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Using Entheseal Length to Infer Locomotor Type

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USING ENTHESEAL LENGTH TO INFER LOCOMOTOR TYPE

A Thesis

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in

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by
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Abstract

An enthesis is a marking (tuberosity or impression) on bone where a muscle or tendon attaches and it can be influenced by age, sex, physical activity, and muscle size. This study ascertains whether entheses, long bones, and their respective ratios can be used as an indicator for mode of locomotion in four primate species: *Ateles geoffroyi* (Geoffroy's spider monkey), *Colobus guereza* (mantled guereza), *Hylobates lar* (lar gibbon), and *Macaca mulatta* (rhesus monkey). Seven entheses on four long bones were chosen based on importance of the muscle in relation to specific locomotor types, use in other studies, and ease of measurement; for each enthesis and accompanying long bone, a ratio was created which indicated the percentage of length the enthesis occupied on the long bone. Body length and not body mass was used in statistical analysis since a correlation analysis showed these two variables as having a significant, positive association. Comparisons were done among species, sex, and location (captive or wild caught specimen) using a Generalized Linear Model (GLM) with Tukey-Kramer's tests and Student's t-tests. The hypothesized pattern for results comparing species will be that *C. guereza* and *M. mulatta* group together, *H. lar* will be separate, and *A. geoffroyi* will be intermediate between *H. lar* and *C. guereza*/*M. mulatta* due to differences in their locomotion. Results show that five out of seven entheses, one out of four long bones, and one out of seven ratios follow the hypothesized pattern. Reasons for the discrepancy between the hypothesized pattern and results include body length and variable locomotor types within each species. Regarding sex, entheses are sexually dimorphic. Location was not a significant factor among species, which allowed captive and wild caught specimens to be combined into a larger sample. These results show that entheses are indicative of sex and are not affected by captivity. Overall, entheseal length is indicative of locomotor type, but long bone length and the ratio are not.

Chapter 1. Introduction

An enthesis is a marking (tuberosity or impression) on bone where muscles or tendons attach and consists of two types: fibrous and fibrocartilaginous. In fibrous entheses, the tendon or ligament attaches directly to the bone, while in fibrocartilaginous entheses the tendon or ligament passes through four zones: dense fibrous connective tissue, uncalcified fibrocartilage, calcified fibrocartilage, and bone (Benjamin *et al*., 2002). Most entheses are of the fibrocartilaginous type, and thus most entheseal studies are conducted on fibrocartilaginous entheses (Benjamin *et al*., 2002). These sites are influenced by age, sex, physical activity, and/or muscle size. Most research done in this field relates to humans by attempting to discover activity or occupational stress markers. However, entheseal studies are not only done on humans and some studies have been done using non-human primates. Results of human studies differ among one another and there is no clear consensus for the effect that age, sex, physical activity/occupation, or muscle size have on entheseal morphology (Acosta *et al.*, 2017; Foster *et al.*, 2012; Godde and Taylor, 2013; Milella, 2014; Milella *et al.*, 2012; Niinimäki and Sotos, 2012; Schlecht, 2012; Shaw and Benjamin, 2007; Villotte and Knüsel, 2012; Villotte *et al.*, 2009; Zumwalt, 2006). While overall conclusions regarding human studies may not always agree, there is consensus that entheses are affected by activity level in some manner. This study takes a new approach by comparing different locomotor types. Specifically, this research attempts to ascertain whether entheses can be used as an indicator for mode of locomotion in four primate species: *Ateles geoffroyi* (Geoffroy's spider monkey), *Colobus guereza* (mantled guereza), *Hylobates lar* (lar gibbon), and *Macaca mulatta* (rhesus monkey).

Ateles geoffroyi, *C. guereza*, *H. lar*, and *M. mulatta* are ideal for this study because they are similar in body mass but differ in modes of locomotion. The locomotion of *A. geoffroyi* is eclectic and includes quadrupedal walking and running, vertical climbing, brachiation and arm-swinging, bipedalism, and leaping (Hirasaki *et al.*, 1993; Mittermeier and Fleagle, 1976). *Colobus guereza* is an arboreal quadruped whose locomotion consists of quadrupedal running and bounding, leaping, and rare arm-swinging (Mittermeier and Fleagle, 1976). *Hylobates lar* is a brachiator that will also occasionally engage in terrestrial bipedalism or quadrupedalism (Chang *et al.*, 2000; Michilsens *et al.*, 2009; Vereecke *et al.*, 2006). *Macaca mulatta* is a quadruped whose range of locomotion includes arboreal and terrestrial quadrupedalism depending on environment, bipedalism, and infrequent climbing and leaping (Demes *et al.*, 2001; Wells and Turnquist, 2001).

Seven entheses on four long bones were chosen based on importance of the muscle in relation to specific locomotor types, use in other studies, and ease of measurement (Acosta *et al.*, 2017; Foster *et al.*, 2012; Godde and Taylor, 2013; Henderson, 2013; Milella, 2014; Milella *et al.*, 2012; Niinimäki and Sotos, 2012; Shaw and Benjamin, 2007; Villotte and Knüsel, 2012; Villotte *et al.*, 2009; Zumwalt, 2006). The seven muscle entheses used are pectoralis major, deltoid, and teres major located on the humerus, biceps brachii located on the radius, brachialis and supinator located on the ulna, and gluteus maximus located on the femur. The deltoid is the only fibrous enthesis used in this study, while the other six muscles form fibrocartilaginous entheses. The function of pectoralis major is flexion, adduction, and medial rotation of the arm (Howell and Straus, 1931; White *et al.*, 2012). The deltoid is a major abductor for the arm (Howell and Straus, 1931; White *et al.*, 2012; Youlatos, 2000). Teres major is a medial rotator, adductor, and extensor of the arm (Howell and Straus, 1931; White *et al.*, 2012; Youlatos, 2000). Biceps brachii is a flexor and supinator of the forearm and also provides weak medial rotation for the arm (Howell and Straus, 1931; White *et al.*, 2012; Youlatos, 2000). Brachialis is a flexor for the forearm (Howell and Straus, 1931; White *et al.,* 2012; Youlatos, 2000). Supinator supinates the forearm (White *et al.,* 2012; Youlatos, 2000). The function of the gluteus maximus is to extend, abduct, and laterally rotate the femur (White *et al.,* 2012; Yirga, 1987).

Due to the different actions that muscles perform, locomotor type will affect the importance of each muscle among *A. geoffroyi*, *C. guereza*, *H. lar,* and *M. mulatta*. For example, a brachiator like *H. lar* will differentially use the forelimb muscles more than the hindlimb. Thus, the forelimb muscles are more important in locomotion, and the stresses, strains, and use will be different compared to a quadruped (Fleagle *et al*., 1981; Miller, 1932). Entheses will be analyzed to determine if the differences in muscle use caused by different locomotor types also cause differences in entheseal length. Therefore, the hypothesized pattern will be that *C. guereza* and *M. mulatta* group together due to similarities in locomotion, *H. lar* will be separate, and *A. geoffroyi* will be intermediate. More specifically, for the forelimb, *H. lar* should have the largest entheseal length, *C. guereza* and *M. mulatta* the smallest entheseal length, and *A. geoffroyi* will be intermediate in entheseal length. For the hindlimb, entheseal length is expected to be the largest in *C. guereza* and *M. mulatta,* the smallest in *H. lar,* and intermediate in *A. geoffroyi*.

This research has paleoanthropological implications. A difficult problem in paleoanthropology is determining all or preferred modes of locomotion in species such as *Australopithecus afarensis, Australopithecus africanus, Australopithecus sediba,* and *Homo naledi* among others (Berger *et al.*, 2010; Berger *et al.*, 2015; Ruff, 2009; Skinner *et al.*, 2015; Ward, 2002, 2013). Bipedality is not in question here. Rather, the question is how frequently *Australopithecus* and *Homo* species were engaging in some type of arboreal locomotion in conjunction with bipedality, and if those other locomotor types can be identified. Comparing entheseal lengths of extant primate species may provide information that could help better resolve this problem. The sexing of fossil hominoids and other primates is also problematic and is usually done through craniodental morphology, body size estimates, or other morphological features (Grine *et al.*, 2012; Lockwood, 1999; Simpson *et al.*, 2008). Since entheses are shown to be affected by sex, entheseal length may also be an indicator for determination of sex or sexual dimorphism (Acosta *et al*., 2017; Foster *et al*., 2012; Milella, 2014; Milella *et al*., 2012; Niinimäki and Sotos, 2012; Schlecht, 2012).

Differentiating entheses between species with different modes of locomotion would allow trends to be seen between modes of locomotion and entheseal length. Also, identifying sexual differences in entheseal length would mean that entheses could be used as an indicator for sex. Comparison between captive and wild caught specimens is done in this study to determine if captive specimens have shorter entheseal lengths than wild caught specimens. The possibility exists that captive individuals may not employ their full range of locomotor type(s) in a restricted environment, compared to wild caught specimens that lived in an open environment with no restriction on locomotor type(s). If no difference is found between captive and wild caught specimens, they could then be combined to increase sample size. Therefore, this study compares entheseal and long bone length, along with a ratio characterized by entheseal length/relevant long bone length, across four primate species to determine if these measurements differ across species, sex, and location (captive vs. wild caught).

Chapter 2. Materials and Methods

2.1. Materials

The sample consists of four primate species: *A. geoffroyi, C. guereza, H. lar*, and *M. mulatta.* Measurements were taken on four long bones and seven entheses. The four long bones measured are the humerus, radius, ulna, and femur. The seven entheses measured are for pectoralis major, teres major, deltoid, biceps brachii, brachialis, supinator, and gluteus maximus. From these measurements, seven ratios were created which consisted of the entheseal length divided by long bone length of the relative long bone. The ratios are an indication of percentage of length an enthesis occupies on the long bone. The seven ratios are pectoralis major/humerus (HPM), teres major/humerus (HTM), deltoid/humerus (HD), biceps brachii/radius (RBB), brachialis/ulna (UB), supinator/ulna (US), and gluteus maximus/femur (FGM).

Skeletal material was studied at six locations in the USA: American Museum of Natural History in New York, New York, Field Museum of Natural History in Chicago, Illinois, Museum of Natural Science in Baton Rouge, Louisiana (Louisiana State University), Museum of Comparative Zoology in Cambridge, Massachusetts (Harvard University), Museum of Southwestern Biology in Albuquerque, New Mexico (University of New Mexico), and Smithsonian National Museum of Natural History in Washington, D.C. Total specimen number and number of specimens per category are located in Table 1.

Table 1. Number of specimens for each sex and location (captive or wild).

	Ateles geoffroyi	*Colobus guereza*	*Hylobates lar*	*Macaca mulatta*
Female captive	2	5	2	19
Female wild	5	6	35	1
Male captive	1	12	3	22
Male wild	1	6	35	2
Total	9	29	75	44

2.2. Methods

At each location, photographs were taken using a Nikon COOLPIX AW100. Measurements of long bone length were done using the VINCA DCLA-1205 300mm sliding digital caliper. Measurements of entheseal length were done using the iGaging Absolute Origin 150mm sliding digital caliper. Maximum length of the humerus, radius, ulna, and femur was measured. Entheseal length for pectoralis major, teres major, biceps brachii, brachialis, supinator, and gluteus maximus was taken on the maximum straight-line length for each enthesis. Deltoid measurements were taken from the inferior aspect of the greater tubercle/surgical neck to the inferior aspect of the deltoid tuberosity. Examples of entheseal measurements are provided in Figures 1-6.

Sex, body length, body mass, and location (captive or wild caught) were also obtained from museum records. *Ateles geoffroyi* and *M. mulatta* did not have enough data for body length or body mass so information was gathered from literature (Fooden, 2000; Ford and Davis, 1992; Glander *et al*., 1991; Hamada *et al.*, 2006; Schultz, 1941). This was done for female *A. geoffroyi* body mass, female *M. mulatta* body length, male *A. geoffroyi* body length and body mass, and male *M. mulatta* body length and body mass. The body length or body mass for individual *A. geoffroyi* or *M. mulatta* specimens that did not have one or both of those values was replaced with the mean of means from information gathered through literature. For example, the mean body mass for female *A. geoffroyi* used in this study is 7.44 kg. Of the seven total specimens, six are individually given a body mass of 7.39 kg, which was the mean of means gathered from literature. The seventh has a mass of 7.71 kg, which was available at the collection. Thus, the total body mass for all seven specimens is 7.44 kg (Table 2). In species where enough data were gathered from the collections (female *A. geoffroyi* body length, female *M. mulatta* body mass, male and female *C. guereza*, and male and female *H. lar*), individual specimens without a mean for body length or body mass were given the sample mean. All measurements except for body mass are recorded in millimeters; body mass is recorded in kilograms. Statistical analyses were then run in SAS 9.4 for all information gathered. Statistical tests included Pearson's correlation analyses, Generalized Linear Model (GLM) including Tukey-Kramer's tests (for species and species by location), and Student's t-test. Tukey-Kramer's test compares each species to the others to determine the source of the GLM's significant results. Since a high number of tests were run for this study, the alpha level has been set to 0.01 to minimize type I errors.

Figure 1. Female *H. lar* teres major (top) and pectoralis major (bottom) entheses.

Figure 2. Female *A. geoffroyi* deltoid enthesis.

Figure 3. Female *A. geoffroyi* biceps brachii enthesis.

Figure 4. Female *H. lar* brachialis enthesis.

Figure 5. Male *C. guereza* supinator enthesis.

Figure 6. Female *H. lar* gluteus maximus enthesis.

Chapter 3. Results

3.1. Summary Statistics and Correlation Analysis

Summary statistics are provided for female, male, and combined sex in Tables 2-4. Correlation analysis was run separately for body length and body mass for *C. guereza* and *H. lar*. Body length and body mass have a significant positive correlation for both *C. guereza* (0.75, p=0.0082) (Table A.2) and *H. lar* (0.53, $p < 0.0001$) (Table A.3). Due to this, only body length was used in all other statistical tests. Body length shows a significant correlation across several measurements (four of 11 on the left-side and five of 11 on the right-side for *C. guereza* and eight of 11 on both the left- and right-sides for *H. lar*), leading to the inclusion of body length in other statistical analyses (Tables A.2 and A.3). Lengths of the left and right side of long bones and entheses were compared by correlation analysis. Results show *A. geoffroyi* (range from 0.71 to 0.99), *C. guereza* (range from 0.87 to 0.99) , *H. lar* (range from 0.90 to 0.98), and *M. mulatta* (range from 0.85 to 0.99) all have significant positive correlations between the left and right-side measurements, which allowed the left and right-side measurements to be combined (Tables A.1-4). The combined measurements were then used to create each ratio.

3.2. First GLM Analysis with Tukey-Kramer's Tests for Species

The GLM evaluates each long bone, entheseal measurement and ratio separately with respect to how species, sex, body length, and location associate with each individual measurement. The GLM was performed on the combined sample of females and males. Two GLM tests were run because male *A. geoffroyi* specimens do not have enough data in measurements for the radius, ulna, biceps brachii, brachialis, and supinator (Table 3). Therefore, the first GLM test included the humerus, femur, pectoralis major, teres major, deltoid, gluteus

Table 2. Female summary statistics for all measurements/ratios. Blank spaces for body length and body mass due to information gathered from literature.

Species	*Ateles geoffroyi*			*Colobus guereza*			*Hylobates lar*			*Macaca mulatta*		
Measurement	n	Mean	SD	n	Mean	SD	n	Mean	SD	n	Mean	SD
Body length (mm)	4	445.33	10.65	8	574.88	32.08	29	466.31	14.37		471.74[1]	
Body mass (kg)		7.44[2]		6	7.79	0.77	26	5.33	0.46	11	6.16	0.96
Humerus (mm)	7	202.97	6.44	10	145.94	5.28	37	234.31	9.55	20	137.68	8.11
Radius (mm)	7	211.43	5.78	7	136.46	7.10	37	256.77	10.34	20	137.11	7.54
Ulna (mm)	7	224.67	5.51	7	151.81	8.93	37	264.70	10.70	20	152.43	9.00
Femur (mm)	7	201.84	9.96	10	189.40	8.30	37	204.27	9.63	20	162.69	9.17
Pectoralis major (mm)	7	35.33	1.62	10	26.01	3.17	37	44.23	3.54	20	21.14	1.29
Teres major (mm)	7	30.51	2.86	10	21.48	1.41	37	35.39	2.75	20	16.09	1.40
Deltoid (mm)	7	75.80	4.38	10	52.61	4.91	37	102.69	4.35	20	48.27	4.47
Biceps brachii (mm)	7	15.11	0.57	7	12.26	0.74	37	18.21	1.36	20	13.75	1.14
Brachialis (mm)	7	24.24	3.17	7	14.80	1.63	37	32.21	1.90	20	13.67	1.44
Supinator (mm)	7	16.01	1.86	7	9.83	1.27	37	21.16	1.41	20	10.03	1.08
Gluteus maximus (mm)	7	42.04	1.86	10	40.20	2.26	37	34.42	2.86	20	34.47	3.13
HPM	7	0.17	0.01	10	0.18	0.02	37	0.19	0.01	20	0.15	0.01
HTM	7	0.15	0.01	10	0.15	0.01	37	0.15	0.01	20	0.12	0.01
HD	7	0.37	0.02	10	0.36	0.03	37	0.44	0.01	20	0.35	0.03
RBB	7	0.07	0.003	7	0.09	0.01	37	0.07	0.004	20	0.10	0.01
UB	7	0.11	0.01	7	0.10	0.01	37	0.12	0.01	20	0.09	0.01
US	7	0.07	0.01	7	0.07	0.01	37	0.08	0.003	20	0.07	0.01
FGM	7	0.21	0.01	10	0.21	0.01	37	0.17	0.01	20	0.21	0.01

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[1] *M. mulatta* body length means from literature: Hamada *et al*. (2006) – 474.68 mm (n=12); Fooden (2000) – 468.8 mm (n=72); Literature mean of means – 471.74 mm; Mean for Table 2 – 471.74 mm.

[2] *A. geoffroyi* body mass means from literature and from specimens used in this study: Ford and Davis (1992) – 7.9 kg (n=97); Glander *et al*. (1991) – 6.62 kg (n=12); Schultz (1941) – 7.64 kg (n=32). Literature mean of means – 7.39 kg; Mean from specimens used in this study – 7.71 kg (n=1); Mean for Table 2 – 7.44 kg.

Table 3. Male summary statistics for all measurements/ratios. Blank spaces for body length and body mass due to information gathered from literature.

Species	*Ateles geoffroyi*			*Colobus guereza*			*Hylobates lar*			*Macaca mulatta*		
Measurement	n	Mean	SD	n	Mean	SD	n	Mean	SD	n	Mean	SD
Body length (mm)		471.75[1]		10	630.69	19.64	34	471.23	18.01		533.81[2]	
Body mass (kg)		7.91[3]		10	9.81	0.75	26	5.89	0.56		8.53[4]	
Humerus (mm)	2	189.45	5.16	17	157.88	6.19	38	237.69	9.05	24	155.18	10.5
Radius (mm)	1	196.00		14	151.76	5.98	38	258.85	11.51	24	154.23	10.94
Ulna (mm)	1	210.00		14	169.86	6.98	38	266.62	12.16	24	172.28	12.92
Femur (mm)	2	194.15	0.07	17	205.64	9.64	38	205.88	8.56	24	186.00	14.31
Pectoralis major (mm)	2	36.65	1.63	17	31.12	3.6	38	45.95	3.19	24	26.11	1.96
Teres major (mm)	2	30.55	2.19	17	24.41	2.84	38	36.79	2.43	24	19.70	2.94
Deltoid (mm)	2	74.90	0.71	17	58.25	4.22	38	104.15	3.9	24	58.50	4.58
Biceps brachii (mm)	1	15.30		14	15.32	1.72	38	18.98	2.87	24	17.19	2.21
Brachialis (mm)	1	19.40		14	17.80	1.4	38	33.40	2.25	24	16.22	1.86
Supinator (mm)	1	15.20		14	11.80	1.96	38	21.95	1.97	24	11.71	1.08
Gluteus maximus (mm)	2	43.40	0.99	17	46.21	4.03	38	35.06	2.35	24	40.54	4.16
HPM	2	0.19	0.01	17	0.20	0.02	38	0.19	0.01	24	0.17	0.01
HTM	2	0.16	0.01	17	0.15	0.02	38	0.15	0.01	24	0.13	0.01

(Table cont'd)

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[1] *A. geoffroyi* body length means from literature: Glander *et al*. (1991) – 466 mm (n=2); Smithsonian National Museum of Natural History – 477.5 mm (n=16). Literature mean of means: 471.75 mm; Mean for Table 3 – 471.75 mm.

[2] *M. mulatta* body length means from literature and from specimens used in this study: Fooden (2000) – 531.8 mm (n=48). Literature mean of means: 531.8; Mean from specimens used in this study: 580 mm (n=1); Mean for Table 3 – 533.81 mm.

[3] *A. geoffroyi* body mass means from literature: Ford and Davis (1992) – 7.91 kg (n=52); Glander *et al.* (1991) – 8.38 kg (n=2); Schultz (1941) – 7.45 (n=20). Literature mean of means: 7.91 kg; Mean for Table 3 – 7.91 kg.

[4] *M. mulatta* body mass means from literature and from specimens used in this study: Fooden (2000) – 7.7 kg (n=25); Schultz (1941) – 8.72 kg (n=7). Literature mean of means: 8.21 kg; Mean from specimens used in this study: 10.73 (n=3); Mean for Table 3 – 8.53 kg.

Species	*Ateles geoffroyi*			*Colobus guereza*			*Hylobates lar*			*Macaca mulatta*		
Measurement	n	Mean	SD	n	Mean	SD	n	Mean	SD	n	Mean	SD
HD	2	0.40	0.01	17	0.37	0.02	38	0.44	0.01	24	0.38	0.02
RBB	1	0.08		14	0.10	0.01	38	0.07	0.01	24	0.11	0.01
UB	1	0.09		14	0.10	0.01	38	0.13	0.01	24	0.09	0.01
US	1	0.07		14	0.07	0.01	38	0.08	0.01	24	0.07	0.01
FGM	2	0.22	0.01	17	0.22	0.02	38	0.17	0.01	24	0.22	0.02

Table 4. Female and male combined summary statistics.

Species	*Ateles geoffroyi*			*Colobus guereza*			*Hylobates lar*			*Macaca mulatta*		
Measurement	n	Mean	SD	n	Mean	SD	n	Mean	SD	n	Mean	SD
Body length (mm)		451.20		18	609.51	36.89	63	468.81	16.39		505.60	
Body mass (kg)		7.54		16	9.05	1.25	52	5.62	0.58		7.45	
Humerus (mm)	9	199.97	8.37	27	153.46	8.23	75	236.02	9.39	44	147.22	12.87
Radius (mm)	8	209.50	7.64	21	146.66	9.65	75	257.82	10.92	44	146.44	12.78
Ulna (mm)	8	222.84	7.28	21	163.84	11.47	75	265.67	11.43	44	163.26	15.00
Femur (mm)	9	200.13	9.27	27	199.63	12.04	75	205.09	9.08	44	175.40	16.87
Pectoralis major (mm)	9	35.62	1.62	27	29.22	4.21	75	45.10	3.45	44	23.85	3.01
Teres major (mm)	9	30.52	2.60	27	23.32	2.78	75	36.10	2.67	44	18.06	2.97
Deltoid (mm)	9	75.60	3.82	27	56.16	5.20	75	103.43	4.17	44	53.85	6.83
Biceps brachii (mm)	8	15.14	0.53	21	14.30	2.07	75	18.60	2.28	44	15.63	2.49
Brachialis (mm)	8	23.64	3.40	21	16.80	2.04	75	32.82	2.15	44	15.06	2.10
Supinator (mm)	8	15.91	1.75	21	11.14	1.97	75	21.56	1.75	44	10.95	1.36
Gluteus maximus (mm)	9	42.34	1.76	27	43.99	4.53	75	34.74	2.62	44	37.78	4.79
HPM	9	0.18	0.01	27	0.19	0.02	75	0.19	0.01	44	0.16	0.01
HTM	9	0.15	0.01	27	0.15	0.01	75	0.15	0.01	44	0.12	0.01
HD	9	0.38	0.02	27	0.37	0.02	75	0.44	0.01	44	0.37	0.02
RBB	8	0.07	0.003	21	0.10	0.01	75	0.07	0.01	44	0.11	0.01
UB	8	0.11	0.01	21	0.10	0.01	75	0.12	0.01	44	0.09	0.01
US	8	0.07	0.01	21	0.07	0.01	75	0.08	0.01	44	0.07	0.01
FGM	9	0.21	0.01	27	0.22	0.02	75	0.17	0.01	44	0.22	0.02

maximus, HPM, HTM, HD, and FGM. The second GLM test was only run on *C. guereza*, *H. lar*, and *M. mulatta* for the radius, ulna, biceps brachii, brachialis, supinator, RBB, UB, and US. While *A. geoffroyi* still has a small sample size regarding the humerus, femur, pectoralis major, teres major, deltoid, and gluteus maximus measurements (Table 4), enough data are available for both sexes to run comparisons.

The first GLM test shows that all measurements and ratios are significantly associated with species and sex. Location and body length are associated with some measurements, but not all (Table 5). Species has the greatest effect, followed by sex (Tables B.1-10). Tukey-Kramer's test was run to compare species and determine significant differences among them. Humerus, pectoralis major, teres major, and deltoid measurements follow the hypothesized pattern; *C. guereza* and *M. mulatta* do not differ from one another, whereas *H. lar* and *A. geoffroyi* differ significantly from one another and from *C. guereza* and *M. mulatta*. Femur and gluteus maximus measurements do not follow the hypothesized pattern and will be elaborated upon later (Tables 6-11; Figures 7-12). Not one of the ratios follows the hypothesized pattern and these results will also be discussed further. However, HD does follow the hypothesized pattern regarding *H. lar* (Tables 12-15; Figures 13-16).

Figures 7-16 illustrate the Tukey-Kramer's test results held in Tables 6-15. The figures show the intersection for the mean values of two species and whether or not those species are significantly different (Table C.1). For example, when comparing *A. geoffroyi* and *C. guereza* for humeral length (Figure 7), each species is associated with a specific line. Every intersection indicates the relationship between two species; significance of the relationship is demonstrated by the color of the line (blue = significant, red = not significant). Additionally, the length of the blue or red line represents the 95% confidence interval for the measurement/ratio mean used in the Tukey-Kramer test of each species (Table C.1). Overall, the graph provides an illustration for determining the grouping of and significance among species.

Table 5. Summary table of p-values in the first GLM analysis (*A. geoffroyi*, *C. guereza*, *H. lar*, and *M. mulatta*).

	Species	Sex	Location	Body length
Humerus (H)	<0.0001	<0.0001	0.8260	<0.0001
Femur (F)	<0.0001	<0.0001	0.1160	<0.0001
Pectoralis major (PM)	<0.0001	<0.0001	0.4847	<0.0001
Teres major (TM)	<0.0001	<0.0001	0.4790	0.0007
Deltoid (D)	<0.0001	<0.0001	0.0046	<0.0001
Gluteus maximus (GM)	<0.0001	<0.0001	0.0032	<0.0001
HPM	<0.0001	<0.0001	0.0056	<0.0001
HTM	<0.0001	0.0004	0.7579	0.1201
HD	<0.0001	<0.0001	<0.0001	0.0003
FGM	<0.0001	0.0087	0.0363	0.3409

Table 6. Tukey-Kramer test results (p-values) among species for the humerus.

Humerus

	C. guereza	*H. lar*	*M. mulatta*
A. geoffroyi	<0.0001	<0.0001	<0.0001
C. guereza		<0.0001	0.8522
H. lar			<0.0001

Table 7. Tukey-Kramer test results (p-values) among species for the femur.

Femur

	C. guereza	*H. lar*	*M. mulatta*
A. geoffroyi	0.0110	0.8280	<0.0001
C. guereza		0.0003	0.3213
H. lar			<0.0001

Table 8. Tukey-Kramer test results (p-values) among species for pectoralis major.

Pectoralis major

	C. guereza	*H. lar*	*M. mulatta*
A. geoffroyi	<0.0001	<0.0001	<0.0001
C. guereza		<0.0001	0.9594
H. lar			<0.0001

Table 9. Tukey-Kramer test results (p-values) among species for teres major.

Teres major

	C. guereza	*H. lar*	*M. mulatta*
A. geoffroyi	<0.0001	0.0002	<0.0001
C. guereza		<0.0001	0.4148
H. lar			<0.0001

Table 10. Tukey-Kramer test results (p-values) among species for deltoid.

Deltoid

	C. guereza	*H. lar*	*M. mulatta*
A. geoffroyi	<0.0001	<0.0001	<0.0001
C. guereza		<0.0001	0.7367
H. lar			<0.0001

Table 11. Tukey-Kramer test results (p-values) among species for gluteus maximus.

Gluteus maximus

	C. guereza	*H. lar*	*M. mulatta*
A. geoffroyi	0.2368	<0.0001	<0.0001
C. guereza		0.2688	0.1407
H. lar			0.9986

Table 12. Tukey-Kramer test results (p-values) among species for HPM.

HPM

	C. guereza	*H. lar*	*M. mulatta*
A. geoffroyi	0.8922	0.9766	0.0003
C. guereza		0.9406	0.0292
H. lar			<0.0001

Table 13. Tukey-Kramer test results (p-values) among species for HTM.

HTM

	C. guereza	*H. lar*	*M. mulatta*
A. geoffroyi	0.7095	0.9258	<0.0001
C. guereza		0.8285	0.0043
H. lar			<0.0001

Table 14. Tukey-Kramer test results (p-values) among species for HD.

HD

	C. guereza	*H. lar*	*M. mulatta*
A. geoffroyi	0.3549	<0.0001	0.0251
C. guereza		<0.0001	0.9937
H. lar			<0.0001

Table 15. Tukey-Kramer test results (p-values) among species for FGM.

FGM

	C. guereza	*H. lar*	*M. mulatta*
A. geoffroyi	0.9990	<0.0001	0.8849
C. guereza		<0.0001	0.8200
H. lar			<0.0001

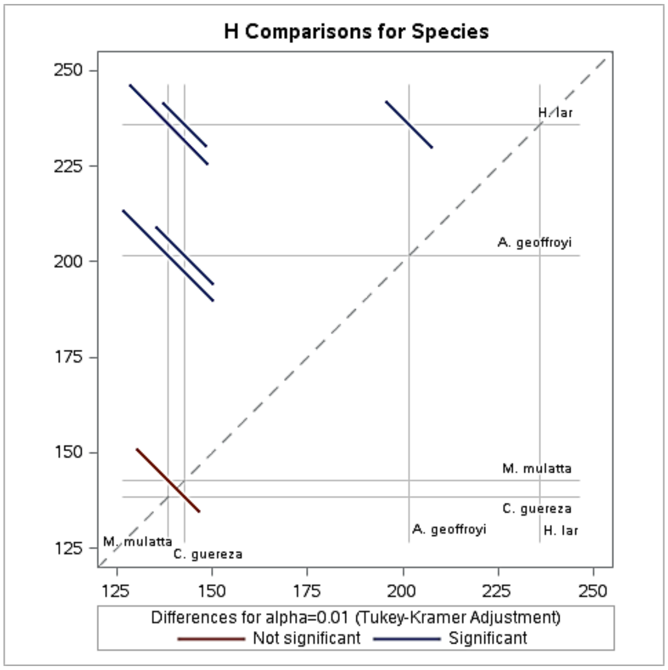

Figure 7. Humerus Tukey-Kramer test illustration (Table 6), x- and y-axes are long bone length. The length of the blue or red line correlates with the 95% confidence interval for the mean value used in the Tukey-Kramer test of each species (Table C.1). The dashed line splits the graph in half.

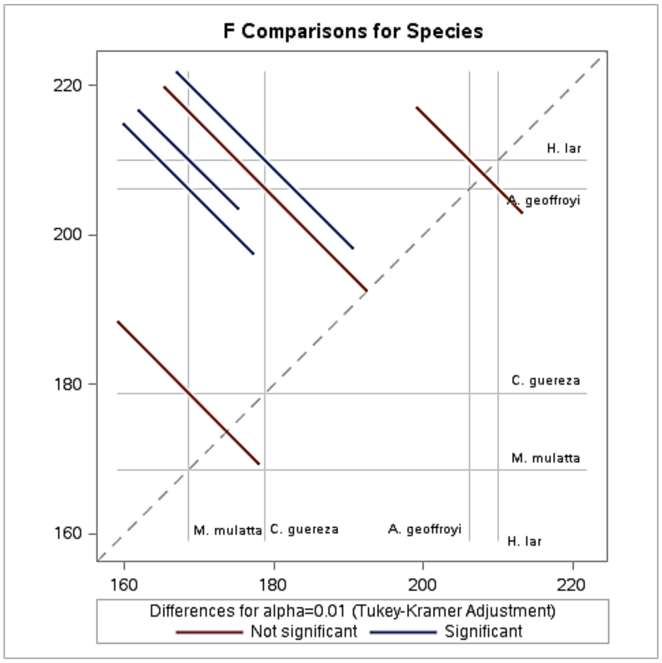

Figure 8. Femur Tukey-Kramer test illustration (Table 7), x- and y-axes are long bone length. The length of the blue or red line correlates with the 95% confidence interval for the mean value used in the Tukey-Kramer test of each species (Table C.1). The dashed line splits the graph in half.

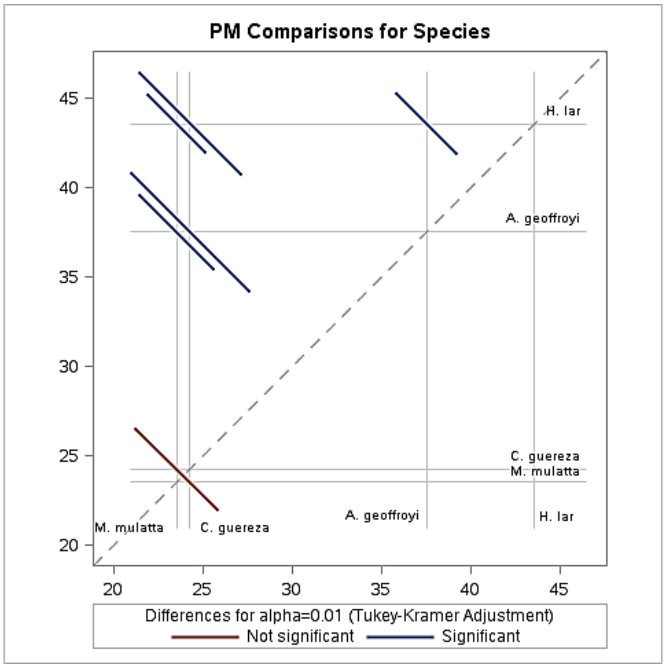

Figure 9. Pectoralis major Tukey-Kramer test illustration (Table 8), x- and y-axes are entheseal length. The length of the blue or red line correlates with the 95% confidence interval for the mean value used in the Tukey-Kramer test of each species (Table C.1). The dashed line splits the graph in half.

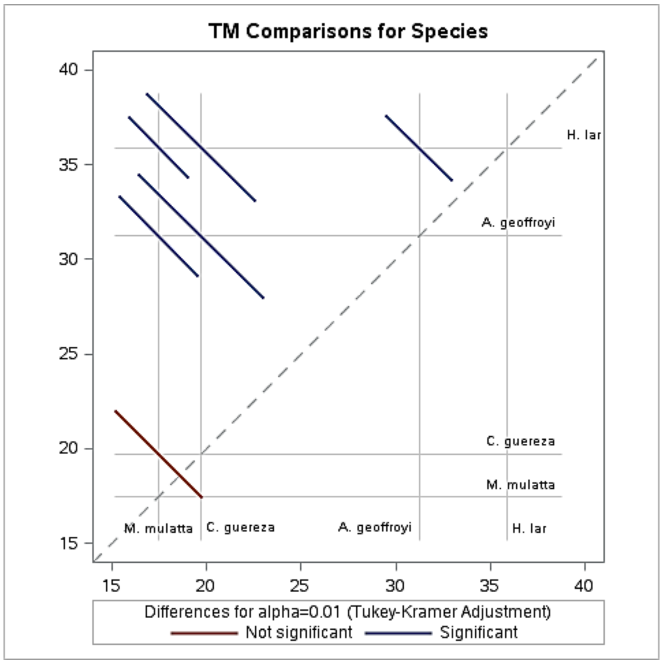

Figure 10. Teres major Tukey-Kramer test illustration (Table 9), x- and y-axes are entheseal length. The length of the blue or red line correlates with the 95% confidence interval for the mean value used in the Tukey-Kramer test of each species (Table C.1). The dashed line splits the graph in half.

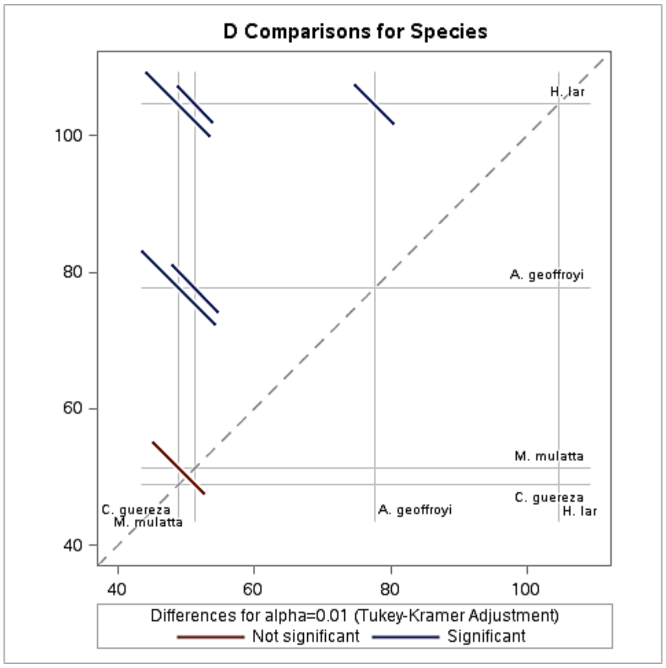

Figure 11. Deltoid Tukey-Kramer test illustration (Table 10), x- and y-axes are entheseal length. The length of the blue or red line correlates with the 95% confidence interval for the mean value used in the Tukey-Kramer test of each species (Table C.1). The dashed line splits the graph in half.

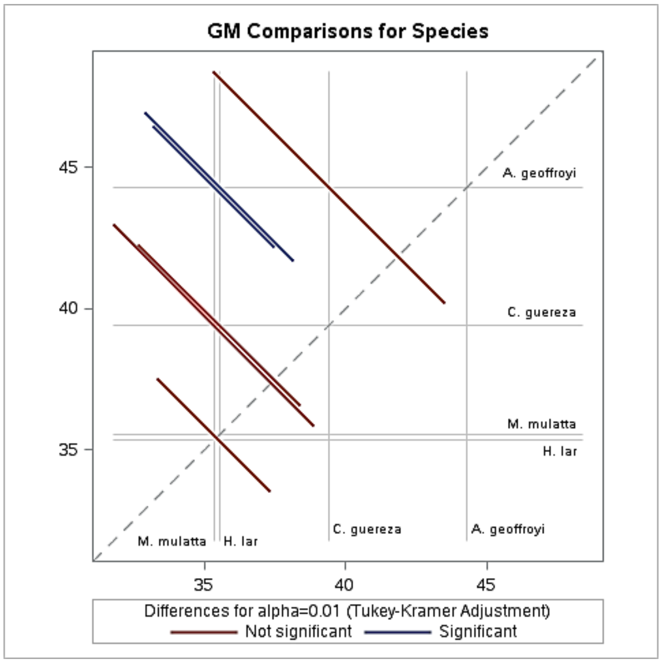

Figure 12. Gluteus maximus Tukey-Kramer test illustration (Table 11), x- and y-axes are entheseal length. The length of the blue or red line correlates with the 95% confidence interval for the mean value used in the Tukey-Kramer test of each species (Table C.1). The dashed line splits the graph in half.

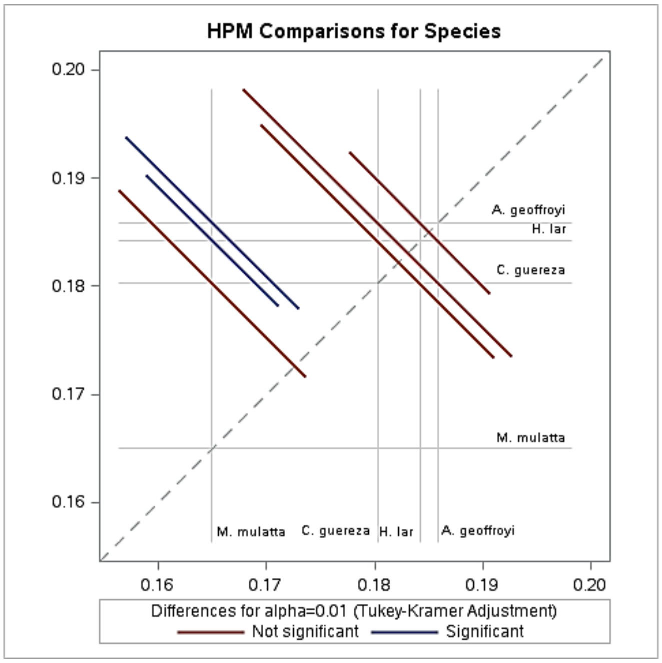

Figure 13. HPM Tukey-Kramer test illustration (Table 12), x- and y-axes are ratio percentage values. The length of the blue or red line correlates with the 95% confidence interval for the mean value used in the Tukey-Kramer test of each species (Table C.1). The dashed line splits the graph in half.

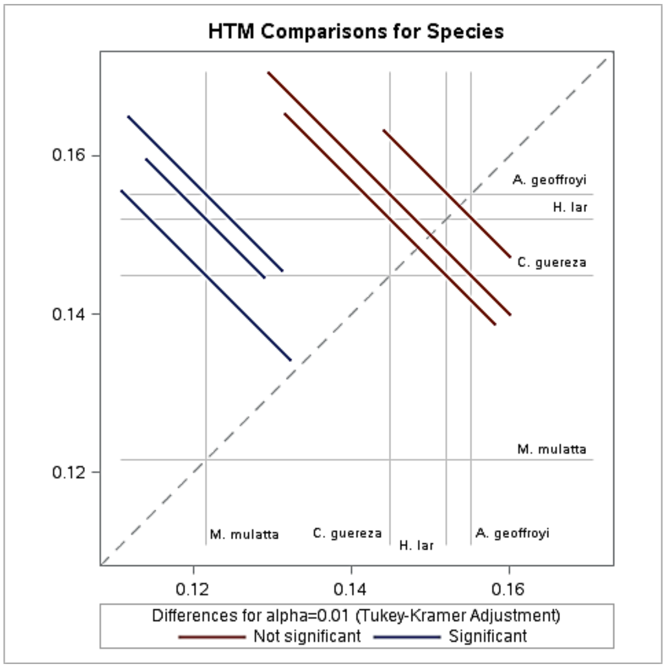

Figure 14. HTM Tukey-Kramer test illustration (Table 13), x- and y-axes are ratio percentage values. The length of the blue or red line correlates with the 95% confidence interval for the mean value used in the Tukey-Kramer test of each species (Table C.1). The dashed line splits the graph in half.

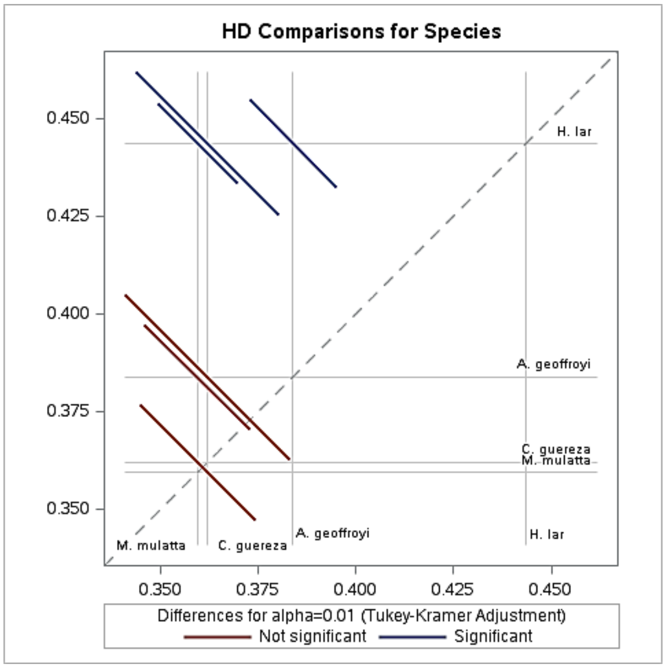

Figure 15. HD Tukey-Kramer test illustration (Table 14), x- and y-axes are ratio percentage values. The length of the blue or red line correlates with the 95% confidence interval for the mean value used in the Tukey-Kramer test of each species (Table C.1). The dashed line splits the graph in half.

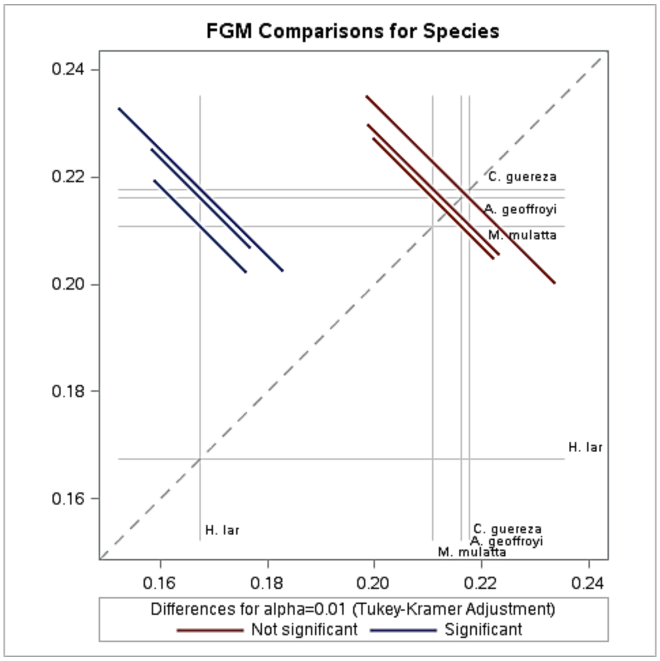

Figure 16. FGM Tukey-Kramer test illustration (Table 15), x- and y-axes are ratio percentage values. The length of the blue or red line correlates with the 95% confidence interval for the mean value used in the Tukey-Kramer test of each species (Table C.1). The dashed line splits the graph in half.

3.3. Second GLM Analysis with Tukey-Kramer’s Tests for Species

The second GLM test shows that all measurements and two of three ratios are associated with species and sex; US by sex closely approaches significance. Species has the greatest effect, followed by sex (Tables B.11-18). Location is associated with three out of eight variables and body length is associated with four variables (Table 16). Tukey-Kramer’s test shows that lengths of the radius and ulna are significantly different across all species (Tables 17-18; Figures 17-18). For the entheseal measurements, brachialis and supinator follow the hypothesized pattern (*C. guereza* and *M. mulatta* are nonsignificantly different, and *H. lar* is significantly different from *C. guereza* and *M. mulatta),* but biceps brachii shows significant differences across all species (Tables 19-21; Figures 19-21). For the ratios, UB follows the hypothesized pattern, but RBB and US do not, grouping together *C. guereza* and *H. lar*, but *C. guereza* also groups with *M. mulatta*. However, *H. lar* does not group with *M. mulatta* for any of the ratios (Tables 22-24, Figures 22-24). All but one result do not follow the hypothesized pattern and will be elaborated upon later. Figures 17-24 are an illustration of the Tukey-Kramer test results held in Tables 17-24 (Table C.2).

Table 16. Summary table of p-values in the second GLM analysis (*C. guereza, H. lar,* and *M. mulatta*).

	Species	Sex	Location	Body length
Radius (R)	<0.0001	<0.0001	0.7356	<0.0001
Ulna (U)	<0.0001	<0.0001	0.4949	<0.0001
Biceps brachii (BB)	<0.0001	<0.0001	<0.0001	0.0002
Brachialis (B)	<0.0001	<0.0001	0.0220	0.0004
Supinator (S)	<0.0001	<0.0001	0.0024	0.0164
RBB	<0.0001	<0.0001	<0.0001	0.0827
UB	<0.0001	0.0004	0.0374	0.6476
US	<0.0001	0.0118	0.0258	0.2585

Table 17. Tukey-Kramer test results (p-values) among species for the radius.

Radius

	H. lar	*M. mulatta*
C. guereza	<0.0001	0.0007
H. lar		<0.0001

Table 18. Tukey-Kramer test results (p-values) among species for the ulna.

Ulna

	H. lar	*M. mulatta*
C. guereza	<0.0001	0.0003
H. lar		<0.0001

Table 19. Tukey-Kramer test results (p-values) among species for biceps brachii.

Biceps brachii

	H. lar	*M. mulatta*
C. guereza	<0.0001	0.0030
H. lar		<0.0001

Table 20. Tukey-Kramer test results (p-values) among species for brachialis.

Brachialis

	H. lar	*M. mulatta*
C. guereza	<0.0001	0.2396
H. lar		<0.0001

Table 21. Tukey-Kramer test results (p-values) among species for supinator.

Supinator

	H. lar	*M. mulatta*
C. guereza	<0.0001	0.1337
H. lar		<0.0001

Table 22. Tukey-Kramer test results (p-values) among species for RBB.

RBB

	H. lar	*M. mulatta*
C. guereza	0.1879	0.0756
H. lar		<0.0001

Table 23. Tukey-Kramer test results (p-values) among species for UB.

UB

	H. lar	*M. mulatta*
C. guereza	<0.0001	0.3022
H. lar		<0.0001

Table 24. Tukey-Kramer test results (p-values) among species for US.

US

	H. lar	*M. mulatta*
C. guereza	0.0286	0.6716
H. lar		<0.0001

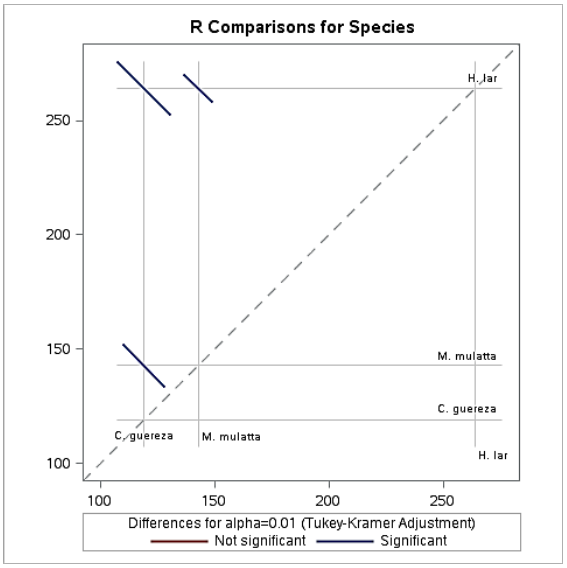

Figure 17. Radius Tukey-Kramer test illustration (Table 17), x- and y-axes are long bone length. The length of the blue or red line correlates with the 95% confidence interval for the mean value used in the Tukey-Kramer test of each species (Table C.2). The dashed line splits the graph in half.

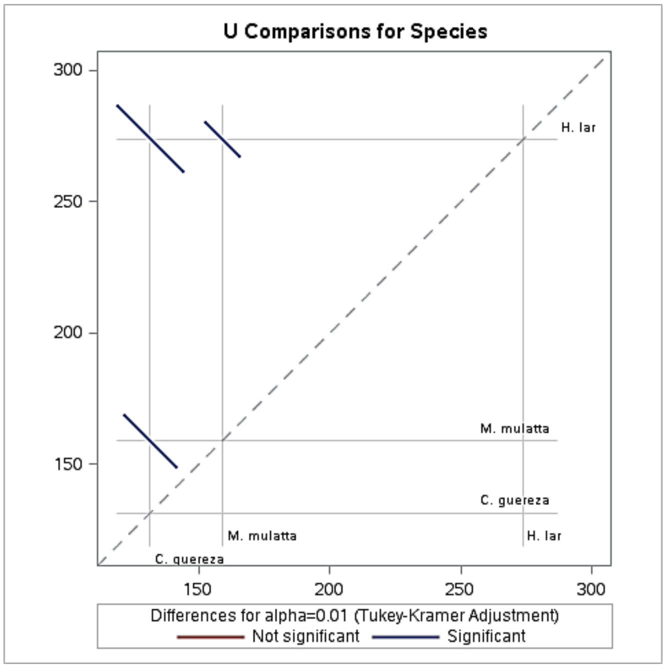

Figure 18. Ulna Tukey-Kramer test illustration (Table 18), x- and y-axes are long bone length. The length of the blue or red line correlates with the 95% confidence interval for the mean value used in the Tukey-Kramer test of each species (Table C.2). The dashed line splits the graph in half.

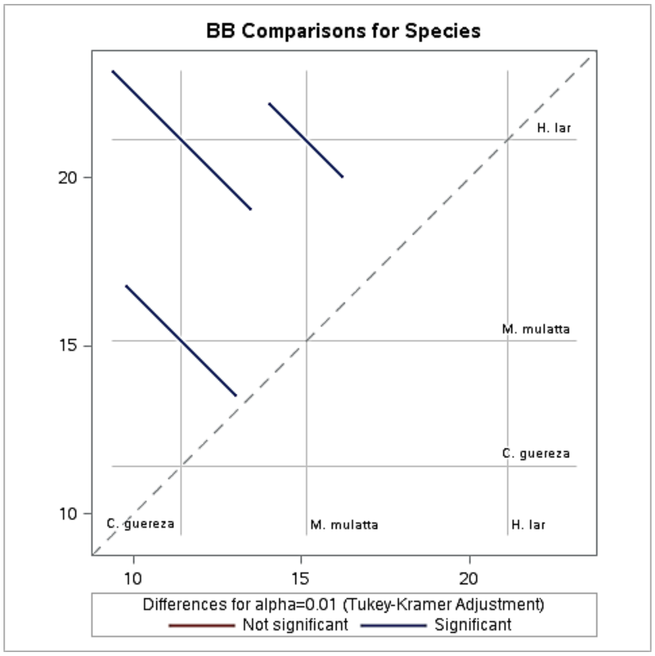

Figure 19. Biceps brachii Tukey-Kramer test illustration (Table 19), x- and y-axes are entheseal length. The length of the blue or red line correlates with the 95% confidence interval for the mean value used in the Tukey-Kramer test of each species (Table C.2). The dashed line splits the graph in half.

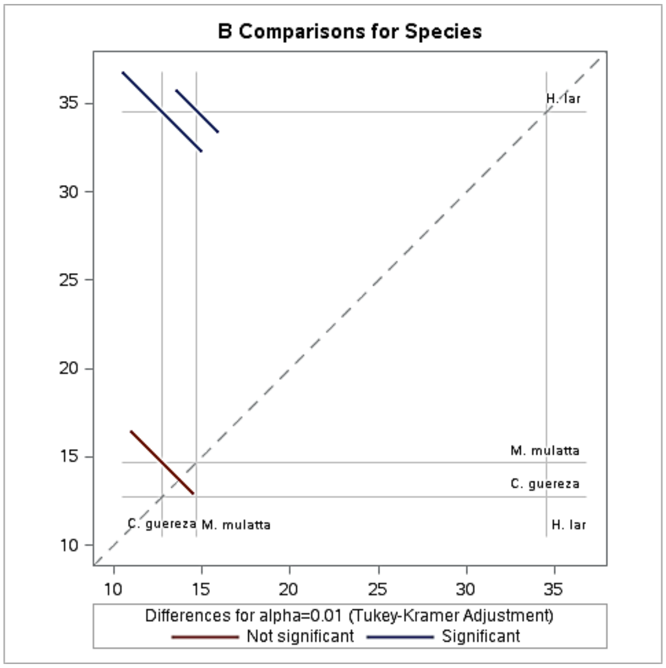

Figure 20. Brachialis Tukey-Kramer test illustration (Table 20), x- and y-axes are entheseal length. The length of the blue or red line correlates with the 95% confidence interval for the mean value used in the Tukey-Kramer test of each species (Table C.2). The dashed line splits the graph in half.

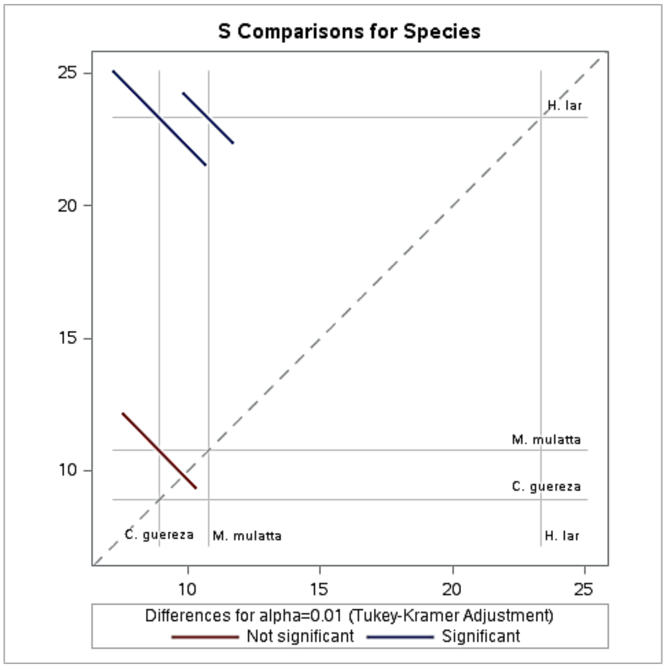

Figure 21. Supinator Tukey-Kramer test illustration (Table 21), x- and y-axes are entheseal length. The length of the blue or red line correlates with the 95% confidence interval for the mean value used in the Tukey-Kramer test of each species (Table C.2). The dashed line splits the graph in half.

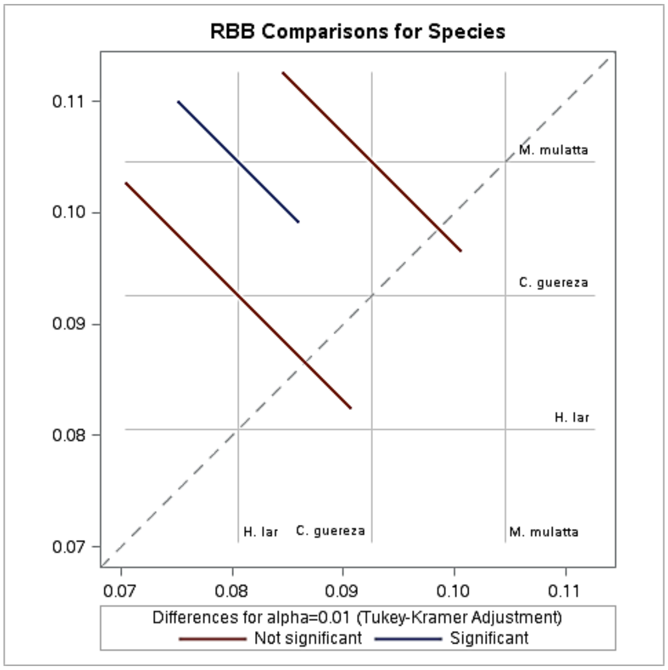

Figure 22. RBB Tukey-Kramer test illustration (Table 22), x- and y-axes are ratio percentage values. The length of the blue or red line correlates with the 95% confidence interval for the mean value used in the Tukey-Kramer test of each species (Table C.2). The dashed line splits the graph in half.

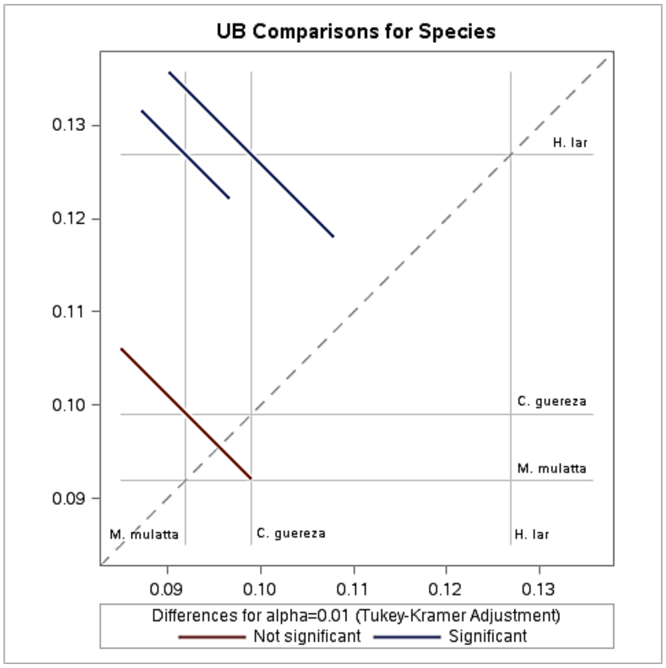

Figure 23. UB Tukey-Kramer test illustration (Table 23), x- and y-axes are ratio percentage values. The length of the blue or red line correlates with the 95% confidence interval for the mean value used in the Tukey-Kramer test of each species (Table C.2). The dashed line splits the graph in half.

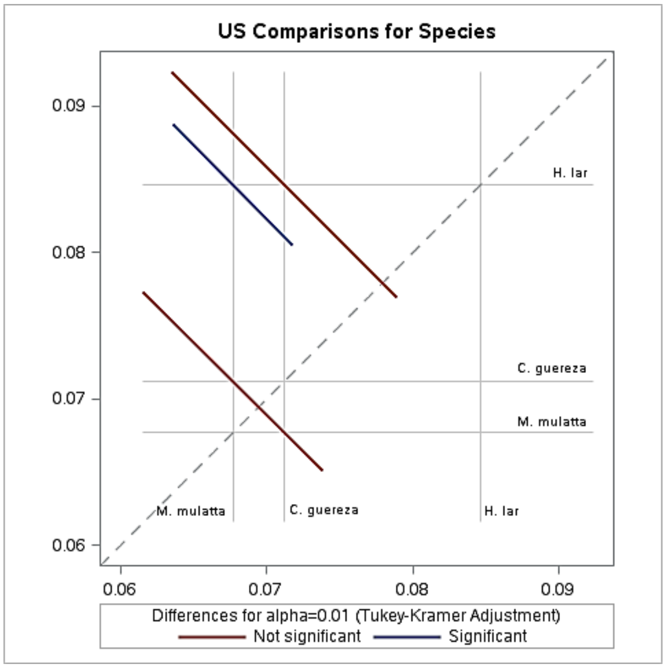

Figure 24. US Tukey-Kramer test illustration (Table 24), x- and y-axes are ratio percentage values. The length of the blue or red line correlates with the 95% confidence interval for the mean value used in the Tukey-Kramer test of each species (Table C.2). The dashed line splits the graph in half.

3.4. Student's T-tests

Student's t-tests were run comparing sex within species since the GLM showed sex is significantly associated with length of long bones and absolute and relative length of entheses. T-tests were only run for *C. guereza, H. lar*, and *M. mulatta* due to insufficient sample size for *A. geoffroyi* (Tables 2 and 3). Results for all long bone and entheseal measurements – except for supinator in *C. guereza* – show significant differences for *C. guereza* and *M. mulatta*, with males larger than females. Regarding the ratios, *C. guereza* shows no significant differences and *M. mulatta* shows differences for HPM, HD, and RBB, with males larger than females (Tables 2 and 3). *H. lar* shows no significant differences for any measurement and ratio (Table 25).

Table 25. T-test p-values from comparing sex within species.

	Colobus guereza	*Hylobates lar*	*Macaca mulatta*
Humerus	<0.0001	0.1207	<0.0001
Radius	<0.0001	0.4128	<0.0001
Ulna	<0.0001	0.4723	<0.0001
Femur	0.0002	0.4451	<0.0001
Pectoralis major	0.0010	0.0305	<0.0001
Teres major	0.0056	0.0220	<0.0001
Deltoid	0.0041	0.1307	<0.0001
Biceps brachii	0.0003	0.1408	<0.0001
Brachialis	0.0003	0.0158	<0.0001
Supinator	0.0265	0.0503	<0.0001
Gluteus maximus	0.0002	0.2994	<0.0001
HPM	0.0240	0.0469	<0.0001
HTM	0.2269	0.0648	0.0139
HD	0.4097	0.9738	0.0002
RBB	0.0191	0.2289	0.0004
UB	0.0335	0.0227	0.0642
US	0.3856	0.0644	0.1914
FGM	0.0561	0.4311	0.1905

Student’s t-test was also run on specific measurements for location since the GLM showed location was significantly associated with several measurements. Tests were run on deltoid, HPM, and HD for *C. guereza* and biceps brachii, supinator, HPM, RBB, and US for *H. lar*. Only these measurements were tested because the species by location Tukey-Kramer’s tests identified which species were the cause of the significant result ($p < 0.01$) seen in the GLM results (Tables 5, 16, D.1-7). A Student’s t-test was not run on gluteus maximus because the Tukey-Kramer test indicated no significant differences within species (Table D.8). Results show significant differences for *C. guereza* across deltoid, HD, and HPM but *H. lar* shows no significant differences (Table 26). However, the Tukey-Kramer test indicates significant differences for *H. lar*; this discrepancy in results between the Student’s t-test and Tukey-Kramer test will be discussed later. Table 27 provides a summary table of all the Tukey-Kramer’s species test results in this study (Tables 6-15, 17-24). This table is added for ease of access for the reader when results are considered in the Discussion section.

Table 26. T-test p-values by location for specific measurements for *C. guereza* and *H. lar*.

	Colobus guereza	*Hylobates lar*
Deltoid	<0.0001	
HD	<0.0001	
HPM	<0.0001	0.0540
Biceps brachii		0.1698
Supinator		0.1235
RBB		0.1731
US		0.1268

Table 27. Summary table for all Tukey-Kramer test results (first and second GLM) in comparison of species. * indicates a significant difference between species, blank space indicates no significant difference, and shaded area indicates not enough information for comparison. Ag = *A. geoffroyi*, Cg = *C. guereza*, Hl = *H. lar*, Mm = *M. mulatta*.

	Ag:Cg	Ag:Hl	Ag:Mm	Cg:Hl	Cg:Mm	Hl:Mm
Humerus	*	*	*	*		*
Radius	■	■	■	*	*	*
Ulna	■	■	■	*	*	*
Femur			*	*		*
Pectoralis major	*	*	*	*		*
Teres major	*	*	*	*		*
Deltoid	*	*	*	*		*
Biceps brachii	■	■	■	*	*	*
Brachialis	■	■	■	*		*
Supinator	■	■	■	*		*
Gluteus maximus		*	*			
HPM			*			*
HTM			*		*	*
HD		*		*		*
RBB	■	■	■			*
UB	■	■	■	*		*
US	■	■	■			*
FGM		*		*		*

Chapter 4. Discussion

4.1. GLM and Tukey-Kramer's Test Results for Species

In general, the entheseal comparisons among species follow the hypothesized pattern for the forelimb, which is that *H. lar* will have the largest measurements, *C. guereza* and *M. mulatta* will group together and have the smallest measurements, and *A. geoffroyi* will be intermediate between the two groups (Tables 27, C.1, C.2). The exception to the hypothesized pattern for entheses is biceps brachii, for which *C. guereza*, *H. lar*, and *M. mulatta* are all significantly different from one another. However, the results for the radius and ulna were unexpected (Table 27). *Colobus guereza*, *H. lar*, and *M. mulatta* are all significantly different from one another, when *C. guereza* and *M. mulatta* were expected to group together based on the hypothesis of how locomotion affects limb structure. The means for lengths of the radius and ulna are similar for *C. guereza* and *M. mulatta*, but the GLM shows that body length is significantly associated with the measurements (Table 16). Therefore, body length is the most likely cause for a significant difference between *C. guereza* and *M. mulatta* since *C. guereza* is larger than *M. mulatta* – although there are not enough data for body length in the *M. mulatta* specimens used in this study because only one specimen out of 44 had body length data available at the collection (Tables 2-4, C.2). However, the radius, ulna, and biceps brachii measurements were the only measurements that did not follow the hypothesized pattern. The GLM indicated that all forelimb measurements – except for supinator – are significantly associated with body length (Tables 5 and 16). If body length does have a significant association with the measurements and is associated with differences between species, why would this cause only three out of nine measurements to not follow the hypothesized pattern and not all of them? Body length may have a greater impact on the radius, ulna, and biceps brachii measurements compared to the other measurements, but this is outside the scope of this article.

The results for the hindlimb, on the other hand, were all unanticipated (Tables 27 and C.1). The results for the femur indicate that *A. geoffroyi* is only significantly different from *M. mulatta*. Therefore, *A. geoffroyi* groups with both *C. guereza* and *H. lar*. While not hypothesized, the result indicates that *A. geoffroyi* groups with both quadrupeds and brachiators. Thus, the eclectic locomotion could be the reason for grouping *A. geoffroyi* with both *C. guereza* and *H. lar*. For the gluteus maximus measurement, the only significant differences seen are for *A. geoffroyi* with *H. lar* and *M. mulatta*. The hypothesized pattern was that *H. lar* would have a shorter gluteus maximus enthesis and not group with *C. guereza* and *M. mulatta* due to *H. lar* not using the hindlimb as frequently in locomotion, but instead all three group together. This result can be attributed to *H. lar*'s femur; since *H. lar* has a longer femur, the enthesis for gluteus maximus will be longer. The ratio provides an explanation for the unanticipated femur and gluteus maximus results for *H. lar,* which will be discussed next.

Miller (1932) states that brachiators like *H. lar* will have the longest bone length in the forelimb, and quadrupedal primates like *C. guereza* and *M. mulatta*, which are mainly walkers and/or runners, will have the shortest bone length in comparison to brachiators. Animals that perform a variety of locomotor types, like *A. geoffroyi*, will be intermediate between those two groups. The reason for these differences is because the way in which the muscles are used varies between locomotor type. Brachiators have longer forelimbs, quadrupedal primates have shorter forelimbs which are closer to the length of their hindlimbs, and intermediate locomotors have intermediate forelimb length between brachiators and quadrupeds because they use a combination of both locomotor types. Fleagle *et al.* (1981) also discovered that muscle responses differ between locomotor types. Thus, the differences among the radius, ulna, femur, biceps brachii, and gluteus maximus lengths can be due to an overlap in locomotor type and muscle response. *Macaca mulatta* and *C. guereza* are both quadrupeds, but they can differ in their form of quadrupedalism depending on the environment and both engage infrequently in other locomotor types. *Colobus guereza* also performs leaping and rare arm-swinging, while its quadrupedal movement generally consists of rapid leaps and bounds (Mittermeier and Fleagle, 1976). *Macaca mulatta* can be a predominantly arboreal or terrestrial quadruped, depending on the environment, along with infrequent bipedalism, climbing, and leaping which would cause variations in locomotion (Demes *et al.*, 2001; Wells and Turnquist, 2001). Therefore, their skeletal and muscular structure would slightly differ even though the general characterization of locomotion is similar (Burr *et al*., 1989; Rodman, 1979). However, this does not explain why *H. lar* is similar to *C. guereza* and *M. mulatta* in the gluteus maximus entheseal length since their locomotor forms differ significantly. *Hylobates lar* has longer forelimbs and hindlimbs, so this could account for part of the unexpected results. Since *H. lar* has very long forelimbs, longer hindlimbs are needed for balance when walking bipedally amongst tree branches or during less frequent terrestrial bipedalism and quadrupedalism (Vereecke *et al.*, 2006). Therefore, the femoral and gluteus maximus measurements do not follow the hypothesized pattern since *H. lar* has a longer femur than *C. guereza* and *M. mulatta*. The gluteus maximus/femur ratio (FGM) provides evidence for gluteus maximus entheseal length being influenced by femoral length more than locomotor type for *H. lar*. The Tukey-Kramer test for FGM indicates significant differences for *H. lar* with *C. guereza* and *M. mulatta* while for gluteus maximus alone *H. lar*, *C. guereza*, and *M. mulatta* show no significant differences (Tables 2-4, 27, C.1).

Larger animals need larger muscles and bones; thus, body length has been posited as an influence on entheseal length and/or rugosity. Several studies have shown that body length is associated with entheseal length and/or rugosity in humans and non-human primates (Godde and Taylor, 2011; Nolte and Wilczak, 2013; Weiss, 2003, 2004, 2007; Weiss *et al.*, 2010), but body length has also been shown to not influence entheseal length and/or rugosity (Niinimäki and Sotos, 2012). The results of this study mirror the inconsistencies of previous entheseal research regarding the influence of body size. Due to these issues, the entheseal/long bone ratio was posited as a possible solution to determine the influence of locomotor type on entheseal and long bone length. The ratio is meant to indicate the percentage of long bone length attributed to the specific muscle enthesis, which is interpreted here as an indicator of use/importance related to locomotor type.

While the entheseal and long bone measurement results generally followed the hypothesized pattern, the results from the ratios did not. The logical line of thinking was that since the entheseal and long bone measurements followed the hypothesized pattern, the ratio would too. However, only one of the seven ratios followed the hypothesized pattern: UB (Table 27). The humerus, pectoralis major, and teres major comparison found that *C. guereza* and *M. mulatta* grouped together, *A. geoffroyi* was intermediate, and *H. lar* was separate and had larger measurements than the other three species, but the HPM and HTM ratios did not follow the same pattern. For both ratios, *A. geoffroyi*, *C. guereza*, and *H. lar* group together and are significantly different from *M. mulatta*. HD also differs from the humerus and deltoid measurements, but it is closer to the hypothesized pattern than HPM and HTM (Table 27). The only difference for HD is that *A. geoffroyi* groups with *C. guereza* and *M. mulatta* instead of being intermediate. One explanation for this could be that the deltoid muscle is more important in brachiation compared to other locomotor types, so while the overall entheseal measurements follow the hypothesized pattern, the percentage of long bone length occupied causes *A. geoffroyi* to group with *C. guereza* and *M. mulatta* instead of being intermediate. Another explanation could be that the results regarding *A. geoffroyi* are skewed because of sample size. Without *A. geoffroyi*, HD follows the hypothesized pattern (Table E.1). However, the results for HPM and HTM would still not follow the hypothesized pattern.

Results show that one forearm ratio conforms with the hypothesis, while the other two do not. For RBB, *C. guereza* grouped with *H. lar* and *M. mulatta*, while *H. lar* was significantly different from *M. mulatta* (Table 27). Unlike the humeral measurements, the radius and biceps brachii did not follow the hypothesized pattern; instead, *C. guereza* and *M. mulatta* are significantly different for both measurements. RBB also differs from the hypothesized pattern but differs due to no significant difference between *C. guereza* and *H. lar*. If locomotion is important in determining long bone and muscle length, then *H. lar* should not be close to grouping with *C. guereza*. HPM, HTM, and US have similar results to RBB, grouping together *C. guereza* and *H. lar*, although HTM also shows a significant difference between *C. guereza* and *M. mulatta* (Table 27). However, as a brachiator *H. lar* should be different from the quadruped *C. guereza* like it is with *M. mulatta*.

Since the femur and gluteus maximus measurement results were unanticipated, the result for the gluteus maximus/femur ratio is similarly unanticipated. For FGM, *A. geoffroyi* groups with *C. guereza* and *M. mulatta* while all three are significantly different from *H. lar* (Table 27). When thinking of the hypothesized pattern, this result is more understandable compared to the other ratios since *A. geoffroyi* frequently engages in quadrupedal locomotion. However, *A. geoffroyi* engages in a variety of locomotor types, so the ratio not reflecting that outcome is surprising. Like HD, part of the problem for FGM could be caused by the sample size of *A. geoffroyi*. If *A. geoffroyi* is removed, then FGM matches the hypothesized pattern (Table E.2). Thus, three out of seven ratios may match what was hypothesized, but that is still less than half that are different from the original hypothesized pattern.

4.2. Student's T-test Results for Sex

Regarding sex, *C. guereza* and *M. mulatta* are polygamous and sexually dimorphic in the long bone and entheseal lengths in this study, while *H. lar* is monogamous with no sexual dimorphism (Table 25). For *C. guereza*, 10 out of 11 measurements were significantly different between the sexes while all 11 measurements were significantly different for *M. mulatta*. As with comparison between the species, the ratios do not match the results of the long bones and entheses. For *C. guereza*, none shows significant differences while *M. mulatta* only had two out of seven with significant differences. For all 18 measurements, *H. lar* had no significant differences. These results are similar to those of Milella (2014), although a different form of entheseal measurement was used in that study. Milella found that entheseal robusticity was an indicator of sexual dimorphism in modern humans, *Gorilla*, and *Pan*. Along with this, entheseal morphology was partially linked to life stages, where older individuals had more robust entheses and differences between the sexes were greater in older individuals. Although this study does not account for age, entheseal length is shown to be sexually dimorphic in *C. guereza* and *M. mulatta*.

The discrepancy for sexual differences between entheseal and long bone lengths with their ratios can be explained by similarities in locomotion. While the overall measurements differ due to sexual dimorphism, the ratios do not. Since the ratio is an indicator of the percentage of long bone length the enthesis covers in a straight line, that percentage should be the same between similar locomotors. As earlier results have indicated, that is not always the case, but that is most likely because the locomotor repertoire between species like *C. guereza* and *M. mulatta* is similar but not identical. However, for comparison within species, their locomotion will be the same, and thus significant differences will not be seen between the sexes for the ratios.

Regarding paleoanthropology, the Student's t-test results for sex indicate that entheseal length can be used as an indicator for sex. However, there are challenges associated with this, such as understanding whether a fossil species is sexually dimorphic or monomorphic in long bone length. While these results favor the use of entheseal length as an indicator for sex, more research must first be carried out before this method can be used for sex estimation. Due to these issues, sexing an individual through entheseal length would not be the definitive answer for the sex of a specimen, but rather, a supplementary analysis to provide another estimate to the overall conclusion.

4.3. Student's T-test and Tukey-Kramer's Test Results for Location

The final variable for discussion is location, which overall did not have a significant association with the measurements (Tables 5 and 16). However, a few measurements were significantly different between captive and wild caught specimens of *C. guereza*: deltoid, HD, and HPM (Tables 26, D.1-3). This is a difficult result to explain because only these three measurements were significantly affected, and only for this species. The GLM also suggested that *H. lar* had significant differences for location, but the Student's t-test results indicate that there was no significant difference (Tables 26, D.4-7). The discrepancy in results regarding the Student's t-test and Tukey-Kramer's test is because the Tukey-Kramer's test is not a straight comparison between captive and wild caught specimens of *C. guereza* or *H. lar,* but instead is affected by other variables like body length. While an important variable, body length is not necessary when testing within a species. Due to this, the Student's t-test is a more accurate method for testing differences in location. Another interesting result is that the GLM found location to be significantly associated with the gluteus maximus measurements, but the Tukey-Kramer test revealed no significant differences within species (Tables 5, D.8). This result suggests that location is associated with gluteus maximus when all species are combined, but not within each individual species.

Since only three measurements within one species were significantly associated with location, the location results for *C. guereza* did not significantly alter the overall results because the deltoid and HD results follow the hypothesized pattern. Therefore, the only Tukey-Kramer species test result that could have been influenced by location is HPM. Even though location was not a factor in this study, the results are intriguing and possibly a more in-depth study comparing captive and wild caught primates would shed some light on what would cause the few differences seen here. Previous research has demonstrated differences between captive and wild caught specimens of the same species relating to behavior or locomotion (Isler and Thorpe, 2003; Sarmiento, 1986; Veasey *et al.*, 1996), but this study has shown that differences between captive and wild caught specimens do not necessarily translate to entheseal changes. Therefore, slight differences in locomotor type between captive and wild caught specimens are not expected to cause great differences in entheseal length. Perhaps no difference between captive and wild caught specimens implies that entheseal length is genetically determined, instead of behaviorally through locomotion. While intriguing, this study has shown that entheseal length does differ due to specific locomotor types, and not locomotion in general. Thus, behavior (i.e., locomotor type) – and possibly genetics – play a role in entheseal length but determining the genetic component of entheseal length is outside the scope of this study.

Zumwalt (2006) provides evidence that specific locomotor type influences entheseal length. This study examined how endurance exercise affects entheseal morphology in sheep and found that it does not. The method used was to place one group on a treadmill each day over a few months and compare them to a control group that did not perform any variation to their natural locomotor type. The results indicating no change in entheseal morphology match the results found in this study when comparing sex and location. The locomotor type of the sheep did not change, just the intensity and frequency of locomotion. Since there was no variation in locomotor type between the two groups – similar to how males and females of the same species will share similar locomotor types – entheseal morphology did not change. Thus, the results of Zumwalt (2006) suggest that intensity of locomotion is not the driving force behind entheseal changes. In this sense, if locomotion is causing entheseal changes, those changes are caused by different locomotor types and not intensity of locomotion.

Chapter 5. Conclusion

The goal of this project was to determine if locomotion is associated with the ratio of entheseal length divided by long bone length, and if this ratio could be used to differentiate or group together species by locomotor type. This aim was achieved through an analysis of entheseal length, long bone length, and the respective ratio. As secondary analyses, sex and location were tested to determine if differences could also be seen for those variables. Taking everything into account, locomotion is related with entheseal length and long bone length, but not necessarily the ratio. Other factors not accounted for in this study, such as age (Milella, 2014; Milella *et al.*, 2012; Villotte and Knüsel, 2012), may play a role. Although entheseal ratios are not as suggestive of locomotion as hypothesized, overall entheseal length is indicative of sex in sexually dimorphic species and can be used as an indicator of sex for paleoanthropological specimens and non-human primates. This study has also shown that for this sample, location is associated with only a few measurements for one species – *C. guereza*. Therefore, future entheseal studies can combine captive and wild caught specimens to increase sample size. Overall, this project has shown that locomotion is associated with entheseal length, but long bone length and the entheseal/long bone ratio are not. Future research can expand upon this work by incorporating more species, specimens, and methodologies to reach a better understanding of the relationship between entheses and locomotion.

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Appendix A. Correlation Results Tables

Results of correlation analyses run comparing body length, body mass, and left and right-side measurements. Analyses only included data gathered at the collections for body length and body mass. Abbreviations: R = right, L = left, hum = humerus, pec major = pectoralis major, bi brachii = biceps brachii, brach = brachialis, sup = supinator, glut max = gluteus maximus.

Table A.1. *Ateles geoffroyi* correlation results among body length, body mass, and left and right side entheseal and long bone lengths. No comparison among body length and body mass with any measurement because not enough information was available. First row for each category is the correlation value, second row is the p-value indicating significance.

	R hum	R pec major	R deltoid	R teres major	R radius	R bi brachii	R ulna	R brach	R sup	R femur	R glut max
L hum	0.99										
	<0.0001										
L pec major		0.96									
		<0.0001									
L deltoid			0.99								
			<0.0001								
L teres major				0.89							
				0.0002							
L radius					0.98						
					<0.0001						
L bi brachii						0.71					
						0.0099					
L ulna							0.98				
							<0.0001				
(Table cont’d)											

	R hum	R pec major	R deltoid	R teres major	R radius	R bi brachii	R ulna	R brach	R sup	R femur	R glut max
L brach								0.96			
								<0.0001			
L sup									0.79		
									0.0024		
L femur										0.99	
										<0.0001	
L glut max											0.97
											<0.0001

Table A.2. *Colobus guereza* correlation results among body length, body mass, and left and right side entheseal and long bone lengths. First row for each category is the correlation value, second row is the p-value indicating significance.

	Correlation value (first row)												
	Probability (p) value (second row)												
	Body length	Body mass	R hum	R pec major	R deltoid	R teres major	R radius	R bi brachii	R ulna	R brach	R sup	R femur	R glut max
Body length	1.00	0.75	0.66	0.81	0.67	0.70	0.86	0.51	0.90	0.81	-0.46	0.73	0.82
		0.0082	0.0105	0.0005	0.0090	0.0049	0.0287	0.3005	0.0135	0.0528	0.3617	0.0029	0.0003
Body mass	0.75	1.00	0.54	0.58	0.51	0.39	0.77	0.86	0.73	0.55	-0.81	0.71	0.53
	0.0082		0.0885	0.0604	0.1055	0.2333	0.2274	0.1380	0.2662	0.4529	0.1929	0.0134	0.0900
L hum	0.61	0.51	0.99										
	0.0198	0.1076	< 0.0001										
L pec major	0.82	0.71		0.98									
	0.0003	0.0147		< 0.0001									

(Table cont'd)

	Body length	Body mass	R hum	R pec major	R deltoid	R teres major	R radius	R bi brachii	R ulna	R brach	R sup	R femur	R glut max
L deltoid	0.62	0.46			0.95								
	0.0171	0.1512			< 0.0001								
L teres major	0.35	0.46				0.87							
	0.2156	0.1518				< 0.0001							
L radius	0.89	0.8					0.99						
	0.0184	0.2013					< 0.0001						
L bi brachii	0.79	0.81						0.89					
	0.0591	0.1925						< 0.0001					
L ulna	0.92	0.79							0.99				
	0.0100	0.2065							< 0.0001				
L brach	0.66	0.75								0.88			
	0.1506	0.2503								< 0.0001			
L sup	-0.54	-0.81									0.95		
	0.2675	0.1856									< 0.0001		
L femur	0.77	0.68										0.99	
	0.0014	0.0207										< 0.0001	
L glut max	0.78	0.52											0.97
	0.0010	0.1029											< 0.0001

Table A.3. *Hylobates lar* correlation results among body length, body mass, and left and right side entheseal and long bone lengths. First row for each category is the correlation value, second row is the p-value indicating significance.

Correlation value (first row)													
Probability (p) value (second row)													
	Body length	Body mass	R hum	R pec major	R deltoid	R teres major	R radius	R bi brachii	R ulna	R brach	R sup	R femur	R glut max
Body length	1.00	0.53	0.38	0.39	0.42	0.27	0.51	0.31	0.51	0.27	0.48	0.45	0.34
		< 0.0001	0.0031	0.0020	0.0008	0.0414	< 0.0001	0.0142	< 0.0001	0.0360	0.0001	0.0003	0.0080
Body mass	0.53	1.00	0.39	0.44	0.42	0.35	0.37	0.43	0.42	0.41	0.57	0.50	0.56
	< 0.0001		0.0029	0.0006	0.0014	0.0092	0.0038	0.0006	0.0010	0.0010	< 0.0001	< 0.0001	< 0.0001
L hum	0.36	0.37	0.97										
	0.0045	0.0051	< 0.0001										
L pec major	0.38	0.42		0.97									
	0.0027	0.0013		< 0.0001									
L deltoid	0.40	0.32			0.95								
	0.0019	0.0185			< 0.0001								
L teres major	0.34	0.31				0.90							
	0.0078	0.0184				< 0.0001							
L radius	0.51	0.42					0.98						
	< 0.0001	0.0011					< 0.0001						

(Table cont'd)

	Body length	Body mass	R hum	R pec major	R deltoid	R teres major	R radius	R bi brachii	R ulna	R brach	R sup	R femur	R glut max
L bi brachii	0.27	0.40						0.96					
	0.0375	0.0020						< 0.0001					
L ulna	0.52	0.37							0.98				
	< 0.0001	0.0038							< 0.0001				
L brach	0.28	0.39								0.94			
	0.0243	0.0021								< 0.0001			
L sup	0.41	0.50									0.92		
	0.0008	< 0.0001									< 0.0001		
L femur	0.48	0.48										0.98	
	0.0001	0.0002										< 0.0001	
L glut max	0.32	0.48											0.91
	0.0128	0.0002											< 0.0001

Table A.4. *Macaca mulatta* correlation results among body length, body mass, and left and right side entheseal and long bone lengths. No comparison among body length and body mass with any measurement because not enough information was available. First row for each category is the correlation value, second row is the p-value indicating significance.

	R hum	R pec major	R deltoid	R teres major	R radius	R bi brachii	R ulna	R brach	R sup	R femur	R glut max
L hum	0.99										
	<0.0001										
(Table cont'd)											

	R hum	R pec major	R deltoid	R teres major	R radius	R bi brachii	R ulna	R brach	R sup	R femur	R glut max
L pec major		0.96									
		<0.0001									
L deltoid			0.99								
			<0.0001								
L teres major				0.93							
				<0.0001							
L radius					0.99						
					<0.0001						
L bi brachii						0.94					
						<0.0001					
L ulna							0.99				
							<0.0001				
L brach								0.85			
								<0.0001			
L sup									0.92		
									<0.0001		
L femur										0.99	
										<0.0001	
L glut max											0.97
											<0.0001

Appendix B. GLM Results

First and second GLM analysis output for all measurements and ratios. Corresponding tables are in Chapter 3: Results Tables 5 (first GLM analysis) and 16 (second GLM analysis). These output tables indicate significance of species, sex, location, and body length for all measurements/ratios. The larger the Type I SS number, the greater the effect that variable has on the measurement/ratio.

Table B.1. Humerus

Variable	DF	Type I SS	Mean Square	F Value	P-value
Species	3	273415.88	91138.6252	1309.00	<0.0001
Sex	1	2533.63	2533.6294	36.39	<0.0001
Location	1	3.38	3.3776	0.05	0.8260
Body Length	1	1753.69	1753.6882	25.18	<0.0001

Table B.2. Femur

Variable	DF	Type I SS	Mean Square	F Value	P-value
Species	3	25319.04	8439.6815	91.89	<0.0001
Sex	1	3745.12	3745.1221	40.78	<0.0001
Location	1	229.75	229.7509	2.50	0.1160
Body Length	1	2562.40	2562.4029	27.90	<0.0001

Table B.3. Pectoralis major

Variable	DF	Type I SS	Mean Square	F Value	P-value
Species	3	13941.14	4647.0466	845.50	<0.0001
Sex	1	387.89	387.8911	70.57	<0.0001
Location	1	2.70	2.6982	0.49	0.4847
Body Length	1	177.15	177.1486	32.23	<0.0001

Table B.4. Teres major

Variable	DF	Type I SS	Mean Square	F Value	P-value
Species	3	9888.43	3296.1436	612.51	<0.0001
Sex	1	188.84	188.8374	35.09	<0.0001
Location	1	2.71	2.7122	0.50	0.4790
Body Length	1	65.16	65.1551	12.10	0.0007

Table B.5. Deltoid

Variable	DF	Type I SS	Mean Square	F Value	P-value
Species	3	86745.57	28915.1900	1983.12	<0.0001
Sex	1	799.11	799.1191	54.81	<0.0001
Location	1	120.90	120.9004	8.29	0.0046
Body Length	1	462.30	462.3035	31.71	<0.0001

Table B.6. Gluteus maximus

Variable	DF	Type I SS	Mean Square	F Value	P-value
Species	3	1916.06	638.6892	77.08	<0.0001
Sex	1	371.74	371.7466	44.87	<0.0001
Location	1	74.44	74.4412	8.98	0.0032
Body Length	1	171.99	171.9988	20.76	<0.0001

Table B.7. HPM

Variable	DF	Type I SS	Mean Square	F Value	P-value
Species	3	0.0258	0.0086	113.45	<0.0001
Sex	1	0.0041	0.0041	54.36	<0.0001
Location	1	0.0006	0.0006	7.93	0.0056
Body Length	1	0.0023	0.0023	29.88	<0.0001

Table B.8. HTM

Variable	DF	Type I SS	Mean Square	F Value	P-value
Species	3	0.02919	0.00973	83.54	<0.0001
Sex	1	0.00151	0.00151	12.99	0.0004
Location	1	0.00001	0.00001	0.10	0.7579
Body Length	1	0.00028	0.00028	2.45	0.1201

Table B.9. HD

Variable	DF	Type I SS	Mean Square	F Value	P-value
Species	3	0.1994	0.0664	303.32	<0.0001
Sex	1	0.0037	0.0037	16.89	<0.0001
Location	1	0.0060	0.0060	27.69	<0.0001
Body Length	1	0.0030	0.0030	13.59	0.0003

Table B.10. FGM

Variable	DF	Type I SS	Mean Square	F Value	P-value
Species	3	0.0868	0.0289	189.08	<0.0001
Sex	1	0.0010	0.0011	7.07	0.0087
Location	1	0.0007	0.0007	4.47	0.0363
Body Length	1	0.0001	0.0001	0.91	0.3409

Table B.11. Radius

Variable	DF	Type I SS	Mean Square	F Value	P-value
Species	2	431426.10	215713.0576	2486.73	<0.0001
Sex	1	2574.09	2574.0904	29.67	<0.0001
Location	1	9.93	9.9273	0.11	0.7356
Body Length	1	3173.39	3173.3956	36.58	<0.0001

Table B.12. Ulna

Variable	DF	Type I SS	Mean Square	F Value	P-value
Species	2	363893.10	181946.5577	1761.73	<0.0001
Sex	1	3301.04	3301.0432	31.96	<0.0001
Location	1	48.37	48.3771	0.47	0.4949
Body Length	1	4516.73	4516.7393	43.73	<0.0001

Table B.13. Biceps brachii

Variable	DF	Type I SS	Mean Square	F Value	P-value
Species	2	428.53	214.2687	80.14	<0.0001
Sex	1	128.64	128.6481	48.12	<0.0001
Location	1	82.44	82.4485	30.84	<0.0001
Body Length	1	40.65	40.6596	15.21	0.0002

Table B.14. Brachialis

Variable	DF	Type I SS	Mean Square	F Value	P-value
Species	2	10338.02	5169.0108	1638.76	<0.0001
Sex	1	119.61	119.6143	37.92	<0.0001
Location	1	16.95	16.9599	5.38	0.0220
Body Length	1	42.07	42.0758	13.34	0.0004

Table B.15. Supinator

Variable	DF	Type I SS	Mean Square	F Value	P-value
Species	2	3879.77	1939.8854	982.54	<0.0001
Sex	1	52.07	52.0753	26.38	<0.0001
Location	1	18.98	18.9806	9.61	0.0024
Body Length	1	11.67	11.6742	5.91	0.0164

Table B.16. RBB

Variable	DF	Type I SS	Mean Square	F Value	P-value
Species	2	0.0350	0.0175	270.67	<0.0001
Sex	1	0.0013	0.0013	21.58	<0.0001
Location	1	0.0014	0.0014	22.37	<0.0001
Body Length	1	0.0002	0.0002	3.06	0.0827

Table B.17. UB

Variable	DF	Type I SS	Mean Square	F Value	P-value
Species	2	0.02917	0.01458	299.00	<0.0001
Sex	1	0.00065	0.00065	13.48	0.0004
Location	1	0.00022	0.00022	4.43	0.0374
Body Length	1	0.00001	0.00001	0.21	0.6476

Table B.18. US

Variable	DF	Type I SS	Mean Square	F Value	P-value
Species	2	0.00667	0.00333	90.10	<0.0001
Sex	1	0.00024	0.00024	6.52	0.0118
Location	1	0.00018	0.00018	5.09	0.0258
Body Length	1	0.00005	0.00005	1.29	0.2585

Appendix C. Tukey-Kramer Adjusted Means Tables

Summary tables for Tukey-Kramer's test adjusted means for measurement lengths/ratio percentage and 95% confidence intervals for each species for the first and second GLM analysis. Corresponding tables and figures are in Chapter 3: Results Tables 6-15, 17-24. The Tukey-Kramer mean measurement lengths and ratio values are different from the overall values due to the incorporation of body length in the test. For the ratios, the number is the value out of one, not the percentage. For example, HPM for *C. guereza* is 0.18, or 18% (Table C.1).

Table C.1. First GLM analysis mean measurement lengths/ratio values and 95% confidence intervals (95% CI) with Tukey-Kramer adjustment for species (Tables 6-15).

	A. geoffroyi		*C. guereza*		*H. lar*		*M. mulatta*	
	Mean	95% CI	Mean	95% CI	Mean	95% CI	Mean	95% CI
Humerus	201.57	193.85, 209.29	138.46	129.06, 147.86	235.89	231.07, 240.71	142.67	137.69, 147.65
Femur	206.13	197.27, 214.99	178.84	168.04, 189.64	210.01	204.48, 215.54	168.55	162.83, 174.27
Pectoralis major	37.53	35.35, 39.71	24.26	21.61, 26.91	43.60	42.25, 44.95	23.53	22.14, 24.92
Teres major	31.23	29.09, 33.37	19.70	17.07, 22.33	35.91	34.58, 37.24	17.46	16.07, 18.85
Deltoid	77.60	74.07, 81.13	48.83	44.52, 53.14	104.59	102.39, 106.79	51.28	49.01, 53.55
Gluteus maximus	44.31	41.64, 46.98	39.42	36.17, 42.67	35.33	33.66, 37.00	35.53	33.81, 37.25
HPM	0.19	0.182, 0.198	0.18	0.170, 0.190	0.18	0.174, 0.186	0.16	0.154, 0.166
HTM	0.16	0.150, 0.170	0.14	0.128, 0.152	0.15	0.144, 0.156	0.12	0.114, 0.126
HD	0.38	0.366, 0.394	0.36	0.342, 0.378	0.44	0.432, 0.448	0.36	0.350, 0.370
FGM	0.22	0.208, 0.232	0.22	0.206, 0.234	0.17	0.162, 0.178	0.21	0.202, 0.218

Table C.2. Second GLM analysis mean measurement lengths/ratio values and 95% confidence intervals (95% CI) with Tukey-Kramer adjustment for species (Tables 17-24).

	C. guereza		*H. lar*		*M. mulatta*	
	Mean	95% CI	Mean	95% CI	Mean	95% CI
Radius	119.00	107.34, 130.66	264.06	258.47, 269.65	142.74	137.13, 148.35
Ulna	131.35	118.63, 144.07	273.81	267.71, 279.91	158.83	152.71, 164.95
Biceps brachii	11.43	9.37, 13.49	21.13	20.15, 22.11	15.14	14.16, 16.12
Brachialis	12.74	10.51, 14.97	34.53	33.47, 35.59	14.69	13.61, 15.77
Supinator	8.92	7.16, 10.68	23.32	22.48, 24.16	10.76	9.92, 11.60
RBB	0.09	0.080, 0.100	0.08	0.076, 0.084	0.10	0.096, 0.104
UB	0.10	0.092, 0.108	0.13	0.126, 0.134	0.09	0.086, 0.094
US	0.07	0.062, 0.078	0.08	0.076, 0.084	0.07	0.066, 0.074

Appendix D. Tukey-Kramer Species by Location Tables

Species by location Tukey-Kramer's test results for all species for deltoid, HD, HPM, biceps brachii, supinator, RBB, US, and gluteus maximus. These tables include the p-values calculated by the Tukey-Kramer's test comparing captive and wild caught specimens of each species. The results indicate which species are associated with the differences for location in the GLM analyses.

Table D.1. Deltoid

	A. geoffroyi wild	*C. guereza* wild	*H. lar* wild	*M. mulatta* wild
A. geoffroyi captive	0.9823			
C. guereza captive		0.0061		
H. lar captive			0.9330	
M. mulatta captive				0.4083

Table D.2. HD

	A. geoffroyi wild	*C. guereza* wild	*H. lar* wild	*M. mulatta* wild
A. geoffroyi captive	0.9209			
C. guereza captive		<0.0001		
H. lar captive			0.7914	
M. mulatta captive				0.9385

Table D.3. HPM

	A. geoffroyi wild	*C. guereza* wild	*H. lar* wild	*M. mulatta* wild
A. geoffroyi captive	0.9992			
C. guereza captive		<0.0001		
H. lar captive			<0.0001	
M. mulatta captive				0.7014

Table D.4. Biceps brachii

	C. guereza wild	*H. lar* wild	*M. mulatta* wild
C. guereza captive	1.0000		
H. lar captive		<0.0001	
M. mulatta captive			0.9604

Table D.5. Supinator

	C. guereza wild	*H. lar* wild	*M. mulatta* wild
C. guereza captive	0.9002		
H. lar captive		0.0019	
M. mulatta captive			0.9995

Table D.6. RBB

	C. guereza wild	*H. lar* wild	*M. mulatta* wild
C. guereza captive	0.9881		
H. lar captive		<0.0001	
M. mulatta captive			0.9859

Table D.7. US

	C. guereza wild	*H. lar* wild	*M. mulatta* wild
C. guereza captive	0.9493		
H. lar captive		0.0035	
M. mulatta captive			0.9989

Table D.8. Gluteus maximus

	A. geoffroyi wild	*C. guereza* wild	*H. lar* wild	*M. mulatta* wild
A. geoffroyi captive	0.8896			
C. guereza captive		0.7688		
H. lar captive			0.9786	
M. mulatta captive				0.1480

Appendix E. HD and FGM Tukey-Kramer Test Results for Species without *A. geoffroyi*

These tables are similar to Tables 14 and 15, but do not include *A. geoffroyi* in the analysis. This is to show that these two ratios follow the hypothesized pattern when *A. geoffroyi* is excluded from the analysis.

Table E.1. HD

	H. lar	*M. mulatta*
C. guereza	<0.0001	0.9160
H. lar		<0.0001

Table E.2. FGM

	H. lar	*M. mulatta*
C. guereza	<0.0001	0.7573
H. lar		<0.0001

Vita

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