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FUNCTION, DESIGN, SCALING, AND SEXUAL DIFFERENCES OF DIMORPHIC CHELAE IN THE LAND CRAB, *CARDISOMA CARNIFEX*

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Abstract. Crab chelae are a model system for studying the relationship between the biomechanics of an organism's structure and its ecological role. This study investigated how chelae dimorphism may correlate with specialization in function in the land crab *Cardisoma carnifex* (Herbst 1791). This was achieved by comparing field observations of preferential claw usage during diurnal activities to a mechanical model derived from anatomical claw measurements, claw closing effort of captured specimens, and calculations of expected closing force. Behavior, mechanical scaling, and effort were also compared between males and females. Foraging, eating, and lead claw entering burrow showed significant differences in claw use frequency. It was also found that the major and minor claws scaled differently with respect to carapace length, with the major claw displaying positively allometric scaling and the minor claw displaying near-isometric scaling. Measurement of claw closing effort with respect to claw length showed high correlation in male minor and female major claws. In males, expected force measurements showed a greater rate of growth in the minor claw than in the major claw with respect to claw length, but in females, expected force in the major claw exhibited a greater rate of growth. A possible explanation for the differences in design between sexes may be that there are functional differences between male and female chelae, such as the primary use of male minor claw and female major claw in gripping objects when stressed.

Key words: biomechanics; Brachyura; functional morphology; force generation; sexual dimorphism

INTRODUCTION

Ecological functions of anatomical structures are often closely tied to the mechanical design of these structures. The relationships between form and function have been studied for centuries in many vertebrates, invertebrates, and plants. Most recently, arthropods–particularly crabs—have been the focus of thorough investigation. Crab chelae, or claws, serve many ecological functions, such as foraging (Schenk and Wainwright 2001), mate acquisition (Schenk and Wainwright 2001), defense (Barnes 1974), offense (Meglitsch 1972), and manipulating objects (Meglitsch 1972). Despite the multipurpose nature of the chelae, they are mechanically simple, and so they are a model system for exploring the relationship between morphology and ecology (Schenk and Wainwright 2001).

Many Brachyuran crabs exhibit claw dimorphism, which can often be attributed to some specialization in function between the claws. The larger claw is commonly designated as the "crusher" claw (major claw) and the smaller claw is designated as the "cutter" claw (minor claw). This dimorphic design is assumed to be a tradeoff between closing speed and force generation, with the

minor claw adapted for speed and the major claw adapted for power (Schenk and Wainwright 2001). The most extreme example of claw dimorphism in crabs is observed in the fiddler crab (family Ocypodidae, genus *Uca)*. In this case, the claw dimorphism is also sexually dimorphic, with only males possessing a large major claw. In this case, form of the major claw is a consequence of sexual selection (Levinton and Judge 1993, Levinton et al. 1995, Levinton and Allen 2005). Diet is also a factor associated with claw design (Yamada and Boulding, 1997). Studies have shown that crabs that feed on fast moving prey have fast, relatively weak claws, while crabs that feed on hard-shelled prey have slow, powerful claws that operate at higher mechanical advantage (Seed 1995, Yamada and Boulding, 1997).

Cardisoma carnifex (Herbst 1791), a member of family Gecarcinidae, is a burrowing land crab that is common on the island of Moorea, French Polynesia (Bickel 1997) as well as throughout the Pacific (Denhoy and Battersby 1992). Adult crabs are eight to thirteen centimeters in carapace width (Denhoy and Battersby 1992), and they are opportunistic scavengers, feeding on leaves, plant parts, detritus, and mud (Bickel 1997). *C. carnifex* individuals of both sexes exhibit dimorphic chelae. Although there have been several studies on its ecology (Denhoy and Battersby 1992; Bickel 1997; Cheng 2000; Elitzur 2001), no claw mechanical studies have been done, and it remains a poorly studied species.

The main objective of this study was to determine relationships between function, closing force generation, and anatomical scaling of the dimorphic claws in *C. carnifex*. The first objective was to observe *C. carnifex* in the field in order to establish the ecological roles of the major and minor claws. I expected to see preferential usage of one claw over the other depending on the activity. Another objective was to determine whether there were differences between the major and minor claws in scaling of claw size relative to crab size and in scaling of claw shape relative to claw size. Based on a study of fiddler crabs by Levinton and Allen (2005), I expected the major claw to scale allometrically, while the minor claw would scale isometrically. Preliminary observations of crabs led me to expect that the major claw would exhibit changes in claw shape relative to claw size, while the minor claw's shape would be independent of size. The third objective of this study was to determine differences in closing force generation between the major and minor claws by measuring claw closing effort and calculating expected closing force at the claw tip by using a mechanical model from anatomical measurements. Again, based on Levinton and Allen's 2005 study of fiddler crabs, I expected the major claw to allometrically scale in force generation as a function of claw length, becoming weaker relative to an isometric scaling of force as claw size increased. In contrast, I expected the minor claw to scale isometrically in force generation. The final objective of this study was to determine whether there were mechanical claw differences between sexes. Since both sexes exhibited claw dimorphism, I expected anatomical scaling and closing force generation between sexes to be similar for the major and minor claws.
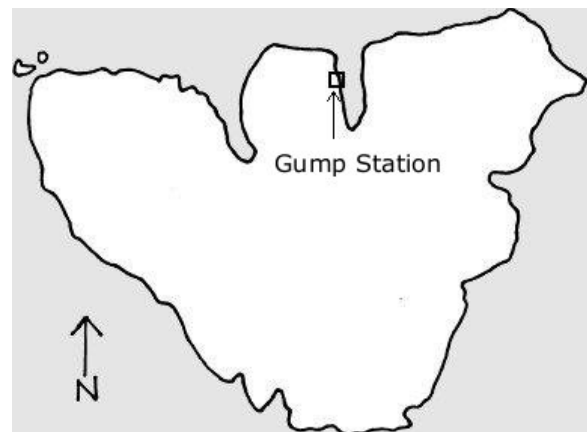

FIG. 1. Map showing the location of the study site at Gump Biological Research Station on Moorea, French Polynesia (17°30' W Lat., 149°50'S Long.)

MATERIALS AND METHODS

Field study sites

Field observations and specimen collection were done at UC Berkeley Gump Station, Moorea, French Polynesia (Fig. 1). Two sites on the station were chosen for their high density of crab burrows. The first site was a plot of land located just north of the waterfront bungalows, which had a large hibiscus tree in the middle of the plot. The second site was located approximately 150 meters south of the docks, which chiefly consisted of a dirt plot surrounded by hibiscus trees.

Field Observations

Land crab behavior was observed either at the bungalow site or the dock site based on visible crab activity and whether there was human or animal activity that would potentially scare the crabs. The crabs were observed from elevated surfaces, as they seemed to be wary of vibrations in the ground as well as motions close to ground level. Also, the crabs either did not seem to detect observers above them or did not perceive them as a threat. Observations were done within three designated times of day: morning (6-7am), afternoon (1-3pm), and evening (5-6:30pm). The duration of each observation period was 15 minutes, starting when the first crab reemerged. Time, location, weather, and temperature were recorded for each period. *Hibiscus tiliaceus* leaves were thrown near crab burrows to encourage crabs to emerge and to observe foraging and feeding behavior.

During each observation period, the activities of the crabs and claw usage during these activities were recorded. The categories of recorded activities were foraging, eating, removing dirt from burrow, threat display, and fighting, as well as the lead claw while retreating into burrows. The activity of removing dirt from burrow was chosen, because the activity of digging could not be directly observed. Claw usage for each activity was recorded as major claw used, minor claw used, or both claws used. Relative crab size (very small, small, medium, large, and very large) and circumstance (near burrow, out in open, alarmed, and in competition with others) were also noted for each recorded activity. For ambidextrous activities that involved alternate usage of both claws, the activity and length of time observed were recorded, as well as the number of times each claw was used in order to determine relative frequency.

Capture and Care

Crabs were captured using three primary methods in order to measure claw closing force and to dissect specimens for anatomical measurements. For the first method, a box was propped up with a stick tied to a string, and hibiscus flowers were placed under the box as bait. As a crab went under the box to retrieve the bait, the string was pulled and the box fell over the crab. This method was found to be the least effective of the three.

As a second method of capture, towels were thrown over crabs that were found in the open in order to immobilize them. This capturing method was used primarily at dawn and after nightfall, because crabs were more often found away from their burrows during these time periods. I found that it was often more effective to run directly at the crabs in order to confuse them than trying to sneak up on the crabs and trying to throw a towel over them.

The final method of capture utilized a fishing line "noose" tied to the end of a long pole. When the noose was placed in front of crabs that were sitting in front of their burrows, the crabs would often grab onto the line as though it was food and tug on it. This would cause the noose to tighten around the crabs' claws, at which point the pole would be yanked upward to capture the crabs.

Crabs were kept in deep tubs or buckets with approximately one to two centimeter of their carapaces, causing them to perform threat displays. Polystyrene wedges of
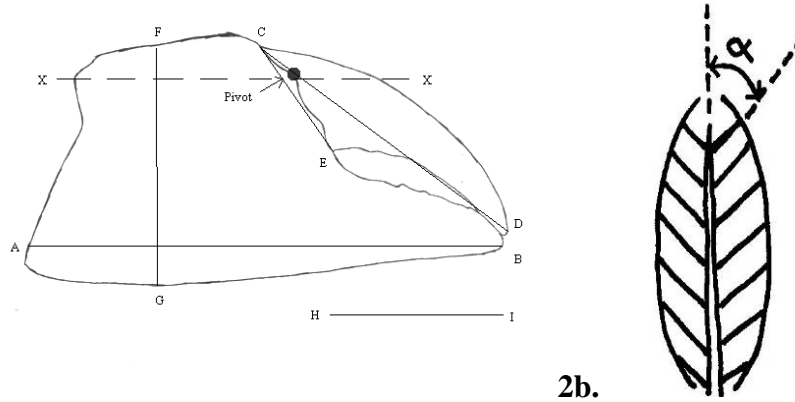
2a.　　　　　　　　　　　　　　**2b.**

FIG. 2a. Major claw of *Cardisoma carnifex*. External claw measurement, as taken by Levinton and Allen, 2005: A-B claw length, C-D dactyl length, C-E dactyl height, F-G manus height, H-I pollex length, manus width measured perpendicular to manus height. **2b.** A section along line X-X, which reveals pennate muscle. Muscle connects to the apodeme at pennation angle α.

seawater, with a flat stone placed at the bottom of the container and *Hibiscus tiliaceus.* leaves, flowers, or carrots placed on the stone for food. Food and water were changed daily.

The areas where the crabs were captured were not limited to the two field study sites, and crabs were captured at various points on the Gump station as well as along the road near the station. 33 specimens were caught over a six week span from September to November.

Closing Effort

Differences in closing force between chelae were indirectly determined by measuring "effort" exerted by the crabs as they were allowed to pinch a deformable surface, in this case wedges of polystyrene, for a given amount of time. In this context, effort is defined as force exerted over a distance, and it is a measure of the total energy put into a system (R. Dudley, pers. comm., 2006). Rough measurements of effort were made by measuring the indentation volumes in the wedges after the wedges were squeezed by the claws. To make the crabs squeeze the polystyrene, the crabs were lifted and held by

dimensions 1.0cm x 3.5cm x 7.0cm were placed in between the tips of each claw, and the crabs were allowed to pinch the wedges for approximately five seconds. The crabs were then returned to their containers, causing them to release their grip.

Displacement volume (V) was calculated by measuring the length (L) of the indentation, width (W), and depths (D_1, D_2) at the two ends of each indentation. Depth measurements were taken by inserting stiff fishing line into the indentations and marking off the top with a permanent marker. The distance from the tip of the fishing line to the pen mark was measured to the nearest .05mm with vernier calipers. Length and width were measured directly to the nearest .05mm with vernier calipers. These measurements were fitted to a model polyhedron with a rectangular base and two parallel, triangular faces. Volume was calculated as the average area of each face multiplied by the length:

$$V = 0.25 \, (D_1 + D_2) \, W \, L \qquad (1)$$

External Claw Measurements

External claw measurements and carapace width were measured in order to determine whether claw scaling was isometric or allometric. In order to prepare crabs for dissection, they were put into containers of seawater and placed in the freezer for approximately two hours, or until they stopped moving. Crabs were sexed by abdomen shape and their carapace widths were recorded. For this study, carapace width was used as a proxy for crab size. Claws were identified as either major or minor and separated from the rest of the body using dissecting scissors. External claw measurements were chosen from Levinton and Allen (2005). Claw length, dactyl length, dactyl height, pollex length, manus height, manus width, and manus length (fig. 2a) were measured to the nearest .05mm using vernier calipers.

Muscle Pennation Angle

Crab chelae can be described as a simple lever system. Pennate muscles attached to an apodeme contract to rotate the dactyl (moveable finger) around a pivot point to either open the claw or close it against the pollex (fixed finger) (Levinton and Allen 2005) (Fig. 2b). An internal morphological property that affects closing force is the pennation angle (α) of the claw closer muscle, which, in arthropods, is the angle at which muscle fibers connect to the apodeme (Schenk and Wainwright 2001). The calculation of force in relationship to pennation angle can be written as (Schenk and Wainwright 2001):

$$F_m = A\ \sigma \sin 2\alpha \qquad (2)$$

F_m is the force exerted by the muscle, A is the muscle cross-sectional area (MCA), and σ is the stress generated per unit MCA. As the equation shows, force generation is maximized as muscle pennation approaches 45° (Schenk and Wainwright 2001).

To stiffen muscles fibers to measure closing muscle pennation angle, the claws were then preserved in the closed position in 10% formol for at least 24 hours. The manus, but not the dactyl, was then cut along line X-X (Fig. 2a) using dissecting scissors for smaller claws or a handsaw for larger claws. Dactyls were removed carefully from the claw, since the closing muscle apodeme usually remained attached to the dactyl. In order to determine pennation angle, the bottom portion of each claw was placed over a vertical strip of tape, with the area where the closing apodeme used to lie placed along one edge of the tape. A string tied to two dissecting pins was pinned down across the claw, parallel to the visible muscle fibers. The claw was then removed and another piece of tape was placed down, with one edge of the tape lying along the path of the string. The string was removed and the intersecting pieces of tape were digitally photographed. The pennation angle was measured by using the program ImageJ to determine the angle of intersection.

Muscle Cross-sectional Area

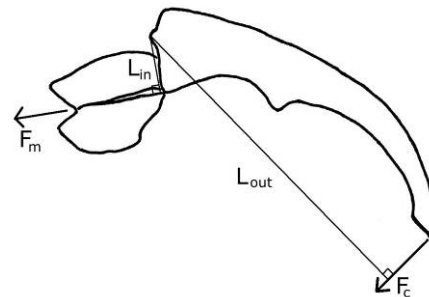Force generation in equation 2 is proportional to a second internal morphological property: muscle cross-

FIG. 3. Diagram of a major claw dactyl and its closer apodeme. Forces and lever arms are labeled for the closing lever system. L_{in} is the in-lever, the distance from the pivot to the apodeme joint perpendicular to muscle contractile force F_m. L_{out} is the out-lever, the distance from the pivot to the dactyl tip perpendicular to force exerted at claw tip, F_c.

sectional area, which is equal to apodeme area (Levinton and Allen 2005). In order to measure apodeme surface area, the closing muscle apodeme was separated from the dactyl after the dactyl was extracted from the rest of the claw. The apodeme was then scraped clean of muscle fibers and digitally photographed along with a known scale. Using these photographs, ImageJ (Rasband, 2006, National Institutes of Health), was used to calculate the apodeme surface area. Surface areas of excessively damaged apodemes were not included.

Mechanical Advantage

The force generated by the muscle is transmitted through the lever system, where the mechanical advantage (MA) of the lever system becomes yet another morphological factor that influences closing force. In a lever system, lever-arm length is the distance from the fulcrum to the force vector, perpendicular to the force. MA is determined by the relative proportion of lever-arm length (in-lever/out-lever) (Levinton and Allen 2005). Values of MA greater than one represent a proportional increase in force exerted on the load and a corresponding decrease in velocity in moving the load, while MA values less than one represent a decrease in force exerted and increase in velocity (Vogel 2003).

In order to measure mechanical advantage of the closing lever system, the in-lever and out-lever of the lever were measured, as shown in figure 3. In-lever distance was measured from the pivot point to the middle of the thick, central line of the apodeme, perpendicular to this central line. Out-lever distance was measured from the pivot point to an imaginary line perpendicular to the dactyl tip, parallel to the dactyl tip. Measurements were taken using vernier calipers to the nearest .05mm. Mechanical advantage was calculated using equation x.

Force Calculation

Expected maximum closing force at the tip of the claw (F_c) was determined by first calculating the expected maximum force exerted by the claw closing muscle (F_m) using equation 2. For the maximum stress value (σ), 200 kilopascals was used. Testing of isometric stress has shown that this value is relatively constant among a variety of animals (Vogel 2003). As F_m is the force input and F_c is the force output in the closing lever described in figure 3, F_m can be determined by multiplying F_c by mechanical advantage (MA).

$$F_c = MA \ F_m \qquad\qquad (3)$$

Statistical Analysis

To obtain claw use frequencies, claw usage data were grouped by time of day recorded and summed together within each group. This avoided an overabundance of frequencies of 1 due to small sample sizes. For each size class, claw usage was sorted by activity. For each activity, claw usage for major claw, minor claw, and both claw were divided by the total claw usage for that activity to obtain a frequency of claw usage.

In order to determine whether different activities had different frequencies of claw usage, the claw usage frequency data were analyzed using Kruskal-Wallis tests for group differences and Tukey-Kramer HSD for multiple paired tests. The Tukey-Kramer tests were corrected for multiple tests at the .95 significance level. Kruskal-Wallis tests were used, because data was not normally distributed, even with transformations. For this analysis, the groups used were the six observed activities, the response was claw frequency, and the tests were done by claw. The activity "lead claw entering burrow" was removed as a group for the analysis of both claws used, because it is physically impossible for these crabs to enter their burrows with both claws leading.

To determine whether claw frequencies differed within activities, the usage frequency data was once again analyzed using Kruskal-Wallis test and Tukey-Kramer HSD. The groups used were the three categories of claw use, the response was claw frequency, and the tests were done by activity. For the analysis of the activity "lead claw entering burrow", the group "both claws" was removed for the same reason stated in the previous paragraph. Kruskal-Wallis and Tukey Kramer HSD were also used to compare relative frequencies of claw usage for ambidextrous activities.

Linear regressions of log-log plots were used to analyze scaling of the anatomical and mechanical data. All regressions were performed by sex in order to determine if there were differences in scaling between sexes. Excluding the field data, all other data were log transformed. First, claw size was analyzed as a function of carapace width. Next, all other measurements (external claw measurements, indentation volume of polystyrene, apodeme surface area, pennation angle, measurements of mechanical advantage, effort exerted, and calculated closing force) were analyzed as a function of claw length. For measurements showing no linear correlation for either claw of either sex, measurements were analyzed using Kruskal-Wallis and Tukey HSD tests, grouped by claw and sex. Specifically, this was done for measurements of mechanical advantage.

RESULTS

Field Observations

Kruskal-Wallis tests showed that for each category of claw use, claw usage frequencies were significantly different between activities (p<0.0001 for both claws used, p=0.0198 for major claw, and p=0.0008 for minor claw) (Appendix A). For activities performed using both claws, the usage frequency of removing dirt was significantly higher than those of threat display, and fighting. For activities performed using only the major claw, usage

frequency for fighting was significantly higher than frequencies for lead claw entering burrow, foraging, eating, and removing dirt. Also, usage frequency during threat display was significantly higher than the frequency during eating. Finally, minor claw frequency of usage in "lead claw entering burrow" was significantly higher than the other five activities.

For Kruskal-Wallis tests of claw usage by activity, eating (p=0.0244), foraging (p=0.0025), and lead claw entering burrow (p<0.0001) showed significant differences in claw usage (Appendix B). For the activity of eating, the frequency of use of both claws was significantly higher frequency than the frequency of use of just the major claw. As for foraging, both claws were used at a significantly higher frequency than both the
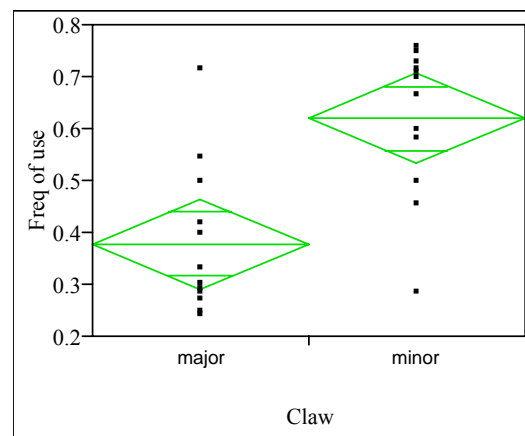

FIG. 4. Claw use frequency of ambidextrous feeding, grouped by claw. Means and quantiles are shown for each group. Analysis by Kruskal-Wallis test showed significant difference between treatments (p=0.0027).

major claw and the minor claw used alone. Finally, for lead claw entering burrow, minor claw frequency of usage was significantly higher than major claw frequency.

Eating was the only ambidextrous activity observed where relative usage rates between claws could be measured. Kruskal-Wallis test showed the usage rate between major and

minor claw to be significantly different (p=0.0024), with minor claw usage frequency (0.621) significantly higher than major claw usage frequency (0.379) (Fig. 4).

Closing Effort

Linear regressions of log-log plots of volume of polystyrene indentation as a function of claw length showed that in males, there was no correlation with the major claw (p=0.7275) but there was a strong correlation with the minor claw (p<0.0001) (Fig. 5). In contrast, females exhibited no correlation with the minor claw (p=0.1308) but did exhibit strong correlation with the major claw (p=0.0069).

External Claw Measurements

Linear regressions of log-log plots of claw length (CL) as a function of carapace width (CW) and external claw measurements as functions of claw length displayed strong correlations (p<0.05) (Fig. 6) for both sexes. For males, the major claw scaled to $CW^{1.395}$ (R^2=.991) and the minor claw scaled to $CW^{1.12}$ (R^2=.988). For females, the major claw scaled to $CW^{1.210}$ (R^2=1.21) and the minor claw scaled

to the $CW^{1.04}$ (R^2=1.04). Excluding female major claw manus width, scaling of external claw measurements ranged from $CL^{0.877}$ to $CL^{1.148}$ (Appendix C). Scaling for female major claw manus width is claw length to the $CL^{0.773}$ (R^2=0.974) (Appendix C).

Muscle Pennation Angle

Linear regressions of log-log plots of muscle pennation angle as a function of claw length displayed no correlation in males (major: p=0.438; minor: p=0.735), but displayed strong correlation in females (major: p=0.0264; minor: p=0.0345) (Fig. 7). Female major claw closing muscle pennation angle scaled to $CL^{-0.204}$ (R^2=0.4382) and minor claw pennation angle scaled to $CL^{-0.234}$ (R^2=0.7352) (Appendix C).

Muscle Cross-sectional Area

Linear regressions of log-log plots of apodeme surface area as a function of claw length showed strong correlations in both major and minor claws of males and females (p<0.05) (Appendix C). In males, major claw apodeme area scaled to $CL^{1.798}$ (R^2=0.629) and minor claw apodeme area scaled to $CL^{2.084}$ (R^2=0.922). In females, major claw apodeme
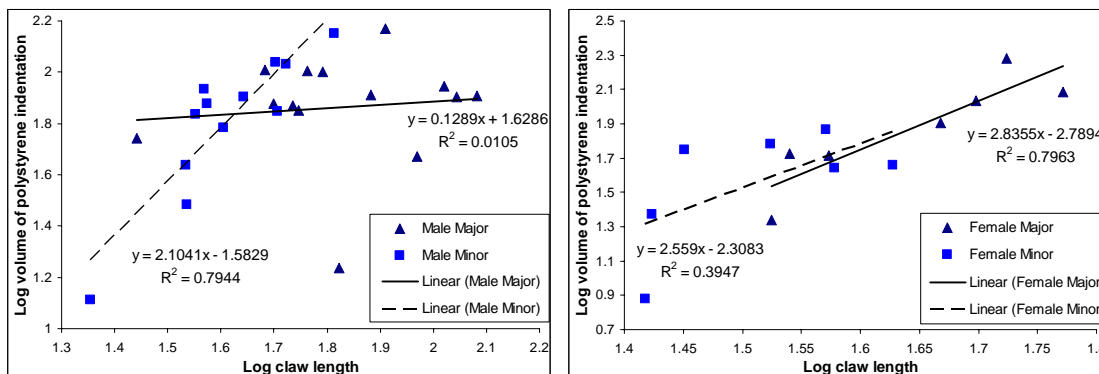

FIG 5. Log-log plot of volume of polystyrene indentation as a function of claw length. Indentation volume was used as a measure claw closing effort. In males, the major claw displayed poor correlation (n=14, p=0.7275), and the minor claw displayed high correlation (n=12, p<0.0001). In females, the major claw displayed high correlation (n=7, p=0.0069), and the minor claw displayed poor correlation (n=7, p=0.1308).
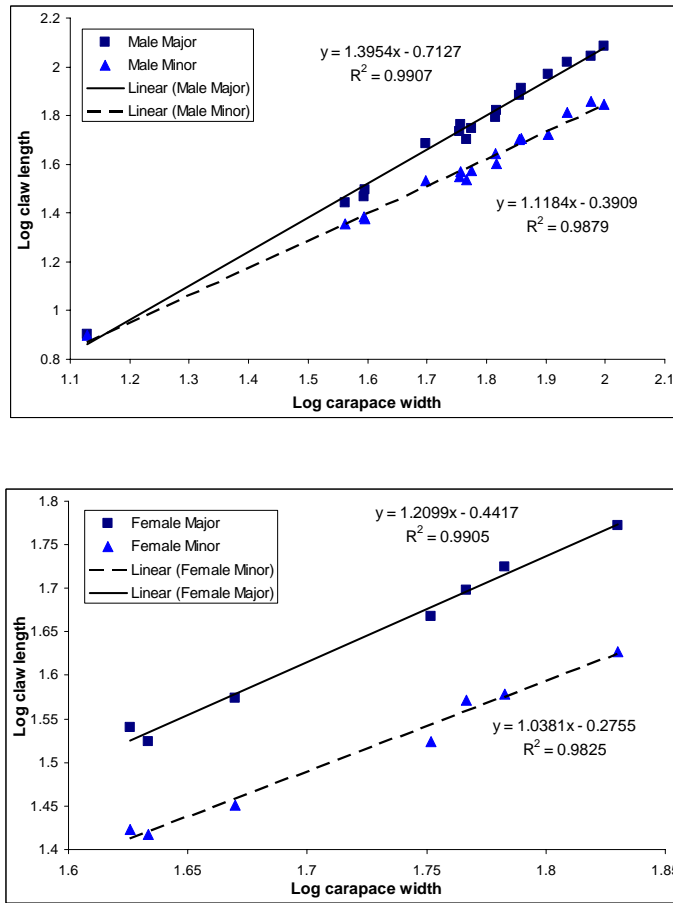
FIG. 6. Log-log plot of the claw length as a function of carapace width. In males, both the major claw and the minor claw displayed high correlations (n=17, p<0.0001 for both graphs). In females, the major claw and the minor claw exhibited high correlations as well (n=7, p<0.0001 for both graphs).

area scaled to $CL^{1.609}$ (R^2=0.896) and minor claw apodeme area scaled to $CL^{1.420}$ (R^2=0.785).

Mechanical Advantage

Linear regressions of log-log plots of the in-lever, out-lever, and mechanical advantage as a function of claw length showed strong correlations for in-levers and out-levers in both major and minor claws of males and females (p<0.05), but showed almost no correlation for mechanical advantage for any claw of either sex (Appendix C). In males, major claw in-lever scaled to $CL^{0.962}$ (R^2=0.983) and minor claw in-lever scaled to $CL^{1.12}$ (R^2=0.976). Major claw out-lever scaled to $CL^{0.936}$ (R^2=0.985) and minor claw out-lever

scaled to $CL^{1.081}$ (R^2=0.976). In females, major claw in-lever scaled to claw length to $CL^{0.986}$ (R^2=0.974) and minor claw in-lever scaled to $CL^{1.248}$ (R^2=0.935). Major claw out-lever scaled to $CL^{0.989}$ (R^2=0.939) and minor claw out-lever scaled to $CL^{1.026}$ (R^2=0.994).

Kruskal-Wallis test and Kramer HSD analysis of mechanical advantage showed that MA in male and female major claws was significantly higher than MA in male and female minor claws (Fig. 8). MA in female major claws was also significantly higher than MA in male major claws.

Force Calculation

Linear regressions of log-log plots of

expected maximum closing force as a function of claw length showed strong correlations in both major and minor claws of males and females ($p<0.05$) (fig. 9). In males, major claw force scaled to $CL^{1.666}$ ($R^2=0.893$) and minor claw force scaled to $CL^{2.194}$ ($R^2=0.845$). In females, major claw force scaled to $CL^{1.684}$ ($R^2=.943$) and minor claw force scaled to $CL^{1.577}$ ($R^2=0.719$).

DISCUSSION

My results show that there are strong anatomical and mechanical differences between the major claw and minor claw. The major claw length scaled allometrically as a function of carapace width, and several external claw measurements scaled allometrically as functions of claw length as well. The minor claw, however, appeared to scale nearly isometrically with respect to both claw length against carapace width and external measurements against claw length.

Positively allometric scaling of the major claw not only demonstrates that the claw becomes proportionally larger relative to the carapace as size increases, but it also shows that there is some degree of shape change as claw size increases. For both sexes, there are relative increases in dactyl and pollex length
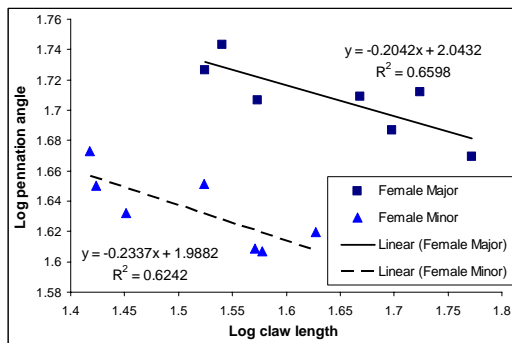
and a relative decrease in manus length with respect to increasing claw length. Empirically, I also observed that the curvature of the dactyl seemed to increase, as well as the relative slenderness of the dactyl and pollex when compared to the claw size. On the other hand, the nearly isometric scaling of the minor claw, especially so in males, shows that minor claw shape is relatively independent of claw size.

Measurements of internal anatomy also exhibited differences in scaling. An example of this is apodeme surface area, which is also defined in this study as the muscle cross-sectional area. As equation 1 showed, force generation at the muscle is directly proportional to muscle cross-sectional area. Analysis of regression involved correlating an area as a function of a distance, so for isometric scaling the expected value would be CL^2. Scaling of apodeme surface area in the major claw was negatively allometric, which suggests that unless there were other compensating factors, larger claws were weaker per square of unit length. However, the minor claw apodeme in male crabs scaled very close to the 2nd power in males, so it
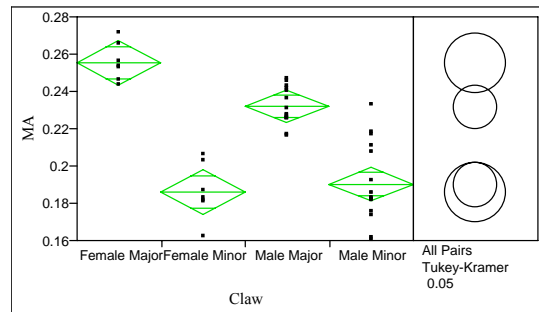
FIG. 8. Mechanical advantage (MA) of claws grouped by claw and sex, showing Tukey Kramer HSD analysis. Means and quantiles are shown for each group. Kruskal-Wallis test showed significant difference between treatments ($p<0.0001$). The major claw treatments in both sexes were significantly greater than minor claws treatments in both sexes. Female major claw treatment was also significantly greater than male major claw treatment ($\alpha=0.05$)

FIG. 7. Log-log plot of pennation angle as a function of claw length in females. . Both the major claw (n=7, p=0.0264) and the minor claw (n=7, p=0.0345) exhibited strong correlations. The graph for pennation angle in males is not shown, because both claws exhibited poor correlations.

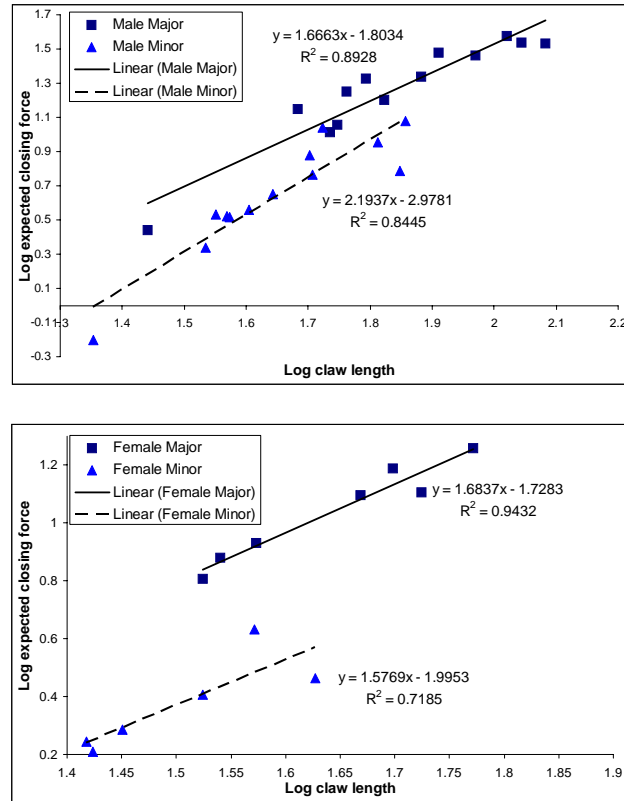**FIG**. 9. Log-log plot of expected claw closing force at claw tip as a function of claw length. In males, both the major claw (n=13, p<0.0001) and the minor claw (n=13, p<0.0001) displayed high correlations . In females, the major claw (n=7, p=0.0003) and the minor claw (n=6, p=0.0330) exhibited high correlations as well.

could be considered isometric. Female minor claw closing apodemes scaled more negatively isometrically than did female major claw closing apodemes, which raises an issue of differences between sexes which will be discussed later in the paper. The male minor claw's isometric scaling means that, with regard to muscle cross-sectional area, force generation per square of unit claw length is independent of crab size.

As mentioned earlier, there are potentially several factors that could provide force generation compensation for negatively allometric scaling of muscle cross-sectional area. One such factor is the muscle pennation angle, which maximizes force production as it approaches 45°. In males, no correlation was found between pennation angle and claw length. However, the mean pennation angle for minor claw was closer to the ideal 45°

(45.141°) than the mean pennation angle for the major claw (53.407°). Thus, in this respect the minor claw closing muscle is more efficient in generating force than the minor claw muscle in males.

Female measurements of pennation angle provided an unexpected result. In females, there are strong correlations between pennation angle and claw length. It is important to note that for this study, there was a low female sample size, with only seven females measured. The smallest female measured had pennation angles of 53.255° major and 47.095° minor and the largest female had pennation angles of 46.701° major and 41.643°. This shows that as female crabs increase in size, force generation efficiency in terms of pennation angle moves from favoring the minor claw to favoring the major claw. The decreasing pennation angle can be

partially explained by observing the anatomical scaling of the manus width ($CL^{0.774}$) in relation to the scaling of the manus length ($CL^{0.886}$). Division of manus length scaling by manus width scaling results in a ratio of $CL^{0.112}$, which may be a significant difference in scaling. Thus, with the manus length growing much more rapidly than the width, pennation angle may have to decrease in order for the muscle to fit inside of the manus. However, this explanation would not apply to the female minor claw, as the ratio of scaling for manus length to manus width is $CL^{-0.057}$. An expected result of this ratio would be that pennation angle would increase with an increase in claw length. However, this ratio may not be large enough to significantly affect pennation angle, and lack of correlation in male pennation angle shows that the ratio of scaling for manus length to manus width may not necessarily have a large effect on pennation angle. More accurate measurements of pennation angle and larger sample sizes may show that like males, pennation angle does not scale in females relative to claw size.

Mechanical advantage is not a factor that determines force generation, but rather it affects force transmission and amplification from muscle to claw tip. It may be important to note that my method of measuring mechanical advantage differs from the methods of previous studies. When I measured mechanical advantage, the two lever arms I measured were perpendicular to the contractile force and the load. This runs contrary to previous studies of mechanical advantage in crab claws, which have measured from the pivot point to the tip of the claw for the out-lever, which is not necessarily perpendicular to the load(see Yamada and Boulding 1997, Schenk and Wainwright 2001, Levinton and Allen 2005), which may lead to inaccurate values of mechanical advantage. This may also have no significant effect when comparing relative values, but it would affect calculations of predicted force. No correlation was found between mechanical advantage and claw length. This could be attributed to variability in claw shape between crabs. However, one-way analysis of mechanical advantage showed significant differences between major and minor claws by sex. As observed by Levinton and Allen (2005) and Schenk and Wainwright (2001), mechanical advantage was significantly higher in the major claw than in the minor claw. This supports the "crusher and cutter" model, where the major claw is designed to be more powerful by being physically larger of the two claws and by operating at higher mechanical advantage.

Recent studies, however, have not explored sex differences in mechanical advantage within species that exhibited dimorphism in both sexes. No significant difference was found between the minor claw MA values between sexes, which suggests similarity in design in this respect. However major claw MA was significantly different between sexes, and female major claws operated at a significantly higher mechanical advantage. This may correlate with differences in major claw function between sexes. Although it was almost impossible to positively identify the sex of crabs observed in the field, I mostly observed territoriality in male crabs, judging sex by claw and carapace size, as well as claw shape. These crabs exclusively fought using their major claws. Assuming that females do not exhibit the same degree of territoriality, perhaps male major claw design may be additionally influenced by pressure exerted by sexual selection. In fiddler crabs, it was found that major claw MA decreased and claw closing speed increased as claw size increased (Levinton and Allen 2005). Levinton and Allen concluded that this decreased MA was related to the increased closing speed and that faster claws may be advantageous during fights between males. While *C. carnifex* does not exhibit scaling of MA in its claw closing system, Levinton and Allen's conclusions may be a possible explanation for lower MA values in the male major claw. Even if the male claw

design did not assist in male-to-male fighting, its exaggerated length may be important as a form of display. In larger males, it appeared as if the dactyl and pollex of the major claw became disproportionately long and slender. A disproportionate increase in length with respect to height would cause a likely decrease in mechanical advantage.

Differences in claw performance based on sex are confirmed by measurement of effort. Recent studies used direct measurements of claw closing force to compare claw differences (Levinton and Judge 1993, Levinton et al. 1995, Yamada and Boulding 1998, Levinton and Allen 2005), but this option was unavailable during this experiment. Instead, effort, an indirect measurement of force, was used. It is important to note that during these tests, it is very likely that the crabs acted under varying degrees of motivation. This means that this test was by no means a measurement of maximum effort, but rather a measure of effort that the crabs chose to exert. In males, minor claw effort displayed high correlation as a function of claw length, while major claw effort displayed very poor correlation. A predicted result would be that both the major and minor claws would exhibit correlations of effort with respect to claw length, and that the correlations would be distinct from each other. A possible explanation for the major claw's poor correlation may be that relative to the minor claw, the major claw requires more energy to operate. Depending on how threatened it felt, the crab may not be inclined to clamp down using full force, especially if it had to do it over a time interval. Another possible reason may be that the structural design of the larger major claws may not be able to support a full exertion of force at the tip. As noted earlier, the dactyl and pollex become relatively long and slender as claw size increases, to the point where they appear relatively fragile. If this were the case, then crabs may be more inclined to exert some closing force that is less than their maximum. This may also show a functional difference between claws, where the minor claw could be predominantly used to clamp on to various objects when the crab is stressed. This was witnessed on several occasions when male crabs would grab tightly onto nearby objects primarily using their minor claws while being handled, holding onto these objects for minutes at a time.

In females, the opposite phenomenon was observed, with major claw effort displaying high correlation and minor claw showing poor correlation. In this case, the major claw may be better adapted to prolonged clamping than the minor claw due to a variety of factors. Muscle cross-sectional area grows more rapidly in the major claw than in the major claw and pennation angle approaches the ideal 45° in the major claw as claw size increases in females. Also, it appears that female major claws do not exhibit the same exaggeration of major claw shape present in males. This may be due to the fact that extremely large females were not found, but it may also be true that extremely large females do not exist. These differences in effort between sexes may suggest that there might be functional claw differences between sexes.

Scaling of expected claw closing force once again displays similarities between the major claw of one sex and the minor claw of the other sex. In males, expected force in the minor claw scaled with claw length to a greater exponent than the major claw. In females, the expected closing force of the major claw grew more rapidly with respect to claw length than the minor claw. If we accept the previously mentioned notion that the male minor claw and female major claw are primarily responsible for strongly gripping onto objects when the crab is stressed, then larger increases in force generation for those claws would be more beneficial to the organism's performance than if closing force scaled in a different manner. The data also showed that out of the four claw and sex combinations, the male minor claw exhibited the greatest rate of growth. A possible explanation for this is that the minor claw's high rate of growth compensates for the

relatively low value of force that the minor claw could potentially generate when compared to the major claw.

Regardless of sex, the major claw did appear to be important in the role of attack and defense. In observed crabs, threat displays were primarily made using primarily what seemed like body size to intimidate other crabs. If the degree of threat display escalated, then the major claw was thrust forward, often culminating in a fight between crabs, which exclusively involved their major claws. The defensive value of the major claw can perhaps be observed by the orientation of the crabs as they enter their burrows. Crabs entered their burrows with their major claw facing the entrance significantly more often than with their minor claw facing the entrance. Although there are many possible reasons behind this, one reason may be that having the major claw at the entrance may provide a greater threat deterrent than the minor claw would. Other possibilities include that the crabs dig with their minor claw, that they eat stored food with a certain claw, or that the crabs are simply programmed to enter their burrows in this manner. An unexpected observation was made several times in the field, when crabs would exit their burrows in one orientation and enter their burrows in the opposite orientation. Again, there could be various explanations for this phenomenon, including the importance of orientation for various activities while inside of their burrows or perhaps the lack of importance of orientation.

While the major claw may be important for attack and defense, the use of claws in other activities seems to be more dependent on both claws being used in conjunction. When crabs foraged, they most often used both claws to secure their grip on their food. This may be attributed to the fact that there was high competition for food at the two study sites, so foraging crabs needed to secure their food and run back to their burrows as quickly as possible to prevent their food from being stolen by other crabs. The act of removing dirt from the burrow during digging is also an activity where both claws were observed to be used at the same time. This is most likely due to the fact that carrying out dirt with both claws at once would be the most efficient way to do this activity.

Unlike the previously discussed activities, eating appears to favor the use of the minor claw. Although the activity was done most frequently using both claws, with the exclusive use of the minor claw second in frequency, the minor claw was used more significantly more frequently than the major claw during ambidextrous feeding. A possible explanation for this is that the minor claw is more efficiently designed for this activity, such as in its ability to shred food. It may also be more energetically favorable to use the minor claw; since it is smaller, it may require less energy to operate. On several occasions while observing feeding in the field, I saw crabs picking at grass and eating with both claws. Although the minor claw was used more frequently, it seemed as if the major claw was primarily used to pull out tougher grass. In other words, the crabs used the additional force generated by the major claw during feeding when it was needed, instead of using it as often as it used the minor claw. The simultaneous use of the major and minor claws also shows how the two claws can overlap in function. Other than the activity of fighting, of which there was not a statistically significant sample size, it appeared that there were no activities that were claw exclusive.

Although the field observations provide a general idea of how *C. carnifex* uses its major and minor claws in nature, the design of the study has provided limited insight as to the direct relationship between claw usage as a function of crab size (due to limited sample size) or as a function of sex (due to the difficulty of identifying sex in the field).

Future studies of crab behavior may involve more vigorous observations of activity in order to determine functional differences by size or sex. One set of activities I could not

observe was the act of digging as well as other activities performed while crabs were in their burrows. Correlating this information with biomechanical data could provide further insight in the relationship between claw design and function. Future biomechanical studies could involve direct measurements of closing force using devices such as force transducers and measuring claw closing speed. Also, similar studies could be done on the other species of crabs present on Moorea.

In summary, the dimorphic chelae in *C. carnifex* displayed differences in function, anatomical scaling and force generation. In addition, although sexual dimorphism may have seemed subtle at first, many differences in claw design were found between sexes, and possible differences in function could be inferred. Through this study, we saw how mechanical design related to ecological function through correlations between dimorphic structures and their functional specialization.

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APPENDIX A

Kruskal-Wallis test and Tukey-Kramer test analysis of claw use frequency against observed activity. * signifies a Kruskal-Wallis P-value between .001 and .05, ** signifies a P-value over .05.

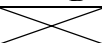| Claw(s) Used	Activity	Group			Mean Freq
Both Claws	Removing Dirt	A			1.000
	Foraging	A	B		0.590
	Eating	A	B		0.500
	Threat Display		B		0.214
	Fighting		B		0.000
* **Major Claw**	Fighting	A			1.000
	Threat Display	A	B		0.595
	Lead Claw Entering Burrow		B	C	0.228
	Foraging		B	C	0.218
	Eating			C	0.132
	Removing Dirt		B	C	0.000
Minor Claw	Lead Claw Entering Burrow	A			0.772
	Eating		B		0.368
	Foraging		B		0.192
	Threat Display		B		0.190
	Fighting		B		0.000
	Removing Dirt		B		0.000

APPENDIX B

Kruskal-Wallis test and Tukey-Kramer test analysis of claw use frequency against claw(s) used, by activity. * signifies a Kruskal-Wallis P-value between .001 and .05, ** signifies a P-value over .05.

Treatment	Tukey-Kramer Test	Group		Mean Frequency
* Eating	Both Claws	A		0.500
	Minor Claw	A	B	0.368
	Major Claw		B	0.132
Threat Display	Major Claw	n/a		0.595
	Both Claws	n/a		0.214
	Minor Claw	n/a		0.190
Foraging	Both Claws	A		0.590
	Major Claw		B	0.218
	Minor Claw		B	0.192
Lead Claw Entering Burrow	Minor Claw	A		0.772
	Major Claw		B	0.228
	Both Claws			n/a
** Removing Dirt	Both Claws	n/a		1.000
	Major Claw	n/a		0.000
	Minor Claw	n/a		0.000
** Fighting	Major Claw	n/a		1.000
	Both Claws	n/a		0.000
	Minor Claw	n/a		0.000

APPENDIX C

Scaling of claw measurements as a function of claw length. Scaling is reported as exponent (e) of base carapace length (CL) to which the measured parameter (X) scales in the equation:

$$X = bCL^e$$

b is a constant. * signifies a P-value between .001 and .05, ** signifies a P-value over .05.

Claw		Measurement	Sex	e	R^2
Major		dactyl length	Male	1.102	0.996
	*		Female	1.148	0.848
		dactyl height	Male	0.966	0.985
			Female	1.068	0.965
		Pollex length	Male	1.091	0.978
			Female	1.139	0.960
		manus height	Male	0.966	0.981
			Female	0.939	0.989
		Manus length	Male	0.901	0.969
			Female	0.886	0.956
		Manus width	Male	0.928	0.971
			Female	0.773	0.974
		in-lever	Male	0.962	0.983
			Female	0.986	0.974
		out-lever	Male	0.936	0.985
			Female	0.989	0.939
	**	MA	Male	0.027	0.075
	**		Female	-0.003	0.000
	*	apodeme area	Male	1.798	0.629
	*		Female	1.609	0.896
	**	muscle pennation angle	Male	-0.048	0.051
	*		Female	-0.204	0.660
Minor		dactyl length	Male	1.094	0.988
			Female	1.073	0.999
		dactyl height	Male	0.974	0.985
			Female	1.046	0.986
		Pollex length	Male	1.109	0.937
			Female	1.108	0.992
		manus height	Male	0.959	0.963
			Female	0.960	0.625
		Manus length	Male	1.050	0.866
			Female	0.877	0.961
		Manus width	Male	0.904	0.992
			Female	0.934	0.939
		in-lever	Male	1.124	0.971
			Female	1.248	0.935
		out-lever	Male	1.082	0.976
			Female	1.026	0.994
	**	MA	Male	0.042	0.017
	**		Female	0.222	0.282
		apodeme area	Male	2.084	0.922
	*		Female	1.420	0.785
	**	muscle pennation angle	Male	0.039	0.010
	*		Female	-0.234	0.624