Functional differences between the major and minor claws of fiddler crabs (*Uca*, family Ocypodidae, Order Decapoda, Subphylum Crustacea): A result of selection or developmental constraint?

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Abstract

We studied the functional differentiation between the major and minor claws of fiddler crabs (*Uca*, family Ocypodidae) by means of a strain gauge apPARATUS and by morphometric estimates of claw function. In *Uca pugnax*, (Smith 1870) closing force is an approximately log-linear function of claw length, but the slope for minor claws is greater than that for the major claws, and the *y*-intercept for major claws is displaced upwards from that of the minor claw. The pattern of closure also differs: major claws impart rhythmic short pulls, whereas minor claws squeeze far more irregularly. The short pulls of the major claw correspond to rapid squeezes observed in videotapes of combat, whereas the irregular pulls of the minor claw match expectations for gathering particles and transferring them to the mouth parts. The mechanical advantage declines steadily with increasing major claw length. These results suggest that the evolution of form of the extremely large major claws in fiddler crabs involved functional shifts, as opposed to a developmentally constrained extrapolation in size of the minor claw.

Keywords: Biomechanics; Fiddler crab; Ocypodidae; Sexual selection; *Uca pugnax*

1. Introduction

It is the purpose of this paper to consider the evolution of a novel structure, the major claw of male fiddler crabs, and to assess the degree to which the rise of such

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a structure was under the control of a developmental constraint, as opposed to being under the control of natural selection for efficient function as a closing device. It has been argued that the evolution of structures may be guided by developmental programs, which might be an internal structural force as important in guiding evolutionary direction as natural selection (Maynard Smith et al., 1985). In deer for example, the now extinct Irish elk had enormous antlers and it has been suggested that these antlers were used in display only, and not for combat (Gould, 1974). It has been further suggested that a developmental program might be responsible for constraining antler size to a certain proportion of body size, which would strongly modify the role of natural selection in controlling antler form (Gould, 1982). This claim would explain why the Irish elk used its enormous antlers for display only: By its size, its antlers would have been constrained to be very large. Display might be the only option, assuming that the large antlers are inefficient in combat. Has display dominated closing function in the evolution of the fiddler crab's giant major claw?

As we shall show below, fiddler crabs are an excellent model system to examine these issues because both claws grow with precisely the same morphology, until some undetermined signal causes one of the two chelae, apparently at random, to continue to enlarge to nearly half of the male's body weight. This major claw is used exclusively for display and combat, but damage in combat is slight to nonexistent. The evolution of the major claw, moreover, must have been caused by sexual selection in an ancestral species, which might have put emphasis on the display value of the claw, at the expense of function, i.e. generation of a closing force. So the question arises: Has the developmental connection between minor and major claws constrained the major claw to continue to grow along the same allometric growth trajectory, simply to evolve a large display structure? If not, are there differences between the two claw types that can be ascribed to function and natural selection? The fiddler crab system is especially valuable as there is complete separation of feeding and sexual function between the two claw types in the male, which allows explicit studies of differentiation of function that are not as approachable in other decapods.

Decapods have chelae that range widely in size, function, and closing strength (Warner & Jones, 1976; Vermeij, 1977). Deposit feeding crabs of the family Ocypodidae typically have small and slender claws that are used to manipulate and carry sedimentary grains (Crane, 1975). By contrast, carnivorous species, including some members of the genus *Ocypode*, have larger more robust claws, sometimes capable of crushing rather thick shells (Vermeij, 1977). In many carnivorous species, the two chelae are differentiated into a cutter and crusher, whose mechanical advantage and closing speed are differentiated. In the lobster *Homarus americanus*, the handedness of this differentiation is determined by environmental factors (Govind & Pearce, 1986). Closing force and biomechanically significant dimensions of a crab chela can also be altered by diet (Smith & Palmer, 1994).

Fiddler crabs of the genus *Uca* show among the strongest degree of cheliped

sexual dimorphism of all the decapods. In all species, female claws are isomorphic, but in the male one claw is extremely large–nearly half of the body weight of the crab (Crane, 1975). The male's major claw grows with strong positive allometry (Morgan, 1923) but the minor claw is similar in size to that of the female (Levinton, unpubl. data) and, as in the female, is used for feeding. The major claw, however, is not used for feeding but is employed in complex waving displays and in combat with other males (Crane, 1975). The lack of two feeding claws puts the male at a disadvantage in food acquisition and some compensations in terms of feeding rate and time spent feeding have been observed (Valiela et al., 1974; Caravello & Cameron, 1987). *Uca pugnax* males can never gain energy as fast as females and respond differently to food abundance, in accordance with expectations of optimal foraging theory (Weissburg, 1993).

Populations of most species of *Uca* have an equal abundance of males with right and left handed major claws, suggesting that the determination of handedness is facultative, as in the cutter-crusher dimorphism of the lobster (Govind & Pearce, 1986). Most likely, a hormonal signal induces the differentiation, and this signal is, in effect, random with respect to side. In small males the removal of one cheliped results in the development of the other into a major claw. After the developmental determination occurs, however, a major claw, even if removed, will develop from the same limb primordium (Yamaguchi, 1977; Ahmed, 1978). In the subgenus *Thalassuca*, however, two species are nearly all right handed (Barnwell, 1982; Jones & George, 1982). Although *Thalassuca* does not appear to be in an ancestral position in the *Uca* clade (C. Sturmbauer, J. Levinton, and J. Christy, unpubl. data), it is not clear whether or not the ancestor of *Uca* was indeterminate in handedness.

The extreme dimorphism of males, accompanied by complete differentiation of function, gives us an excellent opportunity to ask questions about the morphological and functional changes that accompanied the evolution of the major cheliped. Superficially, the major and minor claws are similar in overall dimensions, although the feeding claws have spatulate, setae-laden tips and the major claws have pointed tips and may not occlude in many species. In this paper, we wish to address the question of whether the evolution of the large major claw involved an important biomechanical change in morphology. Owing to the developmental connection between the claws, a null model might suggest that the evolution of the major claw was constrained developmentally along a growth track that was entrenched in the developmental program of the minor claw. In other words, a developmental constraint hypothesis would argue that the dimensions and closing function of the major claw is constrained by a growth pattern that was established during the evolution of the minor claw, whose current form we assume to be the ancestral monomorphic state of *Uca*. This hypothesis cannot be dismissed lightly because the major claw is used for display and generally non-injurious combat. An alternative hypothesis would argue that the function of combat and display caused a bout of natural selection, resulting in an alteration of the major claw's morphology and function.

2. Materials and methods

Adult male *U. pugnax* (Smith 1870) were collected from field populations at the Flax Pond *Spartina* salt marsh (Old Field, New York, USA) in the summers of 1993 and 1994. Crabs were kept in a recirculating sea water system at room temperature, with a tidal and light cycle matching that of Flax Pond, under the control of an electronic cycling device (Chrontrol, Lindberg Enterprises, San Diego, California, USA).

We employed an in vivo technique using the whole animal (as opposed to individual claw preparations), whose claw was inserted with the pollex tip into a fixed brass ring and the dactyl tip into a brass ring connected to a flexible Plexiglas beam. Most of our measurements employed the apparatus described in Levinton & Judge (1993), which employed two strain gauges on the beam, connected to a Wheatstone Bridge and interfaced to a microcomputer via an analog-to-digital connecting board. The Wheatstone Bridge/amplifier was powered by a regulated DC power supply of ±15 V. Gape angle between the dactyl and pollex was kept constant at ca. 35–37°. Because claw gape angle was kept constant for major and minor claws in our study, we assume that the degree of muscle shortening was approximately constant.

We recorded maximum closing force of major and minor claws, using animals of carapace length with a range of 5.2–15.3 mm. For the major claws we measured closing force in 120 individuals (length range was 5.9–40.4 mm), using the apparatus described in Levinton and Judge (1993) but with a regulated DC power supply. For minor claws we used the above apparatus for 39 specimens, but we also employed another flexible beam apparatus with a more slender beam for another 109 crabs, in order to measure the rather smaller closing forces of these smaller claws (length range was 4.0–9.5 mm).

The dimensions of this cantilever were 76.6 mm long × 11.2 mm wide × 1.6 mm thick. Both types of apparatus were calibrated by hanging a range of standard weights on the end of the cantilever and the voltage output was measured by means of the A/D board. The calibration with the D.C. power source was linear and repeatable and the deflected cantilever quickly returned to zero voltage in either apparatus when the weights were removed. In both apparatus types the calibration was linear throughout our range of deflections.

The slender-beam apparatus was cross-calibrated by measuring closing force of 17 crabs on both apparatus types. We discovered that measurements of estimated closing force between the slender-beam apparatus and our old apparatus differed by an average factor of 2.21 but with statistically indistinguishable slope ($n = 17$, $SE = 0.211$), despite the linear response in calibration by weights. We thus multiplied the measurements obtained from the slender beam apparatus by the 2.21 correction factor in all analyses that are presented below. Taking the range of claw lengths for which we have data for the two pieces of apparatus, it was possible to perform an analysis of covariance to compare the data. After the 2.21 correction factor was applied there was no significant difference between size-related trends in closing force, either in slope or intercept ($F = 2.37$, $p = 0.126$).

Thus, we can be confident of measurements for values of natural log claw length greater than ≈1.5. It is not clear. however, why the two pieces of apparatus responded differently. We speculate that it relates to a strong difference of response of the thinner beam under the accelerating closing force of the claw, perhaps relating to a different location of flexure in the beam, relative to the strain gauge. With the application of an accelerating force, the slender beam appears to flex distally with respect to the strain gauge. which would explain the sense of the difference. It is important to note, nevertheless, that the smallest claw lengths (natural log minor claw length less than ≈1.5) are represented by the slender apparatus only, but larger claws, both minor and major, were analyzed on the same apparatus.

As an independent estimate of closing force, we used the morphometric formulation developed by Levinton & Judge (1993), which is the product of the *mechanical advantage index*, which is the manus height divided by dactyl length (Warner & Jones, 1976), and an *index of muscle cross-sectional area*. We developed the index of muscle cross-sectional area by modelling the volume of the manus as an ellipsoid and raising this volume to a power of 2/3. The index of force scaled linearly with log closing force of major claws of *U. pugnax* (Levinton & Judge, 1993).

A limited amount of data was collected by videotaping fiddler crabs in the field. We taped males that grappled with each other with the major claw. We measured the distance between the claw tips, in pixels, as a function of time and report the time it took for closure. Crabs were videotaped at the marshes in Flax Pond, Old Field, New York and at the mouth of the Nissequogue River, Smithtown, New York.

Statistical analyses were performed using SYSTAT (Wilkinson et al., 1992), with the exception of Principal Axes fits, which were done using the methods in Sokal & Rohlf (1995).

3. Results

Closing force for the major and minor claws of *U. pugnax* is illustrated in Fig. 1a. Closing force by the major claw differed clearly from that of the minor claw in two respects. There was an upwards displacement of the major claw fitted line and the slope was shallower. The estimated slope of the major claw log-linear relationship with claw length is 1.20 (SE = 0.079), whereas it is 1.50 (SE = 0.109) for the minor claw. Using a linear model. the slopes of the major and minor claw relationships are significantly different ($F = 29.36$, $p < 0.001$). Fig. 1b shows a similar difference between major and minor claws when considering the morphometric index of force. The major claw log-linear slope was 1.16 ± 0.036 SE, whereas the minor claw slope is 2.06 ± 0.062 SE. Again. the slopes of the major and minor claw relationships differed significantly ($F = 338.49$, $p < 0.001$). While the intercepts between the actual force and index of force plots cannot be compared directly, it is possible to contrast the slope of the major claw log
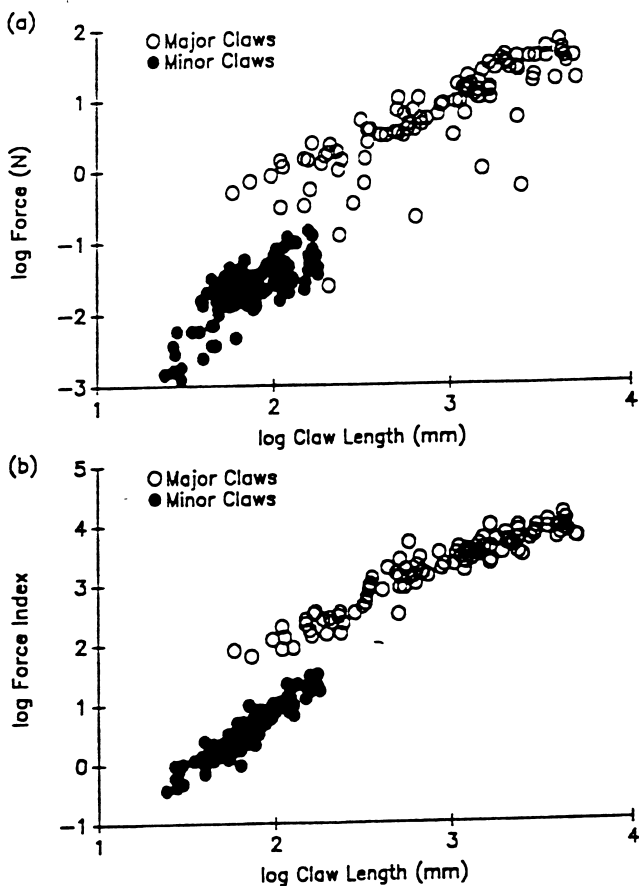
Fig. 1. *Uca pugnax*: (a) Closing force of major and minor claws as a function of natural log of claw length. (b) Index of closing force of major and minor claws as a function of natural log of claw length.

force-log claw length relationship with that of the corresponding morphometric index of force relationship. The values of the slopes were approximately the same and there was no statistically significant difference ($F = 3.23$, $p = 0.07$), and a similar result was obtained for comparison between the actual force and the morphometric force index measurements for the minor claws ($F = 1.60$, $p = 0.21$).

Fig. 2 shows a plot of measured force versus index of force for both major and minor claws. A log-log slope of 1 would suggest that the index corresponds well to the actual measurements, that is, that morphology can be used to accurately estimate force, even when claw morphology changes significantly. We employed a Principal Axis fit (Sokal & Rohlf, 1995) because there is considerable measuring error for both axes. The overall combined slope for both claw types is 0.96, which is close and not significantly different from the expectation of 1 (Principal Axis confidence limits: 0.92, 1.00). The individual slopes for major claws (1.20) and minor claws (0.85) differ barely at the 95% confidence limit, but overall our
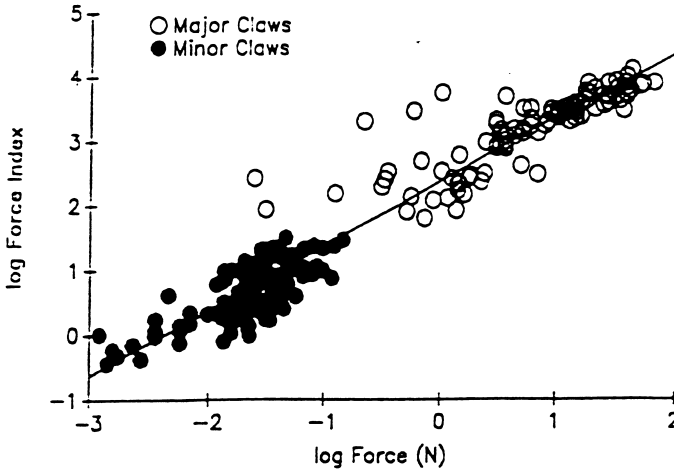
Fig. 2. *Uca pugnax.* Correspondence of actual force measurements with relative force index for major and minor claws. See text for explanation.

results suggest that the same morphological indices can be used to compare relative force among different claw types. The difference might be explained by factors that we did not take into account in our morphometric index of force, such as the angle of insertion of muscle into the apodeme.

We dissected our morphological estimate of closing force into the two components of relative muscle cross-sectional area and mechanical advantage. The relationship of estimated muscle cross sectional area to claw length was quite different for major and minor claws (Fig. 3a); the major claw cross sectional area line was clearly displaced upwards, and the log-log linear slope (1.60 ± 0.019 SE) was less than for that of the minor claws (2.03 ± 0.034 SE). Mechanical advantage of the minor claw showed no trend with claw size, but that of the major claw declined steadily with increasing log claw length (Fig. 3b). The reduced slope relating log force morphometric index to log claw length in the major claw, relative to the minor claw, was therefore explained partially by the declining mechanical advantage. The lack of change in mechanical advantage in the minor claw produced an expected log-linear slope relating log force index to log claw length of ≈ 2.1, which corresponded closely to the change in muscle cross-sectional area. The slope for actual force measurements of the minor claw was less (≈ 1.5) but inspection of the data in Fig. 1a showed a good deal of scatter and an apparent consistent deviation of points below the line in the smaller claw sizes, suggesting a possible local nonlinearity in our results. We must be conservative in our interpretation of these smaller individuals, since, as mentioned above, they come from measurements on an apparatus that could not be directly cross-calibrated in this lower size range. Furthermore, the morphometric index of force of the minor claws fit the expectation and was ≈ 2.1, as mentioned above.

The pattern of claw closure also differed significantly between major and minor
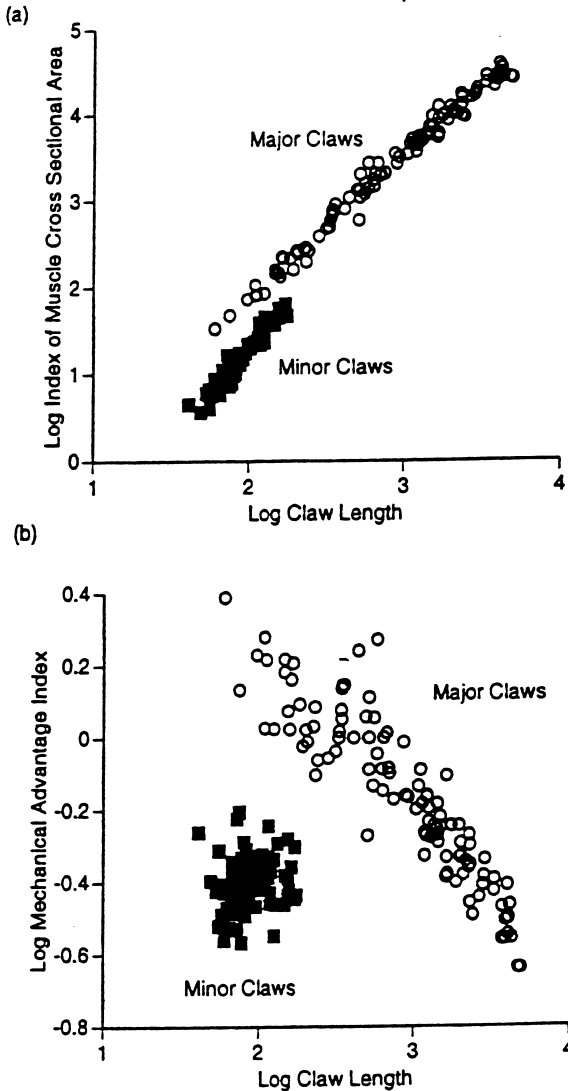
Fig. 3. *Uca pugnax*. (a) Estimated relative muscle cross sectional area for major and minor claws as a function of natural log of claw length. (b) Mechanical advantage index of major and minor claws as a function of natural log of claw length.

claws. Fig. 4a shows a voltage-time trace that is typical for major claws. As found by Levinton & Judge (1993) major claw closure consisted of sharp and symmetrical peaks, much less than a second in duration. Measurements from videotapes of males in combat in the field also revealed short times of closure (time $= 0.10 \pm 0.02$ s SE, $n = 8$). Closure for the minor claws, however, was far more irregular (Fig. 4b), and peak displacement of the beam was often maintained for several seconds. The peak shape was often jagged and far less regular than those found
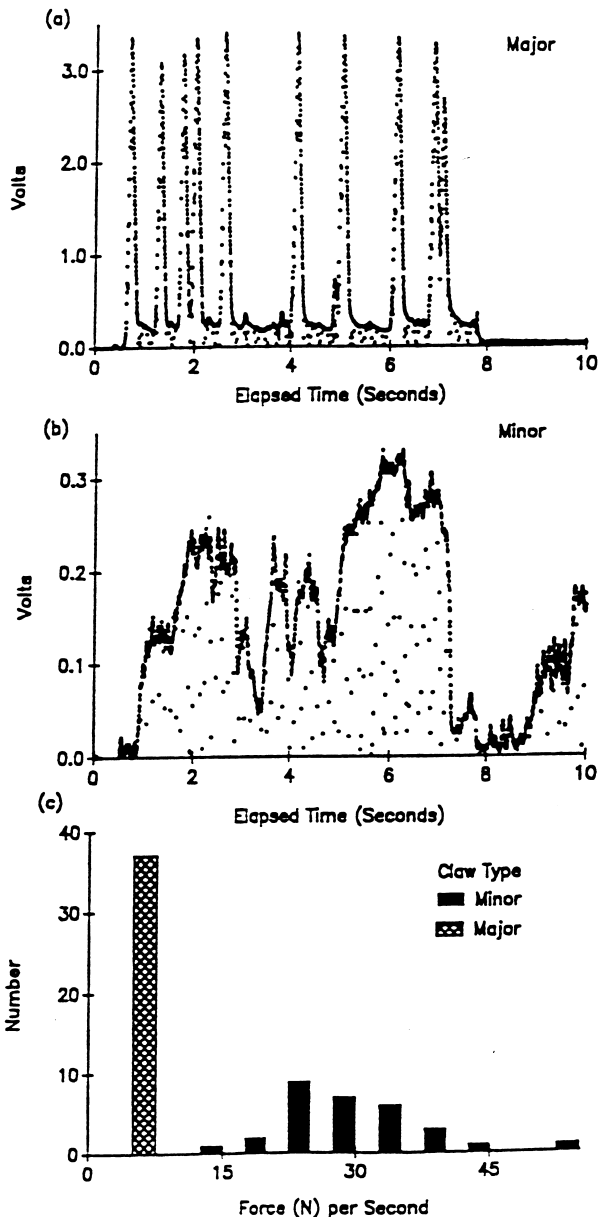
Fig. 4. *Uca pugnax.* (a) Typical voltage trace from closing movements of the major claw; (b) Same for minor claw; (c) Frequency of shapes of voltage trace of major and minor claws. Shape is defined as the peak voltage divided by the number of seconds between parts of ascending and descending legs of the trace that were half of peak voltage. Higher values mean stronger and sharper peaks.
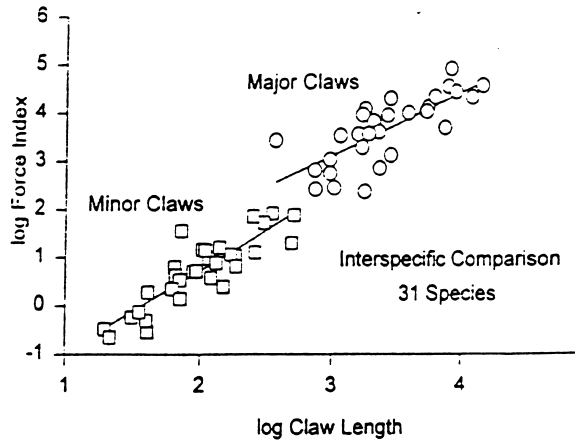
Fig. 5. Index of force as a function of natural log of claw length for male major and minor claws of 31 species of *Uca*. Each point represents the mean of 2-3 adult specimens.

for the major claw. An analysis (Fig. 4c) of a number of traces (Major claw: $n = 37$, Minor claw: $n = 30$) showed a completely non-overlapping distribution of peak shape between the two claw types (Wilcoxon Signed Ranks Test, $Z = -4.78$, $p < 0.0001$).

A simple extension of our work would be to consider comparative data for a number of species of fiddler crabs. Fig. 5 shows a plot of the log of morphometric index of force as a function of log claw length for 31 species, taken from all nine subgenera of the genus *Uca*. As can be seen, the overall pattern is rather similar to the intraspecific pattern we found for *U. pugnax*. An analysis of slopes shows no significant differences between the *U. pugnax* and multispecies slopes when major claws and minor claws are compared respectively. A preliminary analysis suggests that the similarity of estimated variation in closing force can be explained in the same terms as for the case of *U. pugnax*. Among species, there is a negative correlation between major claw log mechanical advantage index and log claw length ($r = -0.55$, $p = 0.004$, $n = 31$), but no significant correlation for the minor claw ($r = -0.19$, $p = 0.489$, $n = 31$).

4. Discussion

Our results demonstrate that the major claw of *U. pugnax* is strongly differentiated in biomechanical function from the minor claw. Where the claw sizes overlap, the major claw is far stronger, which fits with a role in combat. In crab species other than *Uca* with aggressive individuals, sexual dimorphism tends to be more pronounced, males are more aggressive than females, and major claws of males are more powerful than those of females (Warner, 1970; Hartnoll, 1974; Vermeij, 1977). Levinton and Judge (1993) found that the relationship of closing

force of *U. pugnax* to major claw size matched the expectations of a biomechanical model, which suggested that the major claws were fully functional and not just display devices.

The dimorphism of fiddler crabs is unusual because there is a complete differentiation of function. Minor claws are used solely for feeding, whereas major claws are used in display and combat. Thus, we would expect that function of the minor claws would be under the control of natural selection for efficient handling of particles, whereas the major claws would be under the control of sexual selection, where combat and display gain matings. We have never observed male *U. pugnax* damaging other males with the major claws, which begs the question of whether the form of the major claw arose under the strict control of function, or whether its role as a display device made functioning as a grappling device less important. The developmental similarity in juveniles between major and minor claws also suggests perhaps that the strong positive allometry found in major claw growth might just be an extrapolation of form along a growth program that was already constrained in early ontogeny, before the major claw's fate is determined. Our results refute this structuralist hypothesis.

Male *U. pugnax* are constantly grappling with each other during the mating season. Males without burrows often roam through the high-quality high intertidal area and attempt to remove resident males (Crane, 1975; Christy & Salmon, 1984). Grappling is important to success, either in defense or offense. Not only does the strongly increased closing force of the major claw make sense, but the pattern of closing observed in the laboratory also fits with the differentiation of function. Closing by the major claw consists of short bursts, which would allow the crab to grip rapidly onto an opponent the instant that an appropriate hold is obtained. One can liken this to wrestling among humans, where action must occur the moment the appropriate hold is made between opponents. Videotapes of males fighting in the field show that closure of major claws among combatants is quick and of the same order of time as we observed in the laboratory.

By contrast, closure of the minor claws was far more irregular and consisted often of long periods at maximum force, as opposed to the short bursts we observed for the major claw. This pattern corresponds to the irregular gathering and handling of particles required of the minor claw as it closes around a group of sedimentary grains and brings them to the mouth parts. Unlike the major claw, closure for the minor claw exhibits no consistent pattern in the strain gauge measurements except that closure was nearly always for longer periods of time than closure periods of the major claw. While the absolute value of force is greater, the slope of a log-log plot of force on claw length was much less for the major claw than for the minor claw, and this reduction in slope appears to be explained by a monotonically decreasing mechanical advantage with increasing claw length. By contrast, there is no such trend in mechanical advantage for the minor claw. Because a decreased mechanical advantage corresponds to a greater speed of dactyl movement, it may be that the decreased mechanical advantage has something to do with the speed of gripping during combat. This would suggest that gripping speed, and not damage is the main objective of major claw closure in

fiddler crabs. Uca pugnax do not appear to damage their opponents, although damage has been observed in east African U. vocans males (M. Vannini, pers. comm.). A reduced mechanical advantage has the additional value of reducing the relative amount of muscle, which might reduce metabolic load. The striated muscle in the major claw of U. pugnax is a considerable fraction of the total in the body and metabolic energy conservation might be strongly favored. If damage to an opponent were the objective, one might expect that the mechanical advantage would not decline with increasing claw size.

Our results confirm those of Levinton & Judge (1993) that the major claws are fully functional and that simple biomechanically relevant morphometric measurements can be used to assess closing force as a function of claw size. In this study we have been able to extend this conclusion to both claw types with completely differing function. Our results demonstrate that an estimate of muscle cross sectional area and mechanical advantage are necessary and sufficient to explain the variation we see in force exerted by the major claw. In the minor claw, however, differences in mechanical advantage are not important, only muscle cross section matters.

Our interspecific study of 31 species demonstrates that individual differences can be extrapolated to interspecies differences with no apparent respect to the details of taxonomy. We suggest that this relates to the functional aspects of morphological differences between major and minor claws for all species. Such an extrapolation may not be possible on larger taxonomic levels owing to differences in the proportion of long sarcomeres, which also is an important component explaining closing force (Warner & Jones, 1976).

A functional explanation for the divergence in form of the major claw suggests that Uca claw evolution was not guided by a strict developmental program or developmental constraint. In many groups, structures have been recruited in evolution by sexual selection to serve as combined display and combat structures, for example the antlers of deer and the horns of horned beetles. Gould (1982) argued that the trends between body size and antler size in deer need not be adaptive but might be controlled by a developmental program. The Irish Elk had antlers that, albeit giant in size, fit the expected overall relationship between antler size and skull size in deer (Gould, 1974). He argued, however, that the Irish elk's antlers likely did not function in combat and were more likely just display organs. This does not make sense entirely, as one might expect that such a display-only strategy would be lacking in ability to back up the threat. Kitchener (1987) demonstrated from both functional morphological and direct crystallographic evidence that the Irish Elk did indeed fight. A similar argument could be made for fiddler crabs: display must be backed up by a credible ability to fight. Given our results, the major claw is a credible fighting organ although its function may be more to grapple and wrestle, rather than to puncture the carapace. We have never seen a U. pugnax male damage the carapace of another, although, as mentioned above, damage has been observed in combat among U. vocans males.

Further comparative work must therefore be done to understand the function of closing in the major claw. An unpublished study (J. Levinton and M. Weissburg,

in prep.) shows, for example, that the overall lengths of the major claw in many species of *Uca* appear to just be able to cover the carapace, which may signify a function in defense against puncture during combat. The apparent constancy of relationship between major claw length and carapace length opposes the more irregular expectations of sexual selection in a model of intermale combat (Maynard Smith & Brown, 1986). Further investigations will allow us to compare intraspecific and interspecific components of variation between the symmetry of the major and minor claws and between the intraspecific and interspecific variance of traits such as claw length. The latter are especially interesting in the light of predictions that sexual selection might produce more among-taxon variance than natural selection (e.g. West Eberhard, 1983; Maynard Smith and Brown, 1986). An explanation for overall major claw size would then give us a complete picture of function in a structure that has arisen through the process of sexual selection.

Acknowledgements

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