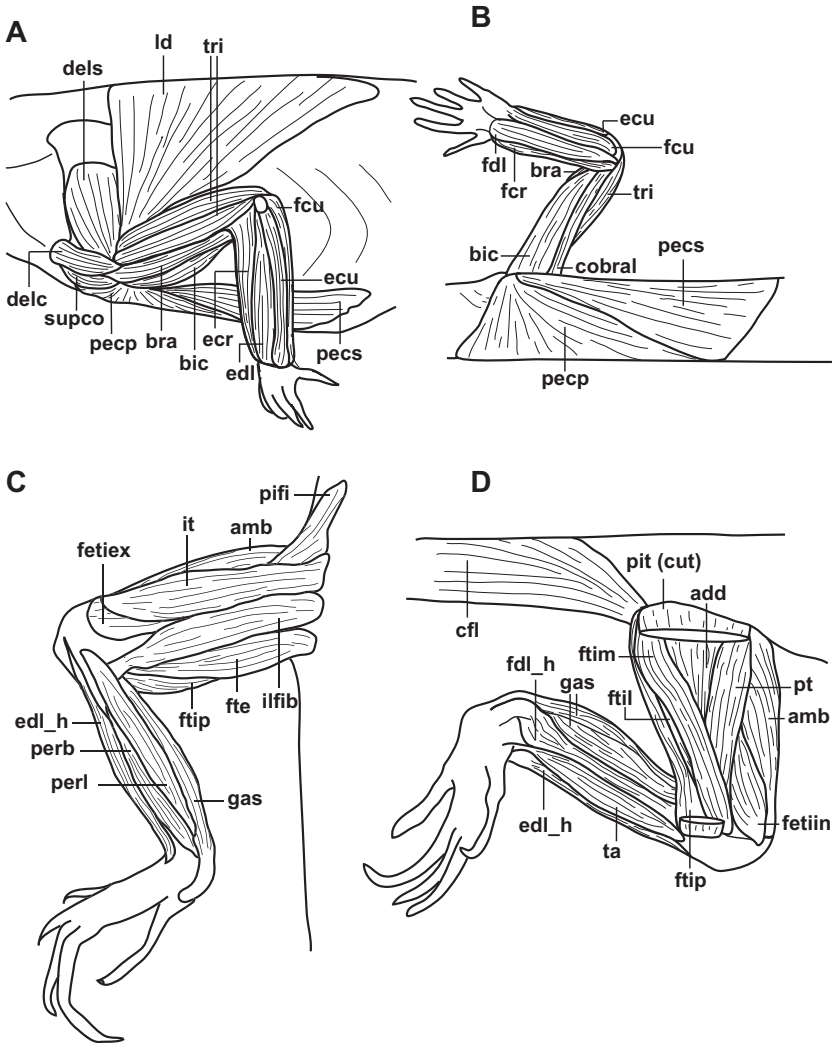


Fig. 1. The appendicular musculature of *Anolis* lizards used in this study. **(A)** Lateral and **(B)** ventral side of trunk and left forelimb, **(C)** dorsal and **(D)** ventral side of left hindlimb are illustrated. Abbreviations: add = M. adductor femoris; amb = M. ambiens; bic = M. biceps brachii; bra = M. brachialis anticus; cfl = M. caudifemoralis longus; cobral = M. coracobrachialis longus; delc = M. clavodeltoideus; dels = M. scapulodeltoideus; ecr = M. extensor carpi radialis; ecu = M. extensor carpi ulnaris; edl = M. extensor digitorum longus (forelimb); edl_h = M. extensor digitorum longus (hindlimb); fcr = M. flexor carpi radialis; fcu = M. flexor carpi ulnaris; fdl = M. flexor digitorum longus (forelimb); fdl_h = M. flexor digitorum longus (hindlimb); fte = M. flexor tibialis externus; fetiex = M. femorotibialis externus; fetiin = M. femorotibialis internus; ftil = M. flexor tibialis internus lateralis; ftim = M. flexor tibialis internus medialis; ftip = M. flexor tibialis internus posterior; gas = M. gastrocnemius; ilfib = M. iliofibularis; it = M. iliotibialis; ld = M. latissimus dorsi; pecs = M. pectoralis superficialis; pecp = M. pectoralis profundus; perb = M. peroneus brevis; perl = M. peroneus longus; pifi = M. puboischiofemoralis internus; pit = M. puboischiotibialis; pt = M. pubotibialis; supco = M. supracoracoideus; ta = M. tibialis anterior; tri = M. triceps complex. The deep muscles as M. coracobrachialis brevis (cobrab), M. iliofemoralis (ilfem), M. puboischiofemoralis externus (pife), M. subcoracoscapularis coracoid portion (subc) and subscapular portion (subs) are not illustrated.

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each joint and 22 muscles from hindlimbs were chosen for measurement (Zaaf et al., 1999; Herrel et al., 2008; Russell and Bauer, 2008; Anzai et al., 2014). These musculatures are illustrated in Fig. 1.

Measurements

Two parameters were measured in each muscle and compared. First, muscle mass was measured as an index of muscular force. Each isolated muscle was dried by blotting and weighed to the nearest 0.01 mg using a Shimadzu balance (AUW-220D; Kyoto, Japan). The length of each muscle moment arm was measured as a second trait. The length was defined as the distance from the center of rotation in each joint to the point of the muscle insertion, which theoretically represents the maximum moment arm (An et al., 1984; Fujiwara et al., 2011). Given the trade-off between torque and excursion, muscles with longer moment arms exert larger torque

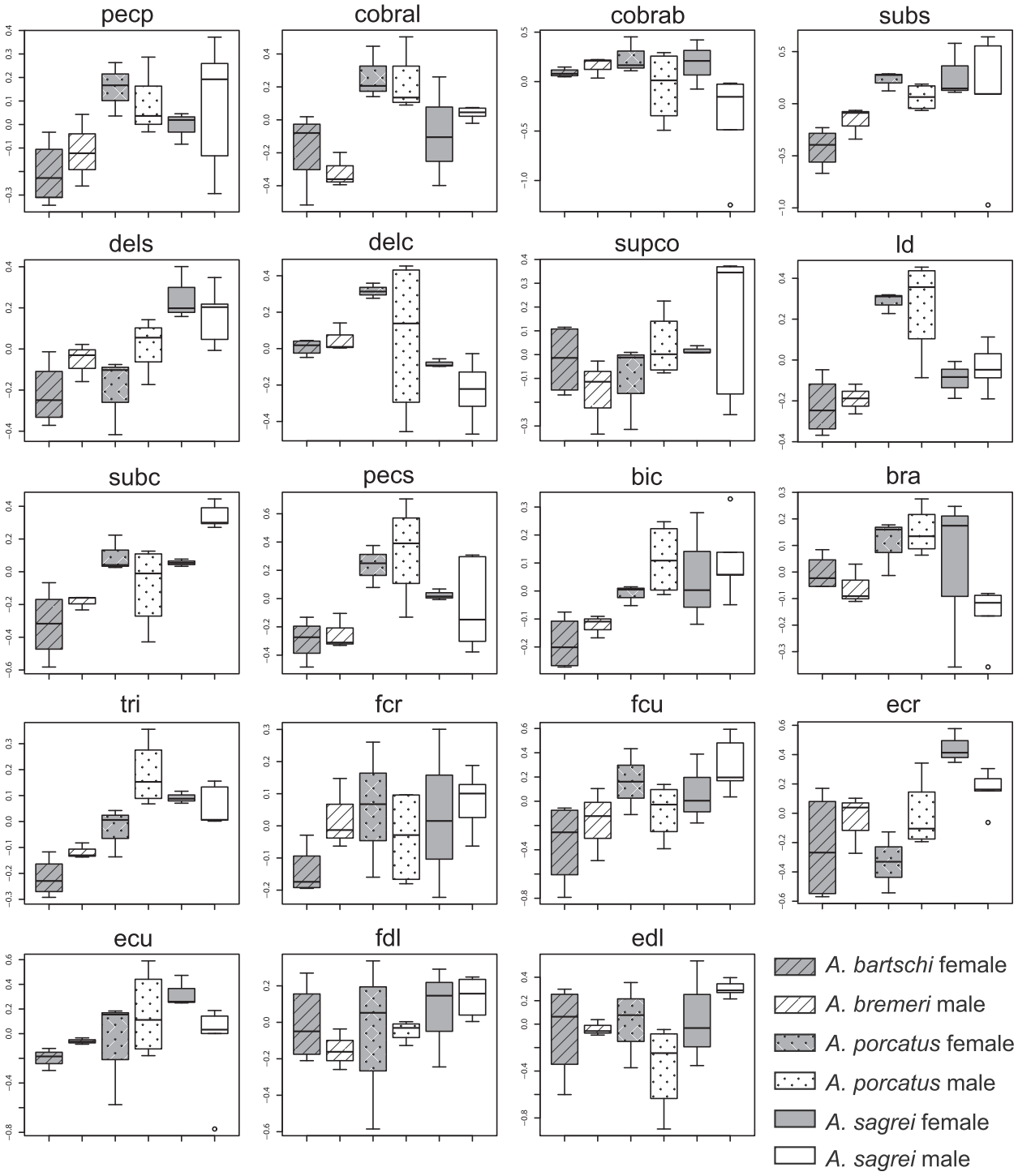


Fig. 2. Boxplots showing the normalized values for the forelimb muscles mass. The vertical axis indicates the residuals from ln-transformed muscle mass regressed against ln-total mass.

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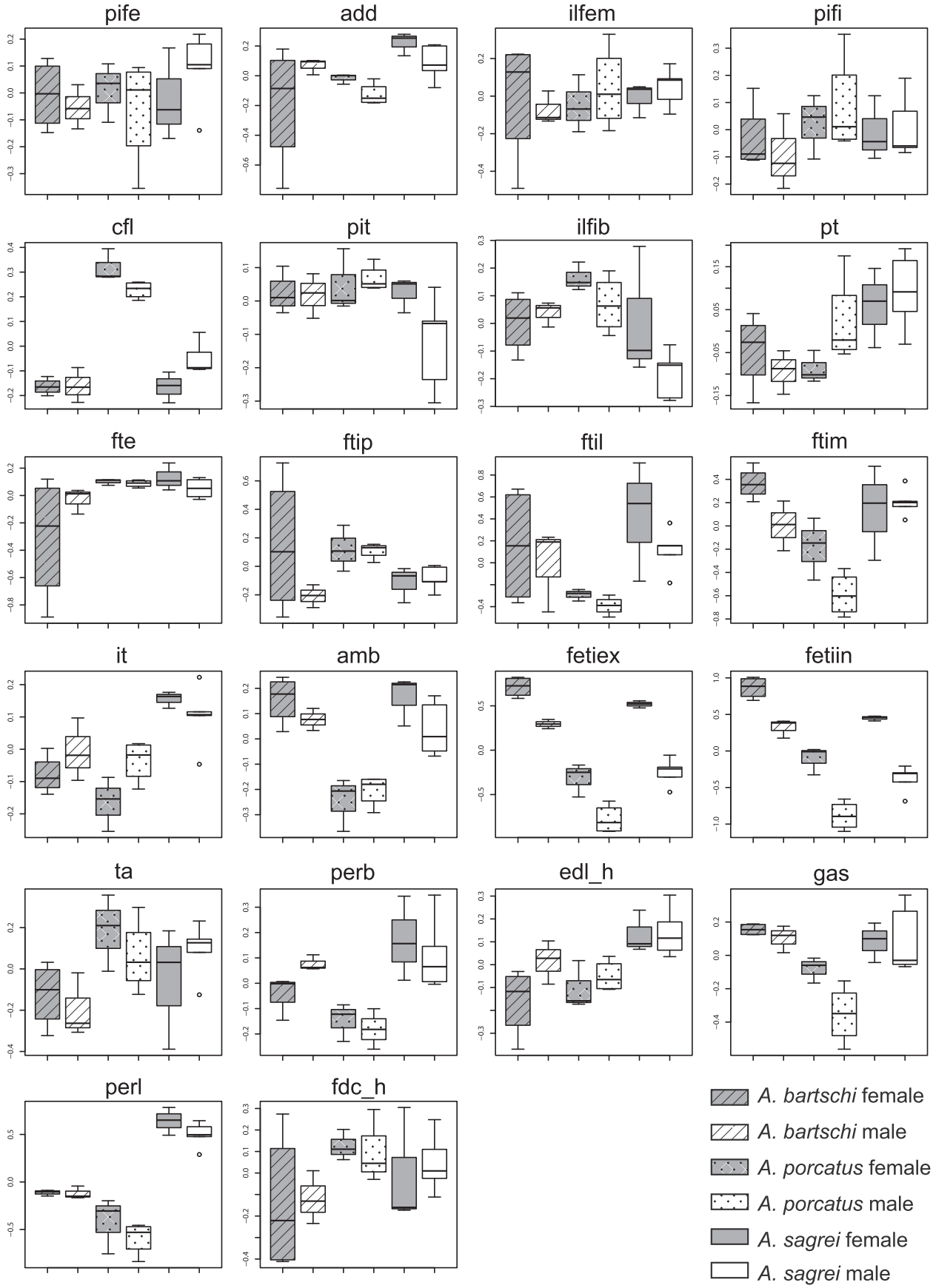


Fig. 3. Boxplots showing normalized values for hindlimb muscles mass.

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and muscles with shorter moment arms produce grater excursion. Lengths were measured using calipers to the nearest 0.05 mm.

Statistical analyses

To remove the effect of body size among different growth stages and/or species, all the muscle measurements were corrected for size. For muscle mass, residuals from the regression of each ln-transformed muscle mass value against the ln-transformed total body mass were used. For the moment arm, the ratio of each measurement to the length of limb bone on which the muscle inserts was calculated. To analyze whether locomotion, display, and sex affect musculoskeletal traits, we used two tests of two-way analysis of variance (ANOVA). One test took locomotion (terrestrial runner or arboreal climber) and sex as crossed factors and other one used sexual display with dewlap (existence or absence) and sex as crossed factors. All statistical analyses were performed using R (version 2.15.0, R Foundation for Statistical Computing, Vienna, Austria) and $P < 0.05$ was the criterion for statistical significance.

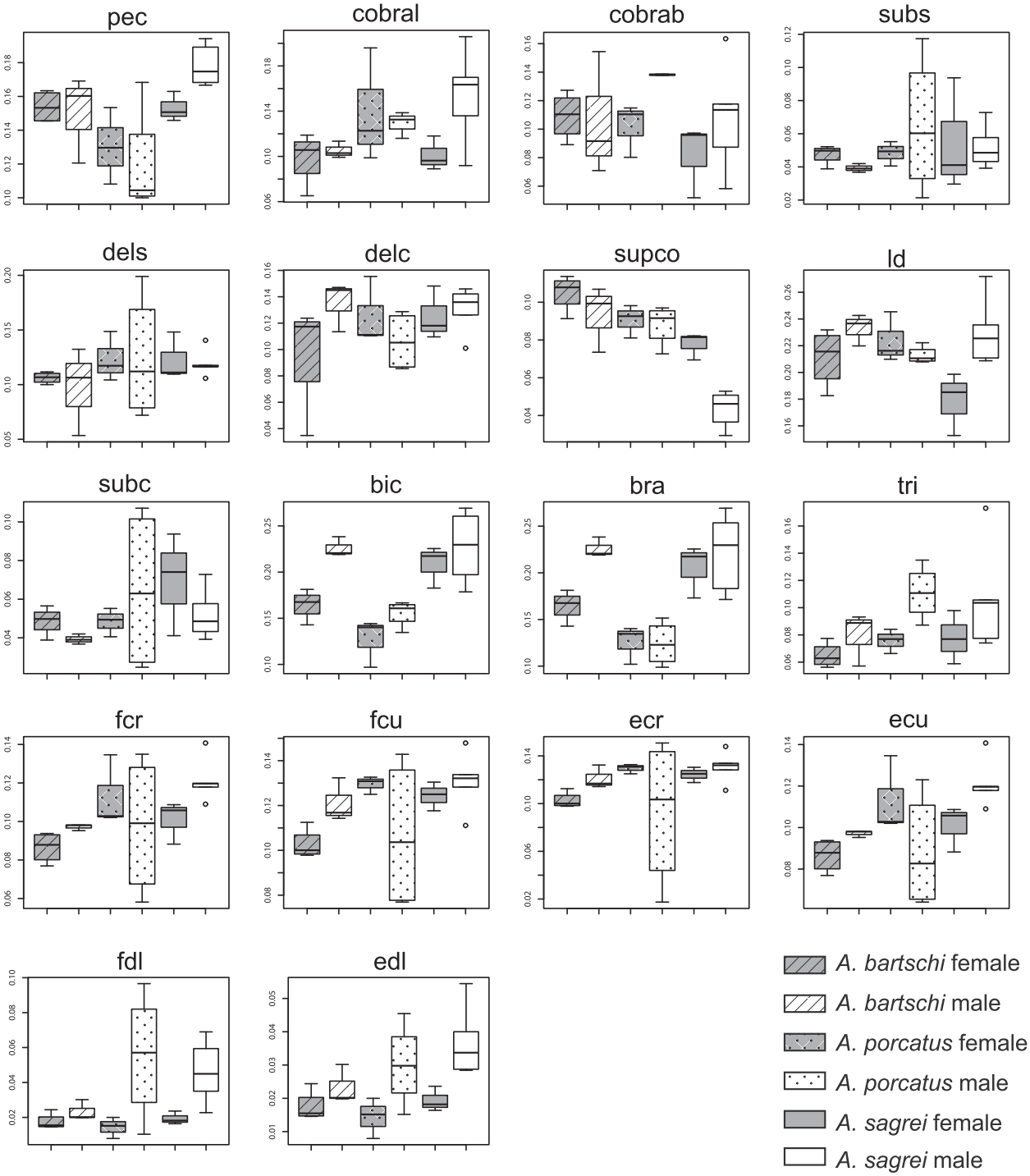


Fig. 4. Boxplots showing the normalized values for the forelimb muscles moment arm. The vertical axis indicates the ratios of the value to length of limb bone that the muscle inserts.

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RESULTS

The results of the comparison of normalized muscle mass are presented in Figs. 2 and 3, and that of the moment arm is shown in Figs. 4 and 5. The all row measurements of muscle mass are shown in Supplementary Table S1, and that of the moment arm is shown in Supplementary Table S2 online. The results of two tests of two-way ANOVA are shown in Table 2, and all of the p-value are presented in Supplementary Table S3 online.

In analyses between different locomotion types, climber species possessed significantly larger mass of M. coracobrachialis longus, M. clavodeltoideus, M. latissimus dorsi, M. pectoralis superficialis, M. brachialis anticus, M. caudifemoralis longus and M. iliofibularis, whereas runner species possessed larger mass of M. flexor tibialis internus lateralis, M.

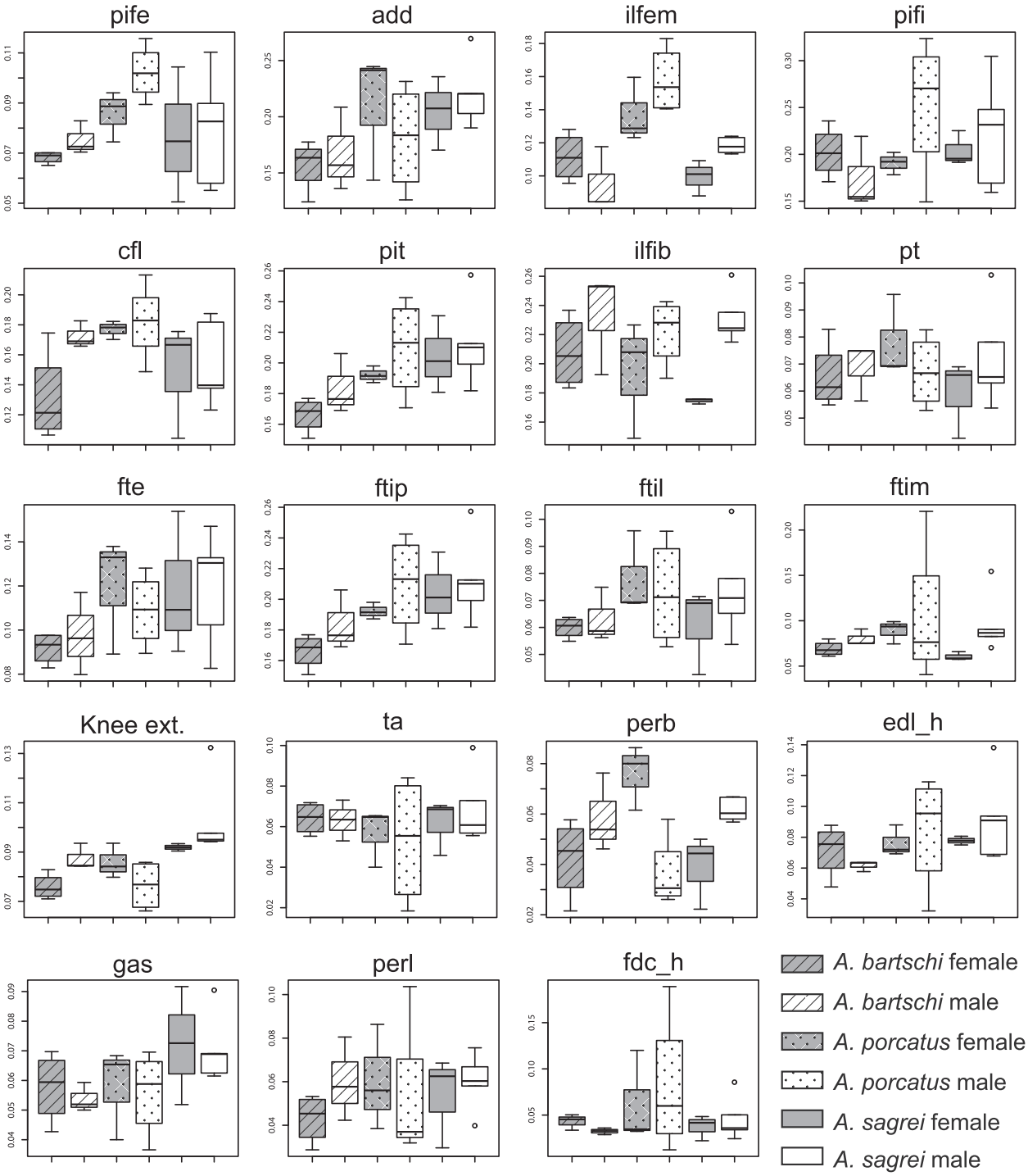


Fig. 5. Boxplots showing the normalized values for the hindlimb muscles moment arm. Result of four knee extensors (M. iliotibialis, M. ambiens, M. femorotibialis externus, M. femorotibialis internus) are illustrated collectively in "Knee ext", as these muscles insert to a common tendon.

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Table 2. Results of two test of two-way ANOVA. Sex, locomotion pattern, existence of display were used as crossed factors. Abbreviations: dis = existence of display; loc = locomotion; int = interaction of two crossed factors. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

	mass						moment arm					
	sex	loc	int	sex	dis	int	sex	loc	int	sex	dis	int
pecP					**			**				
cobral		**			**							
cobrab												
subS					**							
delS					*							
delC		*										
supco							*			*	*	
ld		***			**		*		*			
subC					**							
pecS		**			**			**				
bic				*	***		**	***				
bra		**						***				
tri	*			**	***		*			**		
fcr												
fcu					*				*			
ecr												
ecu									*			
fdl							***	*	**	***		*
edl							*			*		
pife								*				
add											*	
ilfem								***			*	
pifi												
cfl		***	*		**			*				
pit											**	
ilfib		*					**			**		
pt												
fte					**						*	
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ftim	*	***										
it		*							*			
amb		***			*							
fetiex	***	***		***	***							
fetiin	***	***		***	***							
ta					*							
perB		**							***			
edl_h												
gas		***										
perL		***										
fdc_h												

flexor tibialis internus medialis, M. iliotibialis, M. ambiens, M. femorotibialis externus, M. femorotibialis internus, M. peroneus brevis, M. gastrocnemius, and M. peroneus longus. Significant sexual differences in muscle mass were observed in M. triceps, M. flexor tibialis internus medialis, and M. femorotibialis externus and internus. The interaction of two factors was shown only in M. caudifemoralis longus. In terms of moment arm, runner species exhibited longer values in M. pectoralis, M. biceps brachii and M. brachialis anticus, whereas climber species were showed longer moment arms in M. flexor digitorum longus, M. puboischiofemoralis externus, M. iliofemoralis and M. caudifemoralis longus. Intersexual differences were found in M. supracoracoideus, M. latissimus dorsi, M. biceps brachii, M. triceps, M. flexor digitorum longus, M. extensor digitorum longus and M. iliofiblaris. In addition, M. latissimus dorsi, M. flexor carpi ulnaris, M. extensor carpi ulnaris, M. flexor digitorum longus, M. iliotibialis and M. peroneus brevis showed significant interactions between the two factors, sex and locomotion.

In two-way ANOVA analyses using existence of dewlapping display and sex as factors, species with dewlap (*A. sagrei* and *A. porcatus*) possessed larger mass of M. pectoralis profundus, M. coracobrachialis longus, M. subcoracoscapularis scapular portion and coracoid portion, M. scapulodeltoideus, M. latissimus dorsi, M. pectoralis superficialis, M. biceps brachii, M. triceps, M. flexor carpi ulnaris, M. caudifemoralis longus, M. flexor tibialis externus and M. tibialis anterior, whereas species without dewlap (*A. bartschi*) was equipped larger mass of M. ambiens, M. femorotibialis externus and internus. Sexual differences of muscle mass were shown in M. biceps brachii, M. triceps, and M. femorotibialis externus and internus. With respect to moment arm, significantly longer of M. supracoracoideus was shown in species without dewlap, while longer arm of M. adductor femoris, M. iliofemoralis, M. puboischiotibialis, M. flexor tibialis externus and M. flexor tibialis internus posterior were observed in species with dewlap. Significant sexual differences of moment arm were observed in M. supracoracoideus, M. triceps, M. flexor digitorum longus, M. extensor digitorum longus and M. iliofiblaris. No interaction between two factors was found in terms of muscle mass, but the moment arm of M. flexor digitorum longus showed a significant interaction term.

DISCUSSION

Differences among locomotion type

Although some studies indicated the relationship among appendicular musculoskeletal traits and locomotor behavior or habitat use in lizards, these studies analyzed only males, to exclude the effects of sexual difference (Zaaf et al., 1999; Vanhooydonck et al., 2006; Herrel et al., 2008; Anzai et al., 2014). Our data suggest that similar relationships between morphology and ecological traits in females may exist. In terms of muscle mass, the runner species *A. sagrei* and *A. bartschi* were equipped with well-developed extensor muscles in knee and ankle joints in both male and female (Fig. 3). Their large hindlimb extensors are suited for powerful kicking off from the ground or broad surfaces when running (Reilly, 1995, 1998; Herrel et al., 2008). Also, M. flexor tibialis internus lateralis and M. flexor tibialis internus medialis were expanded in runner species. Because these two muscles are apparently used by lizards when running on the ground through femoral adduction (Fieler and Jayne, 1998; Anzai et al., 2014), larger muscles are suited for rapid locomotion by both sexes in running species. In contrast, heavier retractor muscles in shoulder and hip joints and flexor muscles in the elbow were observed in the arboreal climber species, *A. porcatus* (Figs. 2 and 3). Since vertical climbing by lizards requires tension by the front legs to avoid

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backwards tumbling when their hind legs push for propulsion and countering gravity (Zaaf et al., 1999), enlarged elbow flexor muscles and proximal limb retractor muscles adapt lizards to scansorial locomotion in arboreal habitats. With regard to moment arm, *A. porcatus* possessed shorter moment arms in forelimb muscles (M. pectoralis, M. biceps brachii and M. brachialis anticus) and possessed longer moment arms in hindlimb muscles (M. puboischiofemoralis externus, M. iliofemoralis and M. caudifemoralis longus) than the two runner species (Figs. 4 and 5). A shorter moment arm provides a wider excursion angle in joints, thereby facilitating limb movement especially on narrow arboreal substrates (Peterson, 1973; Anzai et al., 2014). The greater flexibility of the elbow joint may be effective for stabilization in complex arboreal environments (Foster and Higham, 2012). In contrast, it is thought that larger torque is required for the hip joint to sustain the body when climbing (Zaaf et al., 1999). Although musculoskeletal traits of limbs in these three species showed different adaptive patterns in a habitat-dependent manner, the male and female tend to be equipped with similar muscular traits related to the locomotor style. This suggests that limb structures of males and females are similarly affected by ecological traits, as both males and females in each species reside in the same habitats (Schettino, 1999).

However, in M. femorotibialis externus and internus, the female in all three species showed significant larger muscle mass than the male (Fig. 3). Male anoles tend to keep a wider territorial home range and to be more active than the female (Vanhooydonck et al., 2005; Johnson et al., 2010), and thus the male is predicted to exhibit morphological traits that are more adaptive for running or jumping, such as long hindlimb and highly developed extensor muscles. Although it is known that males are equipped with a longer hindlimb than females in some *Anolis* species (Butler et al., 2007), unexpectedly our data showed that females are equipped with larger knee extensors than males. Furthermore, the other two extensor muscles on the knee joint (M. iliotibialis and M. ambiens) showed no sexual differences and no interaction between sex and locomotion type in these muscles (Table 2). It means that the four muscles considered as "knee extensors" may have different roles. Although all four muscles are inserted through the same tendon on the head of the tibia, M. iliotibialis and M ambiens arise from aponeuroses from the pelvic bone and extend along the femur superficially, whereas M. femorotibialis externus and M. femorotibialis internus arise from femoral shaft and extend along the femur profoundly. Although several studies have measured electromyography in the hindlimbs of lizards (Reilly, 1995, 1998; Foster and Higham, 2014), no study has analyzed both the superficial knee extensor muscles and the profound muscles. Thus, these "knee extensor" muscles may not only extend knee joint, but also may be related to aspects of locomotion that differ in male and female.

Interspecies and sexual differences among existence/non- of display with dewlap

In forelimb, nearly half of the muscles were enlarged in species with dewlap (*A. sagrei* and *A. porcatus*) compared to *A. bartschi*, which lacks a dewlap. When males of these two species are displaying by extension of the dewlap, they raise their head and lift up their anterior body by their arms. Hence large forelimb muscles in two species may be related to sexual display. However, no sexual differences in mass of forelimb muscles were observed in the three species, with the exception of M. biceps brachii and M. triceps. The lighter forelimb muscles in *A. bartschi* are considered to be a specialization for cave habitats as both males and females show similar morphologies. In addition, knee extensors (M. ambiens, M. femorotibialis externus and internus) were enlarged in *A. bartshci*, thus this species may invest in locomotor behavior to maintain wider territory instead of sexual display behavior.

Elbow extensor muscle, M. triceps, showed statistical sexual differences in both muscle mass (Fig. 2; $P < 0.05$ with locomotion and $P < 0.01$ with display by two-way ANOVA) and moment arm (Fig. 4; $P < 0.05$ with locomotion and $P < 0.01$ with display); male *A. porcatus* in particular showed larger values than female in the boxplots. *Anolis porcatus* tends to keep its arms near the body as this species lives mainly in arboreal narrow habitats and hence when the male performs displaying behavior it needs to extend the elbow in order to raise the head and body. In contrast, *A. sagrei* mainly occurs on broad surfaces such as tree trunks or the ground (Schettino, 1999), they spread their arms widely to increase the stride (Foster and Higham, 2012). Thus, when male *A. sagrei* are displaying with the dewlap, they appear to raise the head and lift the anterior body by adducting their arms to make space for an expanding dewlap. However, no significant sexual differences were shown in humeral adductor muscles, M. pectoralis profundus, M. coracobrachialis longus and brevis. Also no statistical significance of interaction between sex and locomotion or display was indicated in most muscles (Table 2). Although differences in posture when lizards are displaying caused by differences in habitat may lead to sexual dimorphisms, dewlap behavior does not affect limb muscles, at least in *A. sagrei*.

However *A. bartschi*, which does not display with a dewlap, also showed sexual dimorphisms in the moment arm of elbow flexor muscles (Fig. 4), nonetheless non-significant by two-way ANOVA. There could be two explanations why this sexual dimorphism exists. First, the male can produce a larger torque than the female. Second, the female is equipped with larger excursion than the male in elbow flexion. According to Schettino (1999), no differences in ecological habits have been found between males and females in *A. bartschi*, but few ecological studies have been conducted on this species. Although we could not address further why the sexual difference is present, because of the lack of relevant ecological and behavioral data about *A. bartschi*, their sexual differences of body size suggest that male–male combat occurs in this species (Table 1; Lailvaux and Irschick, 2007; Thomas et al., 2009). A similar sexual difference in muscular traits of elbow flexion has been reported in Japanese toad (Oka et al., 1984). Male *Bufo japonicus* are equipped with powerful flexor muscles in the elbow, which relates to clasping behavior to hold females with their forelimbs during the breeding season (Oka et al., 1984). A larger torque of male *A. bartschi* may be related to holding the female during mating, although no extensive observation of mating behavior has been conducted in this species.

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Meanwhile, female *A. bartschi* bears enormous eggs compared to those of other *Anolis* lizards, and additionally lays eggs in crevasses, which differs from most *Anolis* species which oviposit in the soil (Schettino, 1999). These unique reproductive traits may affect the female-specific shorter moment arm on the elbow joint that we describe above. However, we need more detailed observations and ecological researches to discuss the significance of our data with respect to sexual differences in *A. bartschi*. In conclusion, we describe evident sexual dimorphisms in the appendicular musculature of three species of *Anolis* lizards and the possibility that these dimorphisms are affected by various sexual displays using the dewlap and ecological habitats.

ACKNOWLEDGMENTS

We are grateful to Masakado Kawata who organized a cooperative research project on *Anolis* lizards with The University of Havana, and allowed us to use the specimens used in this study. We are grateful to Lazaro Echenique-Diaz and Hiroshi Akashi for helping us collect specimens. Special thanks to Luis M. Diaz for providing helpful information about *A. bartschi*. We also thank Shinichi Fujiwara, Daisuke Koyabu, and Mugino Kubo for helpful advice. Collection and exportation permits were provided by the Centro de Inspección y Contról Ambiental (CICA) of the Agencia de Medio Ambiente de Cuba (Permit No. 2012019).

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(Received February 26, 2015 / Accepted July 22, 2015)

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