Building a dishonest signal: the functional basis of unreliable signals of strength in males of the two-toned fiddler crab, *Uca vomeris*

Candice L Bywater[1*], Frank Seebacher[2] & Robbie S Wilson[1]

[1]*School of Biological Sciences, The University of Queensland, St Lucia QLD 4072, Australia*
[2]*School of Biological Sciences A08, The University of Sydney, NSW 2006, Australia*

* *Author for correspondence* (candice.bywater@uqconnect.edu.au)

Abstract

Males of many species use signals during aggressive contests to communicate their fighting capacity. These signals are usually reliable indicators of an individual's underlying quality, however, in several crustacean species, displays of weapons do not always accurately reflect the attribute being advertised. Male fiddler crabs possess one enlarged claw that is used to attract females and to intimidate opponents during territorial contests. After the loss of their major, claw males can regenerate a replacement claw that is similar in size but considerably weaker. As this inferior weapon can still be used to successfully intimidate rivals, it represents one of the clearest cases of unreliable signalling of strength during territorial contests. We investigated the functional mechanisms that govern signal reliability in the two-toned fiddler crab, *Uca vomeris*. Male *U. vomeris* exhibit both reliable and unreliable signals of strength via the expression of original and regenerated claw morphs. We examined the morphological, biomechanical and biochemical characteristics of original and regenerated claws to establish the best predictors of variation in claw strength. For a given claw size, regenerated claws have less muscle mass than original claws, and for a given muscle mass regenerated claws were significantly weaker than original claws. The mechanical advantage was also lower in regenerated claws compared with original claws. However, the activity of three catabolic enzymes did not differ between claw types. We concluded that the structural and physiological predictors of force production influence the frequencies of reliable and unreliable signals of strength in *U. vomeris*. This study furthers our understanding of the proliferation of unreliable signals in natural populations.

Summary Statement

Our understanding of the spread of unreliable signalling is largely theoretical and often doesn't consider the any functional constraints of an animal’s physiology. Our study examines the structural and physiological characteristics of reliable and unreliable signals of strength.

Keywords

signal reliability, claw regeneration, enzyme activity, muscle physiology, claw biomechanics, performance

Introduction

Males of many animal species use displays of weapons to signal aggressive intent and fighting capacity to opponents in order to avoid the potential costs of combat (Arnott and Elwood, 2010; Berglund et al., 1996; Kokko, 2013). The accuracy of the information transferred between opponents can govern the outcomes of these aggressive displays (Searcy and Nowicki, 2005). Signals of potential strength can effectively change an opponent's behaviour as both competitors in a bout can assess the likelihood of combat success should the dispute escalate to physical contact (Bradbury and Vehrencamp, 2011; Hughes, 2000). Most signals reliably reflect the intrinsic attribute being advertised by the signaller, assuming a strong correlation between the perceived quality (e.g. signal size) and the actual underlying quality (e.g. strength, fighting ability, resource holding potential) (Szamado, 2011a; Szamado, 2011b). For example, dewlap (throat fan) size in many *Anolis* lizards is a reliable signal of strength (Lailvaux and Irschick, 2007). Male anoles frequently engage in prefight displays involving extensions of their dewlaps and while they can be highly variable in size, dewlap size (perceived signal) is highly correlated with bite force (actual quality) (Lailvaux and Irschick, 2007). Theoretical models of signal reliability suggest that on average signals must be beneficial to both signaller and receiver in order to be evolutionarily stable, and signals should also transfer reliable information (Maynard Smith and Harper, 1995; Maynard Smith and Harper, 2003). However this is not always the case and under certain conditions unreliable signals can pervade signalling systems and be maintained in frequencies greater than initially theorised (Szamado, 2000; Szamado, 2008; Szamado, 2011b). Unreliable signals do not transmit accurate information to receivers and occur when the perceived quality (via signal size) becomes decoupled from the actual underlying quality (Lailvaux et al., 2009). Empirical evidence of such signals has been identified in several species of crustaceans via this mismatch of signal size and underlying quality; for example, high variability of claw size to strength relationships in crayfish (Walter et al., 2011; Wilson et al., 2007), bluff displays in stomatopods (Steger and Caldwell, 1983) and discrete phenotypic claw morphs in fiddler crabs (Backwell et al., 2000). In fact one of the best-studied examples of unreliable signalling has been described for the regenerated major claws of male fiddler crabs (e.g. Backwell et al., 2000; Bywater et al., 2014; Lailvaux et al., 2009; McLain et al., 2010).

Male fiddler crabs possess a greatly enlarged (major) claw that is used as a signal during both courtship displays and prefight assessment, and as a weapon during physical contests (Jordao and Oliveira, 2001; Lailvaux et al., 2009; Reaney et al., 2008). Claw size is considered to be the primary signal for male dominance and resource holding potential (RHP), and males with smaller claws retreat prior to physical contact more often than males with larger claws, and receive fewer visits from females (Lailvaux et al., 2009; McLain et al., 2010; Reaney et al., 2008). Following the loss of the major claw due to fighting or predator attacks, crabs can regenerate a replacement, however males with a regenerated claws were found to be competitively inferior compared with original-clawed males (Backwell et al., 2000; Crane, 1975). Although regenerated (leptochelous) claws grow to similar sizes as the original (brachychelous) claws, they lack morphological features like dactyl teeth and tubercules and are comparatively weaker (see Backwell et al., 2000; Lailvaux et al., 2009; McLain et al., 2010). Claw regeneration among male fiddler crabs can be widespread, and between 10-45% of a crab population bear regenerated claws (Bywater and Wilson, 2012; Callander et al., 2012; McLain et al., 2010). Backwell et al (2000) also established that the morphology of regenerated claws never developed to the original quality, even after multiple moult cycles. Fiddler crabs are unable to visually differentiate between the two claw morphs (Backwell et al., 2000; Lailvaux et al., 2009) and during the signalling stages of aggressive contests individuals with weaker regenerated claws are equally successful at acquiring resources (Lailvaux et al., 2009). Yet when combat does occur, individuals with regenerated claws are competitively inferior because claw strength, which is a critical determinant of fighting success, is lower for individuals with regenerated claws (McLain et al., 2010).

Unreliable signals of strength are common within the genus *Uca* and while modelling provides a theoretical understanding of how these signals evolve and remain in populations, the functional and mechanistic bases of these signals is poorly examined. We theorise that the capacity to produce these phenotypes is likely to be constrained by an individual’s underlying physiology. As such, the aim of the present study was to investigate the functional mechanisms underlying the development of unreliable signals of the two-toned fiddler crab, *Uca vomeris* McNeill 1920. We explored structural and physiological processes that may be driving this mismatch between claw size and strength in regenerated claws. Initially we examined whether changes in morphology between claw types were biomechanically constraining force production. We predicted that alterations in shape should affect the leverage of the claw and thereby reduce the maximum strength achievable in regenerated claws. We also assessed whether muscle physiology differed between claw types. We predicted that the reduced muscle strength seen in regenerated claws might be a by-product of reduced metabolic capacity.

Results

Size of the major claw did not significantly differ between claw types ($F_{1,104}$=2.57, t= 1.60, p=0.13). However, claw shape was significantly different between original and regenerated claw types for any given claw size ($F_{3,99}$ = 200.1, t=-23.15, $p < 0.001$) (Fig. 2A). Regenerated claws have longer dactyls and pollexes than original claws, but possessed a relatively smaller manus area. Claw strength increased significantly with claw size ($F_{2,100}$ = 144.8, t= 6.11, $p < 0.0001$), but regenerated claws were weaker than original claws ($F_{2,100}$ = 144.8, t= -16.63, $p < 0.0001$) (Fig. 2B). Claw size was also significantly associated with claw muscle mass, with larger claws possessing more muscle ($F_{3,99}$ = 136.5, t= 16.73, $p < 0.0001$) (Fig. 2C). However, the relationship between muscle mass and size differed significantly between claw types. Regenerated claws possessed significantly less muscle mass than original claws for any given size ($F_{3,99}$ = 136.5, t= -11.72 $p < 0.0001$). Claw strength increased significantly with total muscle mass of the claw ($F_{2,100}$ = 132.5, t= 5.36, $p < 0.0001$), however for a given muscle mass, regenerated claws were significantly weaker than original claws ($F_{2,100}$ = 132.5, t= -11.79 $p < 0.0001$) (Fig. 3A).

Claw strength was also influenced by the velocity ratio of the claw. Regenerated claws had a small velocity ratio as they had longer but thinner dactyls, whereas original claws had higher velocity ratios due to their shorter but wider dactyls ($F_{2,100}$ = 108.7, t= -3.452, $p < 0.0001$) (Fig. 3B). Enzyme activities did not differ significantly between claw types for all enzymes tested (values reported are means with standard error); lactate dehydrogenase (original= 32.28 ± 3.84 units^{-1}ml, regenerated= 37.16 ± 5.61 units^{-1}ml, $F_{1,19}$ = 0.43, p = 0.52), citrate synthase (original= 1.40 ± 0.14 units^{-1}ml, regenerated= 1.24 ± 0.15 units^{-1}ml, $F_{1,20}$ = 0.87, p = 0.36) and cytochrome c oxidase (original= 0.90 ± 0.16 units^{-1}ml, regenerated= 0.92 ± 0.13 units^{-1}ml, $F_{1,21}$ = 0.09, p = 0.77).

Discussion

Functional processes influence the production of the unreliable claw morphs in male *Uca vomeris*. We found that the mismatch between claw size and strength seen in regenerated major claws was affected in part, by both the structure and physiology of the claw. The capacity to generate force is limited by the leverage system of the claw, and is a function of the claw's dimensions (mechanical advantage), the muscle cross-sectional area and muscle characteristics (Levinton and Judge, 1993; McLain et al., 2010). Like previous studies of claw morphs in *U. mjobergi* (Reaney et al., 2008), we found that the regenerated claws of *U. vomeris* had reduced manus areas, longer dactyl lengths. Regenerated claws had significantly lower mechanical advantage than original claws, as a by-product of these changes in claw dimensions, which contributes to the lower closing forces observed.

Additionally, we identified that the differences in strength between claw morphs partially reflect the reduced muscle mass found in regenerated claws. Claw muscle mass fluctuates cyclically as a result of the tissue atrophy required for a crab to moult and grow (Ismail and Mykles, 1992; Skinner, 1966). During ecdysis, the major claw must undergo a large reduction in mass (up to 50% in *Uca pugnax*) in order to be withdrawn through a small joint at the base of the claw (Ismail and Mykles, 1992). Subsequent restoration of the muscle occurs once the new exoskeleton has formed. Muscle mass at any given time during this process, is governed by the balance between the rates of protein synthesis and protein degradation (Mykles, 1997). When synthesis exceeds degradation, protein accumulates and a net loss of protein is seen when degradation is up-regulated (Mykles, 1997). Muscle mass is also influenced by fluxing levels of growth hormones which can regulate rates of protein synthesis and degradation but also by capped numbers of myoblast satellite cells, which constrain the capacity for growth of new muscle tissue (Rai et al., 2014). Muscle atrophy and regeneration is a complex process that occurs on cellular and subcellular levels so it is difficult to pinpoint the direct cause of muscle mass variation. In saying that however, it is likely that tissue atrophy would affect both claw types equally, and the variability we see in muscle mass and strength within each claw type may be partially attributable to an individual's moult stage at the time of testing.

Even when accounting for the differences in muscle mass between claw morphs, regenerated claws were still weaker than original claws. Due to the importance of underlying strength for combat success and given the unreliable nature of regenerated claws as signals of strength, we predicted that differences in muscle physiology might be constraining the development of strong claws. Measuring the enzyme activity of original and regenerated muscle tissue provided a means to estimate the metabolic capacity of the claw muscle. However, we found no differences in the enzyme activity of LDH, CS and COX between regenerated and original claw muscle, which suggests that both claw types have similar cellular metabolic capacity.

This is also consistent with the observation that rates of oxygen consumption of muscle do not differ between claw types (Bywater et al., 2014). However, we would expect catabolic pathways to primarily regulate maximal oxygen consumption rates and not resting rates. Resting oxygen consumption rates are driven by ATP demand for protein synthesis and ATPase activities, and are not generally constrained by maximal enzyme activities (Horton et al., 2006; Seebacher and James, 2008; White and Kearney, 2013). The significant differences observed in whole-claw rates of oxygen consumption could be attributed to the reduced muscle mass found in the regenerated claws. As cell enzyme activity is often correlated with muscle fibre type (Mykles, 1988), we can infer that both claw morphs have similar fibre composition. However, further histochemical and biochemical examination of the claw muscle is required to identify and eliminate fibre composition as a potential driver of variability in claw strength.

While there were no enzymatic differences between claw types, other muscle characteristics may be affecting force production. The contractile ability of muscle fibres is known to influence claw strength. A single muscle fibre consists of longitudinally packed myofibrils and the efficiency of muscle contractions relies upon the complementary movements of thick and thin myofilaments located within each myofibril (Campbell et al., 2006). These filaments occur as small contractile units, called sarcomeres, which repeat along the length of the myofibril. Taylor (2000) found that sarcomere length provides a reliable measure of the size of muscle contractile units in claw muscle and that resting sarcomere length was highly correlated to maximum muscle force. The ratio of thick to thin filaments, as well as filament density, also affects fibre contractile ability and elimination of thin myofilaments during processes like atrophy leads to inefficient myofibril contractions thus reducing the fibre’s ability to generate force (Mykles, 1997; Mykles and Skinner, 1981; Mykles and Skinner, 1982). The arrangement of muscle fibres within the manus may also influence claw strength, as the bi-pennate muscle fibre arrangement found in crab claws increases the capacity to generate force compared to parallel-fibred muscles. Maximum force is dependent on the angle of pennation and a change in the angle of fibre attachment and arrangement effect an equivalent change in mechanical advantage (Alexander, 1983). It would be ideal to examine muscle fibre arrangement in both claw types to see if regenerated claw fibres attach differently. Additionally, the level of muscle innervation also influences myofibril functionality and can differ between individual muscle fibres (Atwood and Bittner, 1971; Dewell and Belanger, 2008; Rai et al., 2014). Innervation is fundamental for initiating myofibril contraction and any outside factors that influence the nerve supply will also affect the contractile ability (Rai et al., 2014). It is possible that regenerated muscles are unable to contract efficiently as a by-product of myofibrillar development or have a reduced nerve supply thereby constraining force production.

Furthering our knowledge of the structural and physiological predictors of force production, and the subsequent capacity to develop reliable signals, should allow for a greater understanding of the proliferation of unreliable signals in natural populations. We suggest that the functional constraints of major claw development, in part, influence the frequencies of reliable and unreliable signals of strength in *U. vomeris*. However, while were able to empirically identify some of the functional predictors driving the variation in force production within the major claw, an explanation for why such a disparity remains between size and strength across claw types is largely theoretical. The regeneration of unreliable major claws in the fiddler crab is widespread and given the importance of claw displays during signalling, and of underlying strength for combat success, it is important to understand how and why these unreliable signals develop. Claw size plays a large role in determining the success or failure of both mating and combat displays in many fiddler crab species, with larger-clawed individuals prevailing more often than not (Callander et al., 2013; Reaney, 2009; Reaney et al., 2008). It is thus unsurprising that an individual regenerating a claw would devote resources into developing a large claw quickly, whilst not investing in the metabolically costly muscle within. Yet, regardless of the explanations behind any physiological changes observed in the regenerated claw, it remains an inferior performer during combat (McLain et al., 2010). With this in mind, it is hard to reconcile the potential negatives of combat failure including loss of territory or mating opportunities, with the benefits an individual may gain from reduced muscle development either via changes in claw shape or muscle quality. An additional question that remains unanswered is why claw dimensions change during regrowth, particularly as these changes negatively impact on closing force, and it would be ideal to examine the internal and external growth patterns of the major claw throughout the regeneration process. Callander *et al* (2013) suggest that it is sexual selection via male-male combat that could be driving shape variation in *Uca mjobergi* as females only responded to claw size and wave rate and did not select mates based on claw shape. If this is the case, claw development during regeneration should be balanced between sexual selection driven by female choice and sexual selection driven by male-male combat. In *U. vomeris* at least, claw development appears skewed by female choice given that claws are large but weak, however evaluating this theory with any confidence is beyond the scope of our study. Many questions regarding the development of regenerated claws and the evolution of unreliable signals remain unanswered and open for further empirical and theoretical investigation.

Methods

Animal collection and morphological measurements

We collected 104 male *Uca vomeris* (original claws=75; regenerated claws=29) for morphological and biomechanical analyses, from two mudflats in south-east Queensland (SEQ), Australia between October 2009 to March 2010. An additional 23 males (original claws=13; regenerated claws=10) were collected for biochemical analyses. Crabs were collected by hand and housed in 40 L tubs (54cm x 40cm x 20cm) containing a gravel substrate and shelter. Tubs were maintained at 23°C ± 1°C (SE) with fewer than 10 individuals per container. All individuals were tested within one week of collection and then returned to their site of capture. We took morphological measurements of each individual including body mass; carapace width (anterolateral angle to anterolateral angle), length and depth; claw muscle mass; claw shape; and claw size. To measure claw size and shape, photographs were taken of each major claw using a digital camera (Sony, model#DSC-W5), against a background of graph paper for calibration. Digital images were analysed using morphometric software (SigmaScan Pro5, Systat Software Inc., San Jose, California, USA) and seven measurements were recorded for each claw (Fig. 1A) (refer to, Bywater and Wilson, 2012). These measurements included: 1) width at heel, 2) width at dactyl/manus joint, 3) length of manus from heel to joint, 4) width of pollex at dactyl joint, 5) width of dactyl (at joint), 6) length of pollex (tip to joint), and 7) length of dactyl (tip to joint). We ran a Principal Components Analysis (PCA) using the seven measurements recorded for all individuals combined to provide an overall measure of claw size (PC1) and shape (PC2). These measures were selected based upon the co-variation and loadings generated for each principal component (Table 1) and only two principal components were retained for analyses based upon the generated scree diagram and ‘elbow’ method. Principal component one was used as a measure of claw size as all vectors loaded in the same direction and 87% of data variation was explained within one component. PC2 accounted for an additional 10% of variation in the data and denoted claw shape, as manus size negatively co-varied with dactyl length. Original and regenerated claws in *U. vomeris* were identified via differences in claw morphology and the presence or absence of claw tubercles as per Lailvaux *et al*. (2009) and Backwell *et al*. (2000) (Fig. 1B,C).

Maximum claw strength of the major claw was measured for all males using a custom-built force transducer which records the flexion of metal plates via a strain gauge (for further details refer to Bywater and Wilson, 2012). Each crab was encouraged to close the tip of it's claw on the transducer plate at least five times, then rested for 5 minutes before repeating the procedure. The greatest claw closing force recorded for each individual was taken as their maximum claw strength. To avoid the claw slipping on the metal plate, and to ensure maximum repeatability, a small piece of thin cloth tape was adhered to the top as a target. The tape did not affect force recordings and was included in all calibrations. The transducer was calibrated daily using known weights and output data were converted from millivolts (mV) into Newtons (N) for analyses. Claw strength was square-root transformed to achieve normality (Quinn and Keough, 2002) and transformed values were used in all analyses.

Biomechanical analyses

We performed an examination of the biomechanical constraints on force production. The claw is a simple lever system; force is applied via the contraction of claw muscle (F_1), which is transmitted through the in-lever (dactyl height, L_1) to the out-lever (dactyl length, L_2) via the dactyl pivot (muscle attachment), to produce a closing force along the dactyl (F_2) (Fig. 1D). When L_2 is longer than L_1, the lever reduces the overall input force, thus claws produce less force when the dactyls are longer. We calculated the velocity ratio (VR; L_1/L_2) at the dactyl tip for original and regenerated claws as an approximation of their mechanical advantage (MA; F_2/F_1). MA represents the ability of a claw to produce force efficiently. We assume the dactyl pivot point to be relatively frictionless, thus MA is nearly equal to VR (Alexander, 1983). Velocity ratios were calculated by dividing dactyl height by dactyl length as per Warner and Jones (1976).

Biochemical analyses

Metabolic enzyme assays were performed on 23 individuals (original, n=13; regenerated, n=10). After morphological and force measurements were collected, the major claw was removed by squeezing the base of the claw near the body, causing the crab to self-autotomize their claw. Muscle tissue samples (~0.05 g) were then dissected out, placed in cryo-Eppendorf tubes and immediately transferred into liquid nitrogen. Samples were maintained at -80°C for up to three weeks until testing occurred. We measured maximal activities of lactate dehydrogenase (LDH), which catalyses the conversion of pyruvate to lactate, thereby releasing ATP in the absence of oxygen. In addition, we measured the activities of two mitochondrial enzymes, citrate synthase (CS) and cytochrome c oxidase (COX), which control flux through the citric acid cycle and the electron transport chain respectively. Muscle tissue was homogenised in nine volumes of cold extraction buffer (pH 7.5) consisting of 50 mmol l^{-1} imidazole, 2 mmol l^{-1} $MgCl_2$, 5 mmol l^{-1} ethylene diamine tetra-acetic acid (EDTA), 0.1% Triton and 1 mmol l^{-1} gluthathione, and samples were kept on ice during processing. The homogenate was further diluted to 1:100 for LDH assays. Enzyme activities were measured using an UV/visible spectrophotometer (Ultrospec 2100pro, GE Healthcare, USA) equipped with a temperature-controlled cuvette holder. All assays were performed at 25°C and carried out in duplicate as per the methods outlined in Seebacher et al. (2003).

Statistical analyses

All statistical analyses were performed using R (Version 2.12.2) or JMP (Version 8). Statistical significance was taken at the level of $p < 0.05$. ANCOVAs were used to compare the differences between claw types for morphological and biomechanical analyses with claw size, claw muscle mass or VR as covariates. ANOVAs were used to compare the activity of enzymes between claw types.

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Competing Interests

The authors declare no competing financial interests.

Author Contributions

C.L.B., R.S.W. and F.S. conceived and designed the experiments, C.L.B. collected and analysed the data, and C.L.B., R.S.W. and F.S. wrote the manuscript.

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Figures

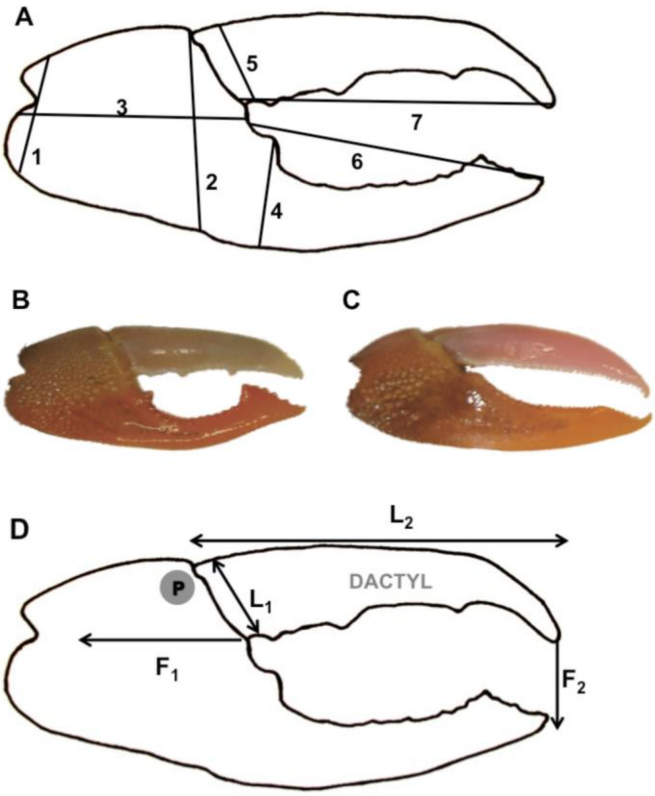

Fig. 1 (A) A diagram showing the seven measurements recorded to describe claw size and shape of the major claws of the two-toned fiddler crab (*Uca vomeris*); an example of the (B) original and (C) regenerated major claws; and (D) a diagram of the forces applied during the closing of the major claw, where L_1 is dactyl height (in-lever), L_2 is dactyl length (out-lever), P is the pivot point for muscle attachment, F_1 represents the force generated from muscle contraction and F_2 represents the closing force along the dactyl. Force is applied via the contraction of the claw muscle (F_1) which transmits through the in-lever (dactyl height, L_1) and the out-lever (dactyl length, L_2) via the dactyl pivot resulting in closing force along the dactyl (F_2) (adapted from Fig. 1.4 in Alexander (1983)).

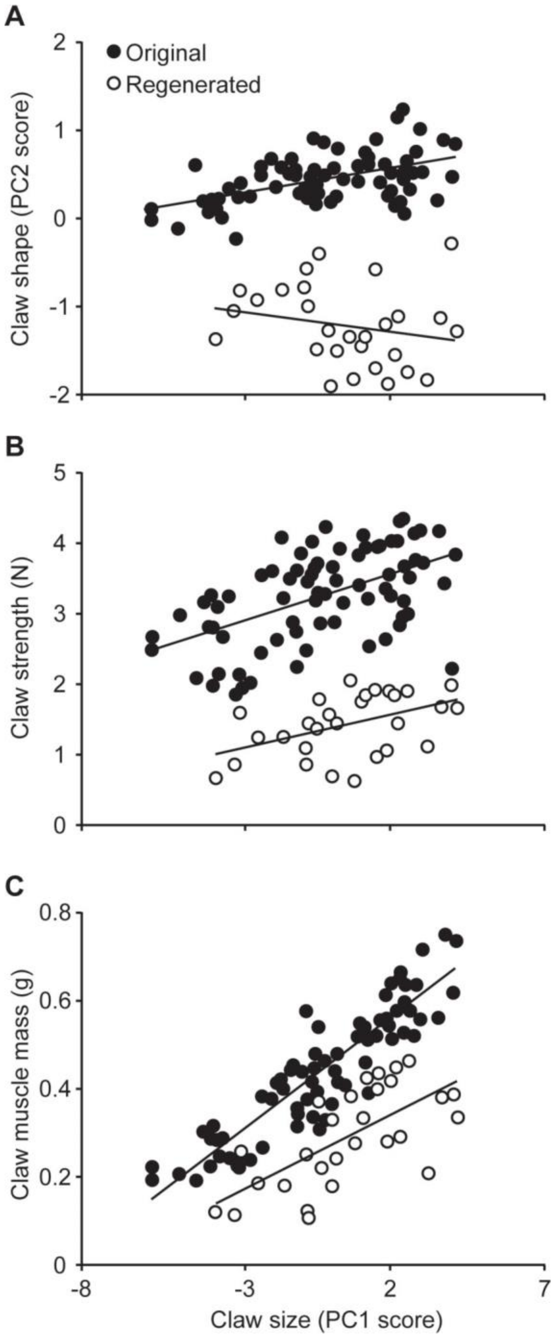

Fig. 2 The relationship between claw size (PC1) and; (A) claw shape (PC2), (B) claw strength (N) and (C) claw muscle mass (g), for male two-toned fiddler crabs (*Uca vomeris*) with original (black) and regenerated (white) major claws. Claw shape in regenerated claws was significantly different between types ($F_{3,99}$ = 200.1, t=-23.15, p < 0.001) whereby regenerated claws had longer dactyls than originals, but with a comparatively reduced manus area (negative PC2 values). Claw strength significantly increased with claw size ($F_{2,100}$ = 144.8, t= 6.11, p < 0.0001) yet differed between claw types ($F_{2,100}$ = 144.8, t= -16.63, p < 0.0001), with

regenerated claws being significantly weaker than original claws. Larger claws had more muscle ($F_{3,99} = 136.5$, $t = 16.73$, $p < 0.0001$), however the relationship between muscle mass and size was significantly different between types. Regenerated claws were significantly lighter than original claws for any given size ($F_{3,99} = 136.5$, $t = -11.72$ $p < 0.0001$).

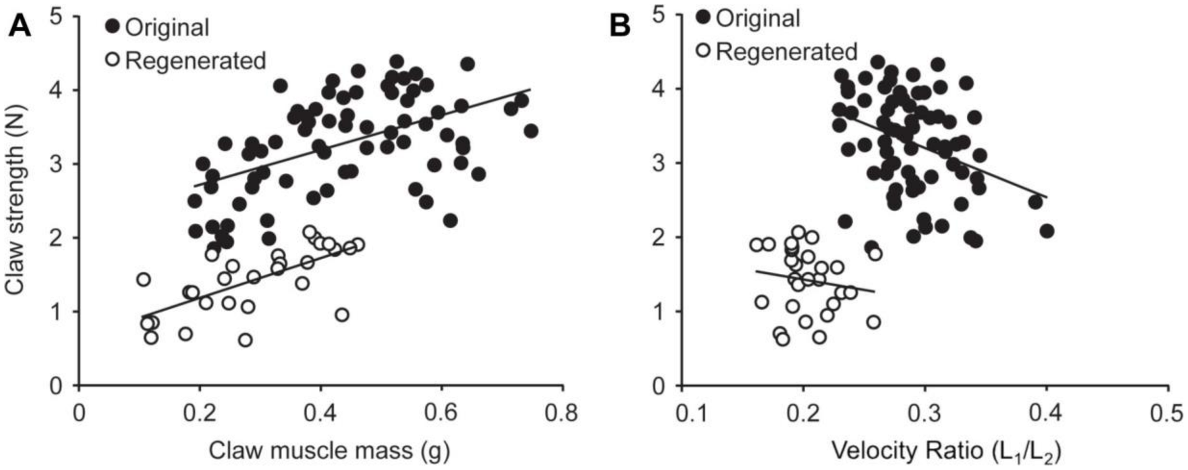

Fig. 3 The relationship between claw strength and; (A) claw muscle mass and (B) velocity ratio, for male two-toned fiddler crabs (*Uca vomeris*) with original (black) and regenerated (white) major claws. Claw strength significantly increased with total muscle mass of the claw ($F_{2,100}$ = 132.5, t= 5.36, $p < 0.0001$), however for a given muscle mass regenerated claws were significantly weaker than original claws ($F_{2,100}$ = 132.5, t= -11.79 $p < 0.0001$). Regenerated claws have relatively long but thin dactyls (small velocity ratio) and are significantly weaker than original claws that have shorter but wider dactyls ($F_{2,100}$ = 108.7, t= -3.452, $p < 0.0001$).

Tables

Table 1 The principal component loadings of claw measurements. Values represent the relative contribution of each of the seven claw measurements towards the data variation explained by each principle component. PC1 represents claw size as all values have similar loadings in the same direction. PC2 represents claw shape and describes variation in claw proportions between the manus and dactyl/pollex.

	Claw measurement	PC1	PC2
1	width at heel	-0.39	-0.20
2	width at dactyl/manus joint	-0.40	-0.16
3	length of manus from heel to joint	-0.37	-0.45
4	width of pollex at dactyl joint	-0.38	0.35
5	width of dactyl (at joint)	-0.37	-0.44
6	length of pollex (tip to joint)	-0.37	0.47
7	length of dactyl (tip to joint)	-0.37	0.44

Table S1. Raw dataset used for all statistical analyses.

id	type	mass	width	length	depth	c1	c2	c3
b1m10	o	3.13	20.26	14.05	10.68	6.16256999	9.0908807	9.86500905
b1m11	o	2	17.58	12.37	8.98	4.80268683	7.37880471	8.42505177
b1m12	o	4.4	22.68	15.73	11.78	6.6638182	10.1650862	11.162953
b1m13	o	2.6	19.69	12.82	10.42	5.20975779	8.53174511	9.2557563
b1m15	o	2.35	19.49	12.89	10.16	4.95476831	7.43007463	8.44571445
b1m17	o	2.57	22.55	12.12	10.35	5.4939387	8.07697164	8.68172229
b1m19	o	3.66	21.19	14.65	10.6	6.70085786	9.81989562	10.7607856
b1m5	o	2.46	18.79	13.03	9.59	5.69563115	7.97273761	9.03506291
b1m6	o	2.9	20.23	14.09	10.92	6.28132394	8.82832395	9.29669957
b1m7	o	5.44	25.01	16.74	13.12	7.06367294	10.9179342	12.5994137
b1m8	o	4.48	24.25	15.51	12.78	7.45694421	10.6998699	11.9133784
b1m9	o	4.3	21.32	14.51	11.72	6.91421313	10.0140459	11.7216844
b2m15	o	4.75	23.68	15.71	13.25	7.11116799	10.5152247	11.8243121
b2m19	o	5.04	23.19	15.74	12.45	7.65843884	11.3395004	12.9139854
b2m2	o	4.35	22.18	15.55	12.28	7.06916466	10.3280102	11.7646055
b2m21	o	4.47	22.44	15.84	11.42	6.66734569	9.93769122	11.3330246
b2m22	o	2.39	18.73	12.68	9.7	4.89759212	7.85627573	8.7903198
b2m30	o	4.31	22.21	15.61	12.19	6.88490584	10.2290428	11.6947284
b2m31	o	2.64	18.66	13.14	10.31	5.67434705	8.47197991	9.68447921
b2m4	o	2.47	19.01	13.17	10.49	4.65257196	7.76479768	9.89359221
b2m6	o	3.54	21.01	14.64	12.04	6.94346489	9.76410894	10.454505
b2m7	o	3.96	22.02	15.47	11.97	6.55498604	9.56658592	10.6327515
b3m10	o	5.76	23.64	16.73	12.41	6.62928261	10.6914302	12.0858224
b3m13	o	7.27	26.39	18.64	14.31	7.50697357	11.5842435	13.7790935
b3m14	o	7.46	28.19	18.65	13.45	8.71044906	12.3235165	14.1547753
b3m16	o	6.28	26.32	17.62	13.22	7.45776878	11.1475017	11.1487091
b3m17	o	7.51	26.98	18.08	14.19	8.33447999	12.6355274	13.8881936
b3m18	o	6.71	26.86	17.77	13.7	7.97313856	11.8889671	13.2059953
b3m19	o	4.86	23.35	16.11	12.31	7.06627609	10.3231549	10.3935978
b3m21	o	7.89	28.17	18.64	19.71	8.82811881	13.1367493	14.3258876
b3m22	o	4.39	22.81	15.77	12.43	6.39536769	9.6232963	11.1909441
b3m23	o	6.16	24.83	16.56	12.9	7.72040587	11.4702752	12.456732
b3m24	o	2.26	18.49	12.66	9.91	4.92498009	7.29586857	8.54433896
b3m25	o	6.46	25.04	17.42	13.3	7.12421318	11.7091849	13.0022161
b3m26	o	6.43	25.85	17.02	13.72	8.0712884	11.5202981	13.7810922
b3m27	o	6.94	26.37	17.52	13	8.21729897	12.2279112	13.148232
b3m28	o	2.64	19.19	13.42	9.83	4.57572742	7.59194822	8.6851618
b3m3	o	7.55	27.07	18.19	13.27	8.62863583	13.0510115	14.1156185
b3m5	o	5.14	24.16	16.03	12.13	7.46765433	10.5577852	11.7684033
b3m6	o	6.35	25.27	17.27	13.47	7.57074694	11.645338	12.4789291
b3m7	o	4.25	21.96	15.25	11.56	6.89459537	10.0758743	11.6478218
b3m8	o	6.91	25.71	17.89	13.36	8.17061787	12.1970465	13.6214986

b4m11	o	3.43	21.48	14.07	10.54	6.68477778	8.88412364	10.0273581
b4m14	o	3.14	20.14	13.6	10.05	6.74980588	9.23170868	9.97371168
b4m15	o	4.26	21.9	15.05	11.69	6.59538853	9.84150155	10.9605576
b4m17	o	4.51	23.29	15.02	10.87	7.60690475	10.4689299	11.2577729
b4m19	o	1.31	15.74	10.38	7.79	4.03462862	5.88131479	6.76051099
b4m2	o	1.6	16.6	11.03	8.79	4.15199615	6.53473731	7.50874734
b4m21	o	3.22	19.54	13.71	10.38	6.26680834	8.82366392	10.1178318
b4m3	o	2.45	19.3	13.1	9.71	5.56037199	7.54156543	8.24568846
b4m4	o	1.95	17.27	11.66	9.37	5.22566051	7.50112877	8.4353877
b4m6	o	3.89	21.53	14.55	11.54	6.6595531	9.66115999	10.9612163
b4m8	o	1.45	16.16	10.61	8.16	4.24139819	5.99988848	6.51070712
b4m9	o	2.21	17.75	12.44	9.66	5.20419146	7.65311912	7.95027297
b5m11	o	8.17	27.04	17.54	14.28	8.9966216	13.385484	14.7038239
b5m13	o	6.52	25.52	18.04	13.61	7.91899818	11.8824431	12.7700561
b5m14	o	6.24	25.42	17.31	13.37	7.63309188	11.4742998	13.0834527
b5m17	o	8.72	29.65	19.17	14.16	9.2094604	13.5237266	15.7713
b5m19	o	4.05	23.19	15.15	11.3	6.58437966	9.95357767	10.9007832
b5m20	o	6.45	25.43	16.88	12.53	7.44782277	12.2679734	13.3291419
b5m21	o	7.22	27.48	18.63	13.64	8.24247951	12.5120198	14.2421394
b5m22	o	6.84	26.29	17.8	13.71	8.51197559	12.4291822	13.0940412
b5m23	o	6.09	24.69	16.99	12.67	8.34707304	11.7721338	12.9987322
b5m24	o	3.51	20.68	14.04	10.39	6.6014749	9.469604	10.734384
b5m25	o	3.47	21.16	14.75	10.95	6.60872389	9.67434698	10.5215873
b5m26	o	6.85	25.7	17.77	13.05	8.1064239	11.9298744	13.0649654
b5m27	o	6.4	23.84	16.77	12.17	8.08093961	12.1867057	14.1235037
b5m28	o	6.73	25.37	17.48	13.06	8.88664952	13.2151924	13.7981074
b5m29	o	5.88	25.29	16.86	12.83	8.01329459	11.8472386	13.4193368
b5m30	o	4.78	23.07	15.99	12.93	6.88962688	10.4031779	11.7849681
b5m31	o	6.48	26.15	17.26	12.6	8.14365475	11.9250399	13.1551245
b5m32	o	6.94	24.52	16.47	12.06	7.9892006	11.755646	13.1872911
b5m33	o	7.17	25.87	17.83	13.08	8.45042249	12.1880693	13.0050803
b5m34	o	7.76	27.13	18.25	13.49	9.09123835	13.0638889	14.3943551
b5m35	o	8.01	26.51	17.88	13.02	9.57806495	13.8485986	14.907689
b5m36	o	4.08	21.56	14.64	10.14	5.92174566	9.54007979	10.579074
b5m37	o	2.33	18.45	12.35	9.37	4.54412517	7.2988658	8.76789099
exm1	r	3.76	23.8	15.87	11.54	6.09094741	9.40348867	9.63685559
exm2	r	2.6	20.55	13.58	10.8	6.82485589	10.1161905	9.92499586
exm3	r	3.05	21.46	14.88	11.11	5.67387197	8.96624432	9.13392183
exm4	r	4.13	24.92	17.25	12.81	5.26752642	7.98061512	7.97987544
exm5	r	5.1	23.18	15.77	13.08	9.31159162	13.3883141	14.0796858
exm8	r	4.79	24.26	16.11	11.52	9.55084141	13.1428643	12.4938294
exm11	r	4.34	23.07	15.89	13.08	7.95166974	12.1400602	11.3135541
exm12	r	4.84	23.61	16.41	12.34	8.92617231	12.8092862	12.924775
exm14	r	3.22	21.71	14.97	11.9	6.02399546	9.88590551	9.92033089
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b3m2	r	5.62	27.04	17.74	13.4	6.12404301	9.29474397	9.87917009

b3m9	r	6.24	27.5	18.04	13.64	7.00629102	10.5691817	10.119364
b4m12	r	2.82	19.53	13.27	10.35	5.15259784	8.1021641	8.26814808
b4m13	r	4.64	24.57	15.71	12.08	6.97199756	10.0237169	9.60407071
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b5m3	r	5.56	24.77	17.07	13.22	6.98997955	10.762021	10.3913376
b5m4	r	6.39	26.62	17.82	13.36	6.58768174	10.2333068	10.2989406
b5m5	r	4.23	23.47	15.41	11.31	6.15530165	9.7157554	9.34743267
b5m6	r	5.91	24.57	17.07	12.58	6.85587837	10.6166181	11.1687807
b5m7	r	4.6	23.66	16.47	13.07	6.34417668	10.0777693	9.66239859
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b6m1	r	4.6	22.61	15.55	11.27	6.29676389	9.87997772	9.19986107
b6m10	r	6.18	24.62	17.5	12.22	7.76231096	11.8368157	12.857881
b6m2	r	4.01	22.59	16.64	12.39	4.27364453	7.17288948	6.92110254
b6m3	r	5.82	26.59	17.1	12.42	7.51660562	11.3478834	12.0651289
b6m4	r	6.87	26.62	18.67	13.7	7.87896538	11.3713205	11.2363934
b6m5	r	5.93	24.99	18.34	13.53	7.76289528	11.0380162	11.6114076

c4	c5	c6	c7	m_a	g	n
4.75888592	3.77064286	11.203822	11.777323	0.32016129	1269.32832	12.4394175
3.53184959	3.23297858	8.16356501	8.06799313	0.40071658	435.35232	4.26645274
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4.5958513	3.74673981	10.8647706	10.9569975	0.3419495	376.83574	3.69299025
4.17600696	3.33306768	9.60539991	9.84822663	0.33844344	394.35944	3.86472251
4.27728196	3.48237911	10.0070424	10.6574363	0.3267558	1071.68854	10.5025477
5.24627069	4.17920896	13.7281602	13.9700197	0.29915555	501.48258	4.91452928
4.35459784	3.56130971	11.1401221	11.8275332	0.30110334	457.76016	4.48604957
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6.51049344	4.95189149	17.9001994	17.5360702	0.28238319	1170.43056	11.4702195
5.59124446	4.77934892	16.0365308	16.2346695	0.29439151	1574.10864	15.4262647
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5.87798766	4.35827975	14.9522401	15.9815245	0.27270739	1807.36855	17.7122118
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5.35236499	4.2452882	14.8001278	15.0394032	0.2822777	1504.82626	14.7472974
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7.69471667	4.95219044	18.8855628	18.5955653	0.26631029	1281.105	12.554829
6.67661846	4.91931622	21.6383979	21.3432723	0.23048557	1254.96	12.298608
6.64306201	4.81834415	20.2089553	21.4087444	0.2250643	332.415	3.257667
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4.07145215	3.12940239	9.60887626	10.2402395	0.30559856	799.29	7.833042
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5.02577626	4.1503664	12.6168314	13.110739	0.31656235	1048.0008	10.2704078
6.17644009	4.50841246	13.9965757	14.405874	0.31295654	1635.11194	16.024097
5.64510744	4.68408594	16.1129837	16.3351235	0.28674934	832.46856	8.15819189
3.0701177	2.63778223	6.53296435	6.74199123	0.39124676	618.08978	6.05727984
3.71796819	2.84944627	8.48923619	8.80609473	0.32357661	894.7554	8.76860292
5.1050973	4.12616005	11.4728433	12.0921892	0.34122523	1321.20604	12.9478192
4.25302025	3.25349976	10.5573604	11.0547572	0.29430766	723.05464	7.08593547
4.11528628	2.99245689	9.70842568	9.73189728	0.30748957	1068.43352	10.4706485
5.67210192	4.20994406	14.8280416	15.2429002	0.27619049	1204.37702	11.8028948
2.94151166	2.54914564	6.83904909	7.39171807	0.34486511	717.78168	7.03426046
4.2721347	3.31709651	9.16027869	9.67769185	0.34275699	786.16538	7.70442072
7.63626914	5.93303601	21.1198534	21.7084141	0.27330582	1186.01287	11.6229261
6.80236548	5.28462298	18.7918259	20.086552	0.26309259	219.12779	2.14745234
6.36772685	4.77896807	16.9842267	17.5814169	0.27181928	1724.63564	16.9014293
7.69048764	5.73564893	22.0884779	22.7772673	0.25181462	1495.22492	14.6532042
5.40987538	4.22559486	14.8373937	15.3445125	0.2753815	615.09301	6.0279115
7.5750282	5.2542966	20.0181517	20.2754755	0.25914542	821.91025	8.05472045
7.58750139	5.59506375	20.0070165	19.4778574	0.28725253	1431.49972	14.0286973
6.97810529	5.55377071	19.6182115	20.2519871	0.27423337	903.15988	8.85096682
6.09172157	5.06497229	18.024282	18.0873907	0.2800278	1588.92993	15.5715133
5.06587786	4.05615322	13.3760108	13.9725255	0.29029492	1235.54473	12.1083384
5.48890248	4.29420007	12.5738655	12.9839958	0.33073024	838.5657	8.21794386
6.81934708	5.5869873	20.8669968	20.5997169	0.2712167	883.89749	8.6621954
7.13436532	5.57049696	17.8172681	17.8871502	0.31142451	1888.87286	18.510954
6.94555891	5.28887964	17.5014394	17.816767	0.29684845	1364.87792	13.3758036
6.93267486	5.04237601	18.6594283	18.2046776	0.27698244	704.45312	6.90364058
5.68308701	4.06099804	15.4659719	15.166028	0.26776939	1090.28024	10.6847464
7.32420703	5.16376138	20.4881614	21.7373527	0.23755245	1026.98953	10.0644974
7.13374132	5.13062622	18.3853514	17.9756935	0.28542021	1144.73632	11.2184159
7.09896543	4.80564258	19.2700097	19.1218775	0.25131646	1063.0522	10.4179116
7.01063305	5.02665568	20.7387116	21.8393495	0.23016508	1406.15447	13.7803138
8.34925873	5.31043393	20.9024455	22.5839764	0.23514167	495.17377	4.85270295
5.71090366	4.08343411	11.5482372	12.2286486	0.33392358	1693.49719	16.5962725
3.88608136	3.11667195	9.23557801	9.81181723	0.31764472	1010.33408	9.90127398
6.39333506	3.92293962	17.1266756	18.3476962	0.21381102	204.09255	2.00010699
6.87415131	4.19544517	15.5728394	16.1549261	0.25970067	316.04205	3.09721209
6.10627133	3.72943547	15.4608944	15.6157962	0.23882455	155.86815	1.52750787
4.99015572	2.77623019	13.3273729	13.7303424	0.20219672	70.95876	0.69539585
8.10876022	5.19096065	23.8208447	25.0425956	0.20728525	397.67907	3.89725489
9.14341461	4.97698873	26.0533118	25.6454278	0.19406924	271.95117	2.66512147
8.31933641	4.58443115	21.6293973	22.4069645	0.20459849	208.05384	2.03892763
8.6833522	4.78491027	24.8819826	25.0395847	0.19109384	281.59605	2.75964129
6.36624	3.77577074	16.5912364	16.7651859	0.22521496	120.21654	1.17812209
8.43182788	4.46356121	26.3986223	26.7754865	0.16670327	123.255	1.207899
6.04405613	4.21277109	17.5465089	16.3406529	0.25780923	70.965	0.695457

7.23756245	4.40982372	22.4206201	21.6110092	0.2040545	306.27	3.001446
5.11286164	3.09221126	13.1768536	13.5164128	0.22877455	253.7612	2.48685976
6.91782967	3.87799954	20.7353544	20.1045776	0.19289137	207.95236	2.03793313
5.73411553	3.34763794	13.8728593	14.4493768	0.23168044	154.67844	1.51584871
7.23649414	4.01444884	20.7349455	20.404998	0.19673851	427.10367	4.18561597
7.61321785	4.47232429	23.2922186	23.4525637	0.19069661	368.59235	3.61220503
7.38223336	4.02191724	22.7619109	21.9574617	0.18316859	36.49716	0.35767217
6.98244372	3.85754043	21.3492249	21.2767179	0.18130336	45.04213	0.44141287
7.11446369	4.28771909	22.3858464	22.4208702	0.19123785	334.70213	3.28008087
6.98370965	4.04735628	19.596632	18.7878311	0.21542435	250.12141	2.45118982
7.7052727	4.49851286	25.8528943	26.1687601	0.17190394	362.79915	3.55543167
7.65645898	3.97398565	24.8617177	24.5666797	0.16176324	361.93017	3.54691567
6.97501707	3.67079843	18.5880105	18.7245108	0.19604242	185.79912	1.82083138
7.3940984	4.74730647	20.0643663	20.9476293	0.22662739	479.43298	4.6984432
5.04175077	2.91225711	12.9035305	13.6421455	0.21347501	41.92812	0.41089558
7.82636423	4.2618333	22.4673345	22.1795315	0.19215164	109.89004	1.07692239
8.46751102	4.34879335	23.1257019	22.6719459	0.19181386	342.13894	3.35296161
6.70749909	4.69233652	21.7233898	21.31556	0.22013668	88.65194	0.86878901

sqrtn	n/g	resid.n	comp1	comp2	negcomp1	negcomp2	pc1
3.52695585	86.2650315	5.35693372	2.1686	-0.59	-2.1686	0.59	0.1798
2.06553933	117.21024	-1.8536918	4.2892	-0.6162	-4.2892	0.6162	0.6734
3.54005297	73.1153735	4.7301192	0.5834	-0.4875	-0.5834	0.4875	0.3984
1.92171545	62.3815921	-3.097833	2.8113	-0.4085	-2.8113	0.4085	0.677
1.96588975	39.5975667	-2.4998869	3.7505	-0.2207	-3.7505	0.2207	2.1348
3.24076344	181.704977	3.90068895	3.2277	-0.3485	-3.2277	0.3485	4.9894
2.21687376	50.9277646	-2.6945955	1.0081	-0.5628	-1.0081	0.5628	-0.7227
2.11802964	92.4958674	-2.2694222	2.8892	-0.2484	-2.8892	0.2484	-0.3129
2.42750699	84.423928	-1.1957746	2.1552	-0.5041	-2.1552	0.5041	0.1383
3.38677125	42.8312901	2.96437569	-0.9679	-0.4353	0.9679	0.4353	0.6132
3.92762838	90.370619	7.21067467	-0.3283	-0.7959	0.3283	0.7959	0.7321
3.61366594	66.4558857	5.2081232	0.4763	-0.9331	-0.4763	0.9331	-1.473
3.65908276	102.518274	5.26523755	-0.1257	-0.1979	0.1257	0.1979	0.3681
2.51724824	42.3282477	-2.3225098	-1.3055	-0.6309	1.3055	0.6309	-2.3321
4.20858786	82.8060392	9.69398167	0.1066	-0.4927	-0.1066	0.4927	-1.0824
3.69943033	89.5080757	5.79521005	0.3879	-0.1718	-0.3879	0.1718	-0.2178
2.12089849	75.2209095	-1.9652831	3.5326	-0.2224	-3.5326	0.2224	0.767
2.84491213	87.973098	0.16242549	0.2986	-0.2951	-0.2986	0.2951	-0.7013
2.00050604	71.720868	-2.9104186	2.5433	-0.2596	-2.5433	0.2596	-1.1097
1.83619831	67.703298	-3.3440488	2.9769	0.2208	-2.9769	-0.2208	0.1985
2.73336039	64.0759779	-0.120848	1.0456	-0.5267	-1.0456	0.5267	-0.9041
3.840221	77.3730186	7.08666572	0.8946	-0.2958	-0.8946	0.2958	0.1579
3.44905422	52.4282724	3.70874782	-0.2658	-0.264	0.2658	0.264	0.1176
3.54327941	43.1585734	3.61224308	-1.9303	-0.2858	1.9303	0.2858	0.6207
3.50693713	37.4386849	3.03772312	-2.6317	-0.3509	2.6317	0.3509	1.5116
1.80490083	25.7930879	-5.41731	-1.3406	0.4813	1.3406	-0.4813	1.5202
4.12557814	63.3434872	7.70764018	-2.746	-0.5306	2.746	0.5306	-0.1949
4.00858042	61.5188247	7.07802773	-2.0363	-0.5333	2.0363	0.5333	0.9623
3.18418451	44.8828287	2.26193429	0.4176	-0.5403	-0.4176	0.5403	0.9198
4.16091564	55.6516201	7.63701161	-3.5469	-0.2203	3.5469	0.2203	-0.1542
3.59964748	102.755448	5.35900168	1.0316	-0.5376	-1.0316	0.5376	1.4018
3.81200617	49.0262854	6.02069148	-0.9786	-0.6174	0.9786	0.6174	0.2542
2.79875722	161.839711	1.51871423	3.8613	-0.1058	-3.8613	0.1058	1.0721
3.20138095	39.2074981	1.60853372	-1.2642	-0.7103	1.2642	0.7103	0.0693
3.95341384	51.0267091	6.80842411	-1.6625	-0.4171	1.6625	0.4171	0.3421
4.01770121	48.7818767	7.07735424	-2.1991	-0.1702	2.1991	0.1702	-0.0065
3.09085474	121.389873	3.11811615	3.5948	-0.1369	-3.5948	0.1369	1.5095
4.17409008	56.2577591	8.01660779	-2.9524	-1.0361	2.9524	1.0361	-0.4657
3.13786663	59.8553617	1.55251712	-0.5004	-0.4576	0.5004	0.4576	0.3276
3.93019923	73.8358795	6.83760842	-1.1949	-0.7484	1.1949	0.7484	0.4496
3.26365945	100.961829	2.65035133	0.1443	-0.8802	-0.1443	0.8802	-1.2254
4.34172143	68.1755696	9.68740976	-2.4163	-0.5062	2.4163	0.5062	-1.1703

2.60398348	40.2895422	-0.5226209	1.6819	-0.3659	-1.6819	0.3659	0.868
3.2047477	65.1262387	2.87774817	1.4851	-0.5901	-1.4851	0.5901	-1.1782
4.00301099	144.491407	8.19909714	0.5324	-0.4496	-0.5324	0.4496	-0.6185
2.85625487	42.1829984	0.00386559	-0.1933	-0.5782	0.1933	0.5782	-0.244
2.46115417	165.499449	0.59941861	5.7486	-0.1048	-5.7486	0.1048	1.0135
2.96118269	210.278248	2.90358767	4.8514	0.1099	-4.8514	-0.1099	0.4973
3.59830782	91.8936777	5.71771254	1.8433	-0.6829	-1.8433	0.6829	-1.2386
2.66194205	87.0508043	0.5775606	3.4337	-0.0121	-3.4337	0.0121	1.2896
3.23583815	127.380152	4.1447487	3.8358	-0.095	-3.8358	0.095	-0.55
3.43553414	84.0063687	4.05254588	0.6969	-0.2597	-0.6969	0.2597	-0.8091
2.65221803	145.036298	1.55861007	5.7094	0.0089	-5.7094	-0.0089	1.4355
2.77568383	91.8286141	1.33926677	3.7493	-0.1984	-3.7493	0.1984	-0.1006
3.40924128	20.770061	1.8531441	-3.7531	-0.9132	3.7531	0.9132	-1.9213
1.46541883	12.3629956	-6.8043004	-1.9505	-0.4664	1.9505	0.4664	-0.5791
4.11113479	58.4218088	8.31662336	-1.1419	-0.7018	1.1419	0.7018	0.7322
3.82795039	27.3176813	4.71928086	-4.1148	-0.8637	4.1148	0.8637	0.7123
2.45518054	18.2553346	-1.7097763	0.7248	-0.3305	-0.7248	0.3305	1.2966
2.83808394	18.3729937	-1.0587685	-2.3069	-0.1737	2.3069	0.1737	-1.3
3.74549026	35.10685	4.67314861	-2.8403	-0.7672	2.8403	0.7672	0.3229
2.97505745	22.1329503	-0.3690302	-2.5416	-0.6748	2.5416	0.6748	-0.6991
3.94607569	58.3202746	6.79211574	-1.5707	-0.9041	1.5707	0.9041	-0.9865
3.47970377	62.54307	4.60830837	1.2485	-0.5293	-1.2485	0.5293	-0.9172
2.86669563	40.6024894	0.6759369	1.156	-0.6876	-1.156	0.6876	-0.4781
2.94316078	25.0642228	-0.5004407	-2.4152	-0.4708	2.4152	0.4708	-1.1457
4.30243583	44.5617574	9.41484581	-2.2686	-1.1642	2.2686	1.1642	-3.2258
3.65729458	37.8703387	4.2011871	-2.4416	-1.2401	2.4416	1.2401	-1.7792
2.62747799	22.2411101	-2.0013249	-1.8474	-0.6286	1.8474	0.6286	-0.6825
3.26875303	37.0740678	2.77896915	0.3544	-0.3877	-0.3544	0.3877	0.4546
3.1724592	24.9244611	0.88806565	-2.4456	-0.0558	2.4456	0.0558	-0.6597
3.34939038	30.2791253	2.31794314	-1.8375	-0.6101	1.8375	0.6101	-1.6191
3.22767897	25.8124667	1.43080735	-2.0284	-0.3166	2.0284	0.3166	-0.3502
3.71218451	27.0255223	4.33119053	-3.0465	-0.5333	3.0465	0.5333	-0.6263
2.20288514	12.8073448	-5.0350684	-4.0131	-0.4853	4.0131	0.4853	-3.1488
4.07385229	94.1365426	9.23161257	1.5468	-0.5751	-1.5468	0.5751	0.7469
3.14662899	109.892053	3.67307844	4.0511	-0.2141	-4.0511	0.2141	1.3752
1.41425139	183.496054	-5.772796	0.6472	0.9962	-0.6472	-0.9962	1.9726
1.7598898	64.6599601	-4.8432812	0.2779	0.3908	-0.2779	-0.3908	-2.8317
1.23592389	47.585915	-5.8749086	1.4636	0.8162	-1.4636	-0.8162	0.4994
0.83390398	55.1901467	-5.9844266	3.0559	1.0389	-3.0559	-1.0389	7.6393
1.97414662	25.9471031	-5.9853885	-4.0018	0.2815	4.0018	-0.2815	-7.2808
1.63251997	23.988492	-7.2868633	-4.1546	1.2781	4.1546	-1.2781	-6.2061
1.42791023	24.6247299	-7.0557738	-2.2655	1.1116	2.2655	-1.1116	-4.2872
1.66121681	19.2577899	-6.9520991	-3.6252	1.1199	3.6252	-1.1199	-6.0444
1.08541333	19.3134769	-6.5433648	0.7605	0.7838	-0.7605	-0.7838	-0.4987
1.09904459	28.2880328	-8.3077521	-3.1931	1.8427	3.1931	-1.8427	1.6156
0.83394065	47.31	-7.0500816	0.7075	0.5518	-0.7075	-0.5518	6.187

1.73246818	27.7141828	-5.5548609	-1.0791	1.4434	1.0791	-1.4434	3.5084
1.57697805	38.7361333	-4.2810917	2.8617	0.8107	-2.8617	-0.8107	0.5514
1.42756195	35.6282015	-6.154649	-0.2776	1.5035	0.2776	-1.5035	1.2291
1.23119808	43.6844009	-5.5086842	2.2963	0.9317	-2.2963	-0.9317	6.1011
2.0458778	28.8464229	-4.1999695	-0.7029	1.3328	0.7029	-1.3328	-1.1164
1.90058018	22.8331544	-5.1401004	-1.511	1.6961	1.511	-1.6961	-0.6821
0.59805699	4.79453308	-8.0887232	-0.8369	1.8185	0.8369	-1.8185	2.8617
0.6643891	14.4725533	-7.6644924	-0.0866	1.9061	0.0866	-1.9061	0.2471
1.81109936	18.4274206	-5.3314542	-1.2008	1.3466	1.2008	-1.3466	-0.3725
1.56562761	22.8017658	-5.6252635	-0.0217	1.2753	0.0217	-1.2753	0.5755
1.88558523	16.762997	-5.6787241	-2.5728	1.7291	2.5728	-1.7291	0.0217
1.88332569	20.7179653	-5.4058809	-1.9528	1.8741	1.9528	-1.8741	0.5732
1.34938185	13.42796	-6.0754613	0.3753	1.496	-0.3753	-1.496	-0.0678
2.16758926	13.8760874	-4.2744115	-1.997	0.2086	1.997	-0.2086	-1.8008
0.64101137	29.1415302	-5.9968707	3.6554	1.3705	-3.6554	-1.3705	5.8767
1.03774871	13.7713861	-7.8385714	-1.8706	1.1924	1.8706	-1.1924	0.9184
1.83110939	16.7815897	-5.6862848	-2.1433	1.5471	2.1433	-1.5471	0.4558
0.93208852	4.6335414	-7.9047545	-1.5578	0.5758	1.5578	-0.5758	-0.5267

pc2	clawmass	sqrt.clawmass	totalmusclemass	sqrtmusclemass	musclesample
-1.021	0.89	0.943398113	0.1442	0.379736751	0.0298
-0.9612	0.45	0.670820393	0.0364	0.19078784	0.0108
-0.908	1.31	1.144552314	0.1714	0.414004831	0.0172
-0.6783	0.74	0.860232527	0.0592	0.243310501	0.0312
-0.4856	0.55	0.741619849	0.0976	0.312409987	0.033
-1.2057	0.65	0.806225775	0.0578	0.240416306	0.0168
-0.8632	1.19	1.090871211	0.0965	0.310644491	0.0224
-0.1992	0.72	0.848528137	0.0485	0.220227155	0.0106
-0.8368	0.89	0.943398113	0.0698	0.264196896	0.0123
-0.8661	1.8	1.341640786	0.2678	0.517493961	0.0353
-1.5209	1.59	1.260952021	0.1707	0.413158565	0.0237
-1.3788	1.34	1.15758369	0.1965	0.443283205	0.0302
-0.379	1.52	1.232882801	0.1306	0.36138622	0.0157
-0.8225	1.92	1.385640646	0.1497	0.386910842	0.0519
-0.7315	1.45	1.204159458	0.2139	0.462493243	0.0507
-0.2811	1.37	1.170469991	0.1529	0.391024296	0.041
-0.2977	0.59	0.768114575	0.0598	0.244540385	0.008
-0.4469	1.39	1.178982612	0.092	0.303315018	0.0261
-0.1583	0.8	0.894427191	0.0558	0.236220236	0.0194
0.6192	0.71	0.842614977	0.0498	0.223159136	0.0189
-0.7618	1.18	1.086278049	0.1166	0.341467422	0.0367
-0.459	1.22	1.104536102	0.1906	0.436577599	0.0718
-0.5168	1.83	1.352774926	0.2269	0.476340215	0.0441
-0.7434	2.48	1.574801575	0.2909	0.539351462	0.0511
-0.9495	2.3	1.516575089	0.3285	0.573149195	0.0924
0.6472	1.79	1.337908816	0.1263	0.355387113	0.0435
-1.0481	2.64	1.624807681	0.2687	0.518362807	0.0438
-1.1944	2.13	1.459451952	0.2612	0.511077294	0.0797
-1.168	1.36	1.166190379	0.2259	0.475289386	0.0472
-0.5616	2.79	1.670329309	0.3111	0.557763391	0.0567
-1.138	1.22	1.104536102	0.1261	0.355105618	0.0349
-1.212	2.06	1.435270009	0.2964	0.544426304	0.0908
-0.1058	0.54	0.734846923	0.0484	0.22	0.0316
-1.3403	2.08	1.44222051	0.2614	0.511272921	0.11
-0.8503	2.22	1.489966443	0.3063	0.553443764	0.047
-0.4547	2.31	1.519868415	0.3309	0.575239081	0.0609
-0.2633	0.61	0.781024968	0.0787	0.280535203	0.0256
-2.0022	2.54	1.593737745	0.3097	0.556506963	0.034
-0.8223	1.64	1.280624847	0.1645	0.405585996	0.0468
-1.5668	1.88	1.37113092	0.2092	0.457383865	0.0418
-1.3732	1.44	1.2	0.1055	0.324807635	0.0288
-0.849	2.33	1.526433752	0.2765	0.525832673	0.0489

-0.6893	0.9263	0.962444804	0.1683	0.41024383	0.0793
-0.8178	1.0388	1.019215384	0.1577	0.397114593	0.0666
-0.7181	1.2992	1.139824548	0.1109	0.333016516	0.0304
-0.9918	1.4489	1.203702621	0.1934	0.439772669	0.0529
0.0119	0.2775	0.526782688	0.0366	0.191311265	0.0233
0.4366	0.3886	0.623377895	0.0417	0.204205779	0.0342
-0.9504	0.9696	0.98468269	0.1409	0.375366488	0.0377
-0.0135	0.5948	0.771232779	0.0814	0.285306852	0.0455
0.0983	0.6029	0.776466355	0.0822	0.286705424	0.025
-0.2879	1.2639	1.124233072	0.1405	0.374833296	0.0343
0.1459	0.2895	0.538052042	0.0485	0.220227155	0.0194
-0.1735	0.538	0.733484833	0.0839	0.289654967	0.0364
-1.5647	3.14	1.772004515	0.5596	0.748064168	0.1036
-0.8285	2.1	1.449137675	0.1737	0.41677332	0.0494
-1.4506	2.03	1.424780685	0.2893	0.537866154	0.0943
-1.866	3.27	1.808314132	0.5364	0.732393337	0.0747
-0.7251	1.21	1.1	0.3302	0.574630316	0.116
-0.2461	2.26	1.503329638	0.4384	0.662117814	0.0583
-1.5929	2.48	1.574801575	0.3996	0.632139225	0.1018
-1.2427	2.25	1.5	0.3999	0.63237647	0.0509
-1.5559	2.11	1.452583905	0.267	0.516720427	0.0925
-0.7356	1.15	1.072380529	0.1936	0.44	0.0994
-1.1544	1.04	1.019803903	0.2024	0.449888875	0.0917
-0.7012	2.27	1.506651917	0.3456	0.587877538	0.0567
-1.7572	2.29	1.513274595	0.4154	0.644515322	0.1682
-2.2619	2.4	1.549193338	0.3532	0.594306318	0.0756
-1.155	2.02	1.42126704	0.3104	0.557135531	0.1059
-0.7764	1.48	1.216552506	0.2882	0.536842621	0.0832
-0.097	2.21	1.486606875	0.4038	0.635452595	0.1497
-0.9954	2.12	1.456021978	0.3705	0.608687112	0.0668
-0.7167	2.39	1.545962483	0.4036	0.635295207	0.1193
-1.0722	2.76	1.661324773	0.5099	0.714072825	0.1091
-0.788	2.93	1.711724277	0.3789	0.615548536	0.0695
-1.1461	1.08	1.039230485	0.1763	0.419880936	0.0532
-0.3168	0.55	0.741619849	0.0901	0.30016662	0.0451
1.5789	0.6601	0.812465384	0.0109	0.104403065	0.004
1.0286	0.6693	0.818107572	0.0479	0.218860686	0.013
1.4777	0.5629	0.750266619	0.0321	0.179164729	0.0139
0.8773	0.4191	0.647379332	0.0126	0.112249722	0.0019
1.3413	1.4273	1.194696614	0.1502	0.387556448	0.0246
2.887	1.5159	1.231218908	0.1111	0.333316666	0.0501
2.3953	1.1664	1.08	0.0828	0.287749891	0.0083
2.6515	1.3386	1.156978824	0.1433	0.378549865	0.0346
1.4915	0.6268	0.791707017	0.061	0.246981781	0.0129
2.9501	2.64	1.624807681	0.0427	0.206639783	0.037
0.1968	1.28	1.13137085	0.0147	0.121243557	0.0016

2.0921	1.85	1.360147051	0.1083	0.329089653	0.0468
1.5313	0.7268	0.852525659	0.0642	0.253377189	0.0399
2.5243	1.3228	1.150130427	0.0572	0.239165215	0.0338
0.8625	0.85	0.921954446	0.0347	0.18627936	0.0097
2.5191	1.59	1.260952021	0.1451	0.380919939	0.0631
3.168	1.77	1.33041347	0.1582	0.397743636	0.0718
2.8861	1.68	1.29614814	0.0746	0.273130006	0.0227
3.4818	1.22	1.104536102	0.0305	0.174642492	0.0136
2.5298	2.05	1.431782106	0.178	0.421900462	0.0828
2.214	1.34	1.15758369	0.1075	0.327871926	0.0456
3.1272	2.31	1.519868415	0.2121	0.460543158	0.0657
3.2516	2.11	1.452583905	0.1712	0.413763217	0.0633
2.675	1.474	1.214084017	0.1356	0.368239053	0.0514
0.5172	2.1752	1.474855925	0.3386	0.581893461	0.1066
1.8454	0.4999	0.707036067	0.0141	0.118743421	0.0067
1.9025	1.9046	1.380072462	0.0782	0.279642629	0.0071
2.538	2.2111	1.486976799	0.1998	0.446989933	0.0584
1.1288	1.838	1.355728586	0.1875	0.433012702	0.0863