

The paradox of the weakening combatant: trade-off between closing force and gripping speed in a sexually selected combat structure

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Summary

1. Previous evidence demonstrates that closing force decreases proportionally as fiddler crab claw size increases. Larger crabs do have greater absolute closing force, but less than would be expected if claw proportions were isometric. In the Mud Fiddler Crab, *Uca pugnax*, this is explained by a decrease in mechanical advantage with increasing claw size.
2. We here re-measure mechanical advantage with a more direct method than used previously; the relationship of mechanical advantage to claw size was similar to the older indirect measure. Because the fiddler crab claw is a simple lever, we predicted that the observed decline in closing force should be compensated by a proportional increase in closing speed.
3. We tested this hypothesis using high-speed video to observe crabs closing their major claws spontaneously under controlled conditions. Closing speed scaled positively to claw length as predicted, and the value of the exponent conformed to expectation from a simple biomechanical model.
4. Evolution of the fiddler crab claw therefore involved a trade-off of closing force for closing speed. An adaptive explanation of relative weakening with increasing body size may lie in the increased ability to rapidly grasp an opponent, a crucial advantage in fiddler crab combat.

Key-words: Biomechanics, mechanical advantage, sexual selection, *Uca pugnax*

Functional Ecology (2005) **19**, 159–165

Introduction

Males of many animal species bear weapons that are used in combat with other males. As success in combat often results in increased mating success, strong sexual selection should result in functional structures that allow one male to subdue or even injure another. It has been argued that intermale combat could lead to runaway selection (Maynard Smith & Brown 1986), as was proposed for the selection for gaudy and colourful structures in male display devices (Fisher 1958; Lande 1981). Would such runaway selection result in structures that lose functionality owing to their extreme form, or even become detrimental to male fitness? This would perhaps make sense if the structure were ornamental, selected by females for reasons other than performance in combat (Berglund, Bisazza & Pilastro 1996). Darwin (1871) suggested as much for pinching beetles (e.g. members of the Lucanidae) whose very large pincers fail to produce much closing force. Darwin

noted: ‘As they are so conspicuous and so elegantly branched, and as owing to their great length they are not well adapted for pinching, the suspicion has crossed my mind that they may in addition serve as an ornament ...’ (Darwin 1871, p. 319).

A similar argument could be made for fiddler crabs of the genus *Uca* (Decapoda: Ocypodidae), small, highly active semiterrestrial crabs found in sheltered areas of marshes and mangrove forests. *Uca* are universally dimorphic; whereas female crabs have two small feeding claws, males have one small (minor) claw and one greatly enlarged major claw that can constitute nearly half the body mass (Crane 1975; Weissburg 1992, 1993). The form of the major claw is reminiscent in size and delicacy to the pincers of Lucanid and *Dynastes* (Hercules) beetles. Males wave the often brightly coloured chela in species-specific displays, a behaviour that has been shown to be more related to attracting females than to communicating among males (Pope 2000). Male chela size may itself be attractive to females, although evidence of preference for larger-clawed males is contradictory (Yparraguirre 1981; Salmon 1984) in part because the size at which males are successful in

mating appears to be context-dependent (Zucker 1986; Jennions & Backwell 1998).

Berglund *et al.* (1996) used a qualitative game theory argument to conclude that the strategy proposed by Darwin was unlikely. Success in contests between males required that an individual have a substantive ability to fight behind the putative threat posed by a large ornament. In addition to signalling to females, male fiddler crabs use their major claw to fight with other males (Crane 1975; Salmon & Hyatt 1983; Pope 2000). Combat between crabs involves a stereotyped set of behaviours that includes threats, contact and grappling (Hyatt & Salmon 1979a,b). Combat does not usually result in serious injury in many species (Crane 1966; Hyatt & Salmon 1979a,b; Jennions & Backwell 1996), but in others injury is a possible outcome (Jones 1980). In some species of fiddler crab, larger males keep territories at shore levels where higher-quality breeding burrows attract females for mating. In such areas of the intertidal roving individuals often attempt to usurp residents, with larger males having greater success in evicting smaller crabs (Crane 1975; Pratt, McLain & Lathrop 2003). In this case the benefits of success in combat are clear; larger males are more likely to obtain and defend a breeding burrow in a location preferred by females (Christy 1982, 1983). This observation leads to the prediction that larger males should have increasingly robust claws. Combined with experience, a relatively larger claw should result in enhanced fighting effectiveness.

Crab chelae function as a simple lever system; contraction of pinnate muscles attached to a blade-shaped apodeme rotates a movable finger (dactyl) about a fulcrum, resulting in closure against a fixed finger (pollex) (Fig. 1). The force applied to the apodeme by the muscles is transmitted through the in-lever to the out-lever, producing a closing force along the dactyl. Following more general considerations of muscle force generation (Alexander 1975), closing force in a crab chela is proportional to muscle cross-sectional area (MCA), which is equal to apodeme area (Warner & Jones 1976; Schenck & Wainwright 2001). Claw closing force is also a function of the mechanical advantage (MA) of the lever system, which is determined by the relative proportions of the lever arms (in-lever/out-lever) on

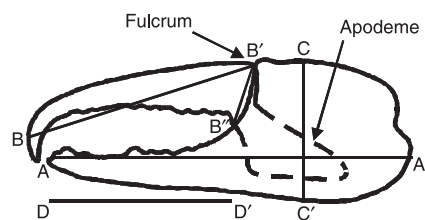


Fig. 1. Major claw of male *Uca pugnax*. Measurements taken from crabs used in the study: A–A', claw (propodus) length; B–B', dactyl (out-lever) length; B'–B'', dactyl height (in-lever); C–C', manus height; D–D', pollex length. Manus width was measured perpendicular to manus height; manus length equals claw length minus pollex length.

either side of the fulcrum (Elnor 1978; Elnor & Campbell 1981). Variation in closing force with claw size is therefore a function of the product of MCA and MA.

The logic that a bigger claw is better for combat due to an associated increase in closing force collides with our knowledge of claw morphology, creating an apparent paradox. A biomechanical study of fiddler crab claw closing force demonstrated that the major claws of males are fully functional; the pattern of closing force with changing body size fits a simple model based upon expectations from MCA and MA (Levinton & Judge 1993). Consistent with predictions from the model of Berglund *et al.* (1996), the major claw of fiddler crabs does not represent an empty threat. However, while absolute closing force of the major claw does increase with increasing claw size, large crabs are not as strong as one would expect. As male fiddler crabs grow, the proportions of their major claws change such that MA (and as a consequence, relative closing force) declines steadily with increasing claw size, resulting in proportionally weaker chelae (Levinton & Judge 1993). This negative relationship between size of the major claw and MA is true of all *Uca* species measured thus far (Levinton, Judge & Kurdziel 1995). Although proportional claw closing force could be maintained in the face of declining MA by compensatory (positive) allometry of MCA, in fact MCA does not even exhibit isometry as crabs grow, exacerbating the problem (Levinton & Judge 1993). In contrast, the minor (feeding) claws of both male and female fiddler crabs are isometric with respect to both MA and MCA (Levinton *et al.* 1995) and relative closing force remains constant as individuals increase in size.

Declining closing force with increasing claw size would at first glance seem maladaptive, since strength should be an essential function as males grapple in combat. However, patterns of this sort are not unique to fiddler crabs and can be explained functionally. Many carnivorous crustacea, such as the American Lobster, *Homarus americanus*, are dimorphic and have differentiated cutting and crushing claws. The crusher claw usually has not only greater muscle mass (and presumably MCA), but also a higher MA than the cutter claw, which is used to rapidly manipulate and slice food items (Govind & Pearce 1986). Such species therefore have two separate implements specialized for different aspects of food manipulation and preparation. The differentiation of function between claws probably involves a trade-off between closing force and closing speed (Elnor & Campbell 1981; Schenck & Wainwright 2001). In a similar way, increased claw closing speed is a possible advantage that might accrue to male fiddler crabs as a result of steadily decreasing MA with increasing body size. Functional trade-offs such as this are common in other lever systems, particularly the four-bar linkage jaw systems of fishes (Westneat 1990).

The purpose of our study was to determine whether there is indeed a trade-off between closing force and

closing speed mediated by changes in MA of the major claw of the Mud Fiddler Crab *Uca pugnax* (Smith), commonly found in temperate salt marshes of the Atlantic coast of the United States. We also ask if the magnitude of this putative trade-off fits expectations from a simple biomechanical model based on claw morphology, as was observed previously for closing force (Levinton & Judge 1993; Levinton *et al.* 1995). We believe that this is one of the first times such a trade-off in a biomechanical lever system has been explicitly tested in a quantitative fashion.

Materials and methods

Adult male *U. pugnax* were collected from a sand flat at the Flax Pond salt marsh in Old Field, New York, USA (Levinton & Judge 1993). Crabs were held in recirculating seawater at 25 °C for 48 h prior to experimentation and fed Tetramin fish flakes *ad libitum*.

Previous work documenting the relationship between claw (propodus) length and closing force in *U. pugnax* relied on indirect measures of MCA and MA to model expected force production (although the correspondence between predicted and actual force measurements was quite good) (Levinton & Judge 1993; Levinton *et al.* 1995). We calculated MCA and MA for newly collected male crabs ($N = 73$) both indirectly after Levinton & Judge (1993) as the cross-section of an ellipsoid defined by manus length, width and height, and the ratio of claw height to pollex length, respectively, and directly as the apodeme area and ratio of dactyl height at the dactyl base (in-lever) to dactyl length (out-lever) (Fig. 1). Specimens were preserved in 70% ethanol, and measurements of apodeme area were made following dissection of the dactyl with attached apodeme from the propodus. Length measurements were made to the nearest 0.02 mm with digital callipers and apodeme area was estimated from digital images (Scalar Corp., Vacaville, California, USA, USB computer microscope ($\times 1$)) with NIH Image (v. 1.61) calibrated against a scale photographed at the same time. Slopes of the equations relating claw length (CL) and MCA, MA and an index of closing force (ICF = MCA \times MA) calculated by both methods were compared with analysis of covariance (ANCOVA) on log-transformed data, with claw length as the covariate.

An index of claw closing velocity (ICV) analogous to the ICF (Levinton & Judge 1993) can be calculated from the morphological measurements described above. The velocity of the dactyl tip is proportional to the shortening velocity of the muscles attached to the apodeme, and inversely proportional to the mechanical advantage. If muscle shortening velocity scales isometrically with length, ICV is equal to the product of muscle length and $1/MA$ (Richard & Wainwright 1995). We estimated length of the claw closer muscle as $MCA^{1/2}$ (where MCA = apodeme area), assuming that length scales to area with a slope of 0.5. Given the previous success of Levinton & Judge (1993) in predicting claw

closing force with a variant of this measure (see also results below), we feel that this assumption is reasonable. We compared the predicted relationship between ICV and CL with actual closing speeds measured for the major claws of live crabs ($N = 102$).

It was not possible to get reliable measures of closing speed in the field because fighting between males cannot be accurately videographed from a standard angle with a standard length scale. These measurements were therefore done in the laboratory using the same type of apparatus previously used to measure closing force (Levinton & Judge 1993). The tips of the pollex and dactyl were placed in two brass rings, one (pollex) attached to the end of a fixed beam and the other (dactyl) to a thin flexible beam in a cantilever device similar to the one used by Levinton & Judge (1993). The distance between the two rings was adjusted with a set screw as a function of claw size to keep the gape angle between pollex and dactyl constant at 36°. Crabs spontaneously closed their major claw in a series of rhythmic contractions. We recorded the crabs with a MotionScope high-speed video camera (Redlake Inc., San Diego, CA) set at 125 frames s^{-1} . The monitor output allowed us to calculate the number of frames, and therefore the time period, over which claw closure occurred. For each crab, we estimated average angular velocity for the first full closure event as the claw gape angle ($36^\circ = 0.628$ rad) divided by time ($n = 1$ measure per individual), and the linear velocity of the dactyl tip as the product of angular velocity and dactyl length. This approach permitted accurate estimates of velocity since time was measured precisely and claw closing distance was well controlled. We estimated functional relationships between predicted and observed closing velocity and claw length with reduced major axis (Model II) regression on log-transformed data using the iterative LOSS function in SYSTAT (v. 10). Given that both x and y are subject to error variation of differing scale, this approach is preferred over simple linear or major axis regression (Ricker 1973; Sokal & Rohlf 1995).

Results

Consistent with previous results (Levinton & Judge 1993; Levinton *et al.* 1995), morphological estimates made on a new sample of *U. pugnax* using a more direct measure of muscle cross-sectional area (apodeme area) and length of in-lever (width of dactyl at the base) demonstrate that relative closing force of the major claw declines with increasing claw size for male fiddler crabs (Fig. 2, $r^2 = 0.62$). Closing force estimated with the different morphometric indices scaled to claw length with exponents much less than the value of 2 that is expected under isometry (ICF = $CL^{1.17}$ using methods from Levinton & Judge 1993; and $CL^{1.36}$ with the new direct measurements of MCA and MA). The difference between the two estimates is not statistically significant ($F_{1,142} = 1.65$, $P = 0.201$), and both are similar to actual measurements of claw closing force for

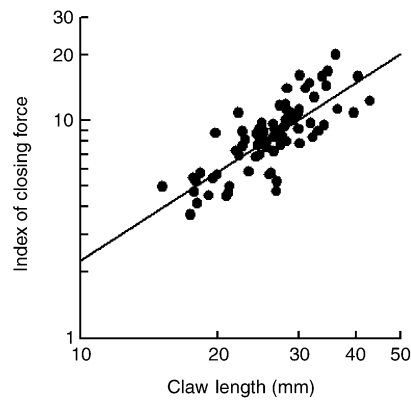


Fig. 2. The relationship between relative index of closing force and claw length for *Uca pugnax*, calculated with direct measures of apodeme area and mechanical advantage ($N = 73$).

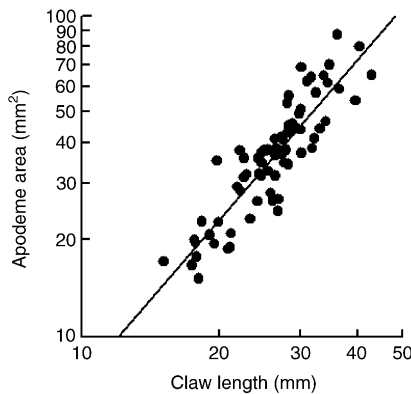


Fig. 3. The relationship between apodeme area and claw length for *Uca pugnax* ($N = 73$).

U. pugnax (e.g. Levinton *et al.* 1995). As fiddler crabs grow, the proportional decrease in closing force of the major claw results from allometric relationships of both MCA and MA to claw length. Apodeme area scales to claw length as $CL^{1.65}$ (Fig. 3, $r^2 = 0.78$) and is not statistically different from the indirect estimate derived from external morphometrics after Levinton & Judge (1993) ($MCA = CL^{1.60}$; $F_{1,142} = 0.26$, $P = 0.615$). Both estimates are less than the expected value of 2, which assumes that MCA increases proportionally with the square of claw length. Mechanical advantage also decreases with increasing claw size, indicating that the out-lever (dactyl length) is increasing more rapidly than the in-lever (dactyl height) as claw size increases (Fig. 4, $r^2 = 0.38$). In this case, the estimate of MA calculated directly (dactyl height/dactyl length, $CL^{-0.29}$) differs significantly from the indirect measure (manus height/pollex length, $CL^{-0.42}$) used previously by Levinton & Judge (1993) ($F_{1,142} = 5.74$, $P = 0.018$). Although there is more scatter in the data, we assume that the new direct measure provides the best estimate of MA, and therefore used this measure when calculating expected claw closing velocities.

As predicted by the biomechanical model, observed closing velocity was positively related to claw length (Fig. 5). Qualitative examination of the video record-

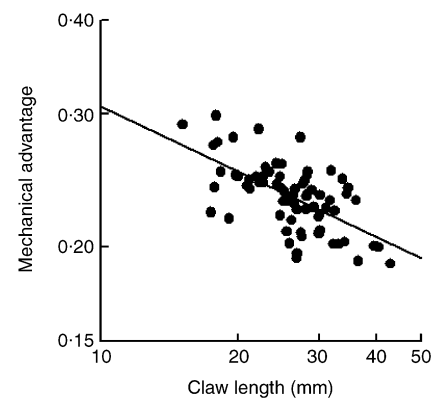


Fig. 4. The relationship between mechanical advantage and claw length for *Uca pugnax* ($N = 73$).

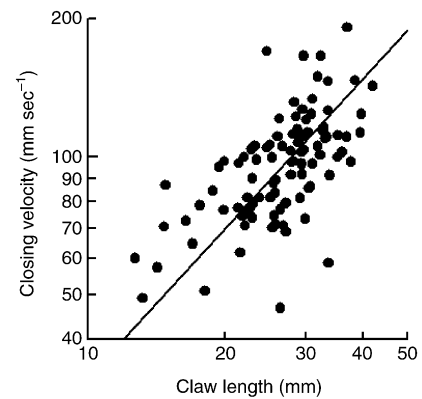


Fig. 5. The relationship between closing velocity of the dactyl tip and claw length for *Uca pugnax* ($N = 102$).

ings suggests that calculating a single value for velocity is somewhat idealized since claw closing speed was slightly reduced at the beginning and end of each event. Nevertheless, agreement between the predicted and observed data is quite good. Our expectation was that closing velocity would scale to claw length as $CL^{1.20}$ (reduced major axis regression) while the actual observed relationship was $CL^{1.08}$. There are currently no standard methods analogous to ANCOVA for comparing the slopes of lines fitted using Model II regression. As a first approximation, we note that the 95% confidence intervals for the two estimated slopes overlap substantially (predicted: 1.09, 1.30; observed: 0.90, 1.27), although the interval around our estimate of observed velocities is rather wide. We also acknowledge that our assumption about muscle shortening velocity scaling isometrically with length is unlikely to be correct. As a general rule, a decreasing rate of muscle contraction with increasing body size has been observed for a variety of taxa including mammals (Rome *et al.* 1990), fish (Anderson & Johnston 1992; Richard & Wainwright 1995) and crustaceans (Josephson & Stokes 1994; Nauen & Shadwick 1999). The degree to which muscle shortening velocity decreases is variable and not always large, but this phenomenon would lead to an overestimate of predicted closing speeds and may explain the

slight discrepancy between our predicted and observed results. Ontogenetic changes in the angle of insertion or sarcomere length of the pinnate muscle fibres would also affect claw closing force and speed, however, angle of insertion has been found to be invariant with respect to size for multiple species of crab (Schenck & Wainwright 2001; Taylor 2001) and the sarcomere lengths of muscle fibres in the major and minor claws of *U. pugnax* specifically do not differ (Govind, Quigley & Mearow 1986). These data suggest that size-specific changes in claw biomechanics can be adequately explained by our simple morphological model.

Discussion

Our results demonstrate that closing speed of the major claw of *U. pugnax* increases with claw size by approximately the factor expected based on allometric changes in MCA and MA. The simple lever system of the fiddler crab claw dictates a trade-off between closing force and closing speed; as MA decreases with increasing claw size, closing force must decrease while closing speed increases. As a consequence, fiddler crabs (and other chelae-bearing crustaceans) cannot simultaneously maximize force and speed through changes in the biomechanical system. It is important to test this prediction quantitatively because there is no guarantee that mechanical proportions are the only dictators of claw dynamics. For example, Taylor (2001) demonstrated in cancer crabs that although claw closing force increased with claw size, maximum muscle stress (force per unit area) decreased. He suggests the existence of a constraint that might be general among crabs, although we see little evidence for this in *U. pugnax* (Levinton & Judge 1993; Levinton *et al.* 1995).

Trade-offs between force and speed have been observed in other crustaceans. American Lobsters, for example, have evolved a system in which one claw is specialized for closing force and the other for closing speed (Govind, Mellon & Quigley 1987). Functional trade-offs are also evident in different biomechanical systems. Variation among taxa in the four-bar linkage jaw system of labrid fishes constitutes a trade-off between jaw closing force and closing speed (Westneat 1990), and has been used to trace the phylogenetic history of feeding evolution in this group (Westneat 1995). In high-energy environments of Pacific coral reefs, labrid fishes tend to have pectoral fins with high aspect ratios (Bellwood & Wainwright 2001), in contrast to the fins of fish living in more protected waters. Presumably this difference reflects a trade-off between the fin proportions needed for 'flying' as opposed to 'rowing' (Westneat 1996).

The observed trade-off between claw closing force and speed in fiddler crabs raises the question of why males apparently do not have reduced success in combat as a result of becoming proportionally weaker as they grow, or conversely, what is the advantage to larger males of increased claw closing speed? Alterna-

tively, the explanation may not be one of functionality driven by natural selection, but rather of a runaway process of female choice for highly ornamented individuals, with claw function of secondary importance. A similar suggestion has been made for the evolution of deer, most notably for the Irish Elk. While the extinct Irish Elk had antlers that were not unusual in proportion to body size, they nevertheless were enormous and appeared to be ornamental. Gould (1974) argued that the large palmate antlers most likely had a display function and that Irish Elks probably did not fight by butting antlers. Even so, large antlers do not always guarantee success in combat and mating. In some cases, a dimorphic strategy allows males of one phenotype to succeed in one part of a mating season, while a less robust and well-armed male does better in another (Eberhard 1977). Smaller male deer with accordingly smaller antlers may be less exhausted towards the end of the rutting season, and may beat better-endowed males who succeeded earlier in the season by virtue of their larger antlers. Other honest signals of condition might be used when body size is not a good indicator (Clutton-Brock & Albon 1979). Still, there must presumably always be some real combat function behind antlers. Indeed, Kitchener (1987) provided convincing evidence that Irish Elk antlers were in fact used in intermale contests. Similarly, given the use of the fiddler crab claw in male combat (Crane 1975) and evidence for preservation of closing function (Levinton & Judge 1993), we reject the idea that the chela is merely an ornament with little functional value.

Nevertheless, if damaging opponents were an objective of combat one might assume that male fiddler crabs would at a minimum maintain relative claw closing strength with increasing claw size. Unfortunately, we do not have a systematic account of the frequency and intensity of damage inflicted in fighting between males, let alone data related to body size. Our own personal observations with *U. pugnax* and *U. pugilator* show that grappling and pushing between crabs typically results in little damage to the participants. This impression is confirmed by many observations of the same species by Ann Pratt (personal communication). Patricia Backwell (personal communication) has noted that thousands of observations of combat in *U. annulipes* and *U. perplexa* have not resulted in many instances of damage or autotomy of the major cheliped (autotomy is common in decapod crustaceans and is considered to be an adaptive reflex response to injury (Juanes & Smith 1995)). She has also observed another species with many autotomized chelae on the sediment surface, however, whether these cast-off claws are the result of combat or predation is uncertain. John Christy informs us (personal communication) that marks reflecting damage from fighting can occur in *U. pugilator*, and Stefano Cannicci (personal communication) has noted extensive damage to participants in an experiment that induced combat between males of *U. vocans*. Clearly, further research is required to examine the scope of

damage from combat between *Uca* males in an organized fashion. It would be particularly interesting to know whether variation in the exponents relating closing force to claw size correlates to an index of combat damage among species. In other words, do males of species exhibiting high rates of damage (e.g. *U. vocans*) also maintain greater relative claw closing force as they grow, compared with species where damage from fighting is uncommon?

We can only speculate at present on the forces driving the trade-off between claw closing force and closing speed in male *U. pugnax*. However, given the apparent lack of damage inflicted during combat in this species we are left with the conclusion that claw closing speed is at a premium. Male combat success may be predicated more on grappling speed than on crushing force that damages an opponent. A typical combat encounter occurs in a breeding area between a roving male seeking possession of a burrow and the resident he is trying to displace (Crane 1975). To be successful, the roving male must rapidly grab the resident and extricate him before he is set in his hole. In other cases two fighting males, both residents of burrows, interact on the sediment surface with a stereotyped series of pushing encounters and grappling, which is sometimes followed by one male grabbing and driving the other to the ground (Hyatt & Salmon 1979a). Michael Rosenberg (personal communication) has observed in Panama male *U. deichmanni* and *U. terpsichores* grabbing and flipping rivals, followed by the speedy retreat of the losing crab. In each of these cases, greater claw closing speed would allow the winning male to quickly grab and throw his opponent before he was ready to respond. This advantage is analogous to the rapid move of an aggressor in Greco-Roman wrestling or other martial arts such as 'Push-Hands'. It is also possible that the proportionally longer dactyl in large males affords an increased probability of getting a good grip on an opponent in order to flip him over.

Our overall argument for a functional trade-off between claw closing force and speed is part of a general theme of trade-offs and constraints in sexually selected characters. Horns of male African antelopes function as visual displays for attracting females, but must also serve as a defence against predators (Packer 1983). Females tend to have simpler horns that function only for defence; the dual functions of ornament and armament may impose a limit on the showiness of the male's horns. Many reproductively active male frogs use a vocal display and some gather in conspicuous leks to attract females (Ryan, Tuttle & Rand 1982). However, multiple predators are also guided to their prey by the frogs' mating calls, imposing counter-selection on call frequency and volume (Ryan 1985). Male Wolf Spiders, *Hygrolycosa rubrofasciata*, court females by drumming dry leaves with their abdomen. Energy expenditure for drumming males is 22 times the resting rate, resulting in loss of body mass and increased mortality, particularly among poorly fed individuals (Kotiaho *et al.*

1998; Kotiaho 2000). The idea that the reproductive benefits of further trait exaggeration are eventually balanced by costs to fitness such as increased mortality or reduced growth rate is a central premise of the theory of sexual selection (Fisher 1958; Zahavi 1975, 1977; Kirkpatrick 1982), and understanding how the evolution of sexually selected traits is limited by numerous potentially competing factors remains an important goal of evolutionary biologists (Andersson 1994). We here provide a quantitative framework for exploring how simple mechanical properties constrain the evolutionary trajectory of a sexually selected trait, and suggest that extending our results in a broader phylogenetic context will be an important step towards this goal.

Acknowledgements

We thank Michael Campagna, who helped collect some of the data in this project. We also thank David Conover for providing the high-speed video apparatus. Michael Judge designed the beam system used to measure closing speed. Finally, and most importantly, we thank two anonymous reviewers who discovered important errors in our original analyses and helped us to get a better grip on our arguments. This is Contribution 1133 from the Program in Ecology and Evolution, State University of New York, Stony Brook.

References

- Alexander, R.M. (1975) *Biomechanics*. Chapman & Hall, London.
- Anderson, M.E. & Johnston, I.A. (1992) Scaling of power output in fast muscle fibers of the Atlantic cod during cyclical contractions. *Journal of Experimental Biology* **170**, 143–154.
- Andersson, M. (1994) *Sexual Selection*. Princeton University Press, Princeton, NJ.
- Bellwood, D.R. & Wainwright, P.C. (2001) Locomotion in labrid fishes: implications for habitat use and cross-shelf biogeography on the Great Barrier Reef. *Coral Reefs* **20**, 139–150.
- Berglund, A., Bisazza, A. & Pilastro, A. (1996) Armaments and ornaments: an evolutionary explanation of traits of dual utility. *Biological Journal of the Linnean Society* **55**, 385–399.
- Christy, J.H. (1982) Burrow structure and use in the sand fiddler crab, *Uca pugilator* (Bosc). *Animal Behavior* **30**, 687–694.
- Christy, J.H. (1983) Female choice in the resource-defense mating system of the sand fiddler crab, *Uca pugilator*. *Behavioral Ecology and Sociobiology* **12**, 169–180.
- Clutton-Brock, T.H. & Albon, A.D. (1979) The roaring of red deer *Cervus elaphus* and the evolution of honest advertisement. *Behaviour* **69**, 145–170.
- Crane, J. (1966) Combat, display and ritualization in fiddler crabs (Ocypodidae, genus *Uca*). *Philosophical Transactions of the Royal Society of London B* **251**, 459–472.
- Crane, J. (1975) *Fiddler Crabs of the World*. Princeton University Press, Princeton, NJ.
- Darwin, C. (1871) *The Descent of Man, and Selection in Relation to Sex*. John Murray, London.
- Eberhard, W.G. (1977) Fighting behavior of male *Golofa porteri* beetles (Scarabeidae: Dynastinae). *Psyche* **84**, 292–298.
- Elnor, R.W. (1978) The mechanics of predation by the shore crab, *Carcinus maenas* L. on the edible mussel, *Mytilus edulis* L. *Oecologia* **36**, 333–344.

- Elner, R.W. & Campbell, A. (1981) Force, function and mechanical advantage in the chelae of the American lobster (*Homarus americanus* Decapoda: Crustacea). *Journal of Zoology London* **193**, 269–286.
- Fisher, R.A. (1958) *The Genetical Theory of Natural Selection*. Dover Publishers, New York.
- Gould, S.J. (1974) The origin and function of 'bizarre' structures: antler size and skull size in the 'Irish Elk', *Megaloceros giganteus*. *Evolution* **28**, 191–220.
- Govind, C.K. & Pearce, J. (1986) Differential reflex activity determines claw and closer muscle asymmetry in developing lobsters. *Science* **233**, 354–356.
- Govind, C.K., Quigley, M.M. & Mearow, K.M. (1986) The closer muscle in the dimorphic claws of male fiddler crabs. *Biology Bulletin* **170**, 481–493.
- Govind, C.K., Mellon, D. & Quigley, M.M. (1987) Muscle and muscle fiber type transformation in clawed crustaceans. *American Zoologist* **27**, 1079–1098.
- Hyatt, G. & Salmon, M. (1979a) Combat in the fiddler crabs *Uca pugilator* and *Uca pugnax*: a quantitative analysis. *Behaviour* **65**, 182–211.
- Hyatt, G. & Salmon, M. (1979b) Comparative statistical and information analysis of combat in the fiddler crabs, *Uca pugilator* and *Uca pugnax*. *Behavior* **68**, 1–23.
- Jennions, M.D. & Backwell, P.R.Y. (1996) Residency and size affect fight duration and outcome in the fiddler crab *Uca annulipes*. *Biological Journal of the Linnean Society* **57**, 293–306.
- Jennions, M.D. & Backwell, P.R.Y. (1998) Variation in courtship rate in the fiddler crab *Uca annulipes*: is it related to male attractiveness? *Behavioral Ecology* **9**, 605–611.
- Jones, A.R. (1980) Chela injuries in the fiddler crab *Uca burgersi* Holthius. *Marine Behavior and Physiology* **7**, 47–56.
- Josephson, R.K. & Stokes, D.R. (1994) Contractile properties of a high frequency muscle from a crustacean. I. Activation patterns *in vivo*. *Journal of Experimental Biology* **187**, 261–274.
- Juanes, F. & Smith, L.D. (1995) The ecological consequences of limb damage and loss in decapod crustaceans: a review and prospectus. *Journal of Experimental Marine Biology and Ecology* **193**, 197–223.
- Kirkpatrick, M. (1982) Sexual selection and the evolution of female choice. *Evolution* **36**, 1–12.
- Kitchener, A. (1987) Fighting behaviour of the extinct Irish elk. *Modern Geology* **11**, 1–28.
- Kotiaho, J. (2000) Testing the assumptions of conditional handicap theory: costs and condition dependence of a sexually selected trait. *Behavioral Ecology and Sociobiology* **48**, 188–194.
- Kotiaho, J., Alatalo, R.V., Mappes, J., Nielsen, M.G., Parri, S. & Rivero, A. (1998) Energetic costs of size and sexual signalling in a wolf spider. *Proceedings of the Royal Society of London B* **265**, 2203–2209.
- Lande, R. (1981) Models of speciation by sexual selection on polygenic traits. *Proceedings of the National Academy of Science USA* **78**, 3721–3725.
- Levinton, J.S. & Judge, M.L. (1993) The relationship of closing force to body size for the major claw of *Uca pugnax* (Decapoda: Ocypodidae). *Functional Ecology* **7**, 339–345.
- Levinton, J.S., Judge, M.L. & Kurdziel, J.P. (1995) 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? *Journal of Experimental Marine Biology and Ecology* **193**, 147–160.
- Maynard Smith, J. & Brown, R.L.W. (1986) Competition and body size. *Theoretical Population Biology* **30**, 166–179.
- Nauen, J.C. & Shadwick, R.E. (1999) The scaling of acceleratory aquatic locomotion: body size and tail-flip performance of the California spiny lobster *Panulirus interruptus*. *Journal of Experimental Biology* **202**, 3181–3193.
- Packer, C. (1983) Sexual dimorphism: the horns of African antelopes. *Science* **221**, 1191–1193.
- Pope, D.S. (2000) Testing function of fiddler crab claw waving by manipulating social context. *Behavioral Ecology and Sociobiology* **47**, 432–437.
- Pratt, A.E., McLain, D.K. & Lathrop, G.R. (2003) The assessment game in sand fiddler crab contests for breeding burrows. *Animal Behaviour* **65**, 945–955.
- Richard, B.A. & Wainwright, P.C. (1995) Scaling the feeding mechanism of largemouth bass (*Micropterus salmoides*): kinematics of prey capture. *Journal of Experimental Biology* **198**, 419–433.
- Ricker, W.E. (1973) Linear regression in fishery research. *Journal of the Fisheries Research Board of Canada* **30**, 409–434.
- Rome, L.C., Sosnicki, A.A. & Goble, D.O. (1990) Maximum velocity of shortening of three fibre types from horse soleus muscle: implications for scaling with body size. *Journal of Physiology* **431**, 173–185.
- Ryan, M.J. (1985) *The Tungara Frog: a Study in Sexual Selection and Communication*. University of Chicago Press, Chicago, IL.
- Ryan, M.J., Tuttle, M.D. & Rand, A.S. (1982) Sexual advertisement and bat predation in a Neotropical frog. *American Naturalist* **119**, 136–139.
- Salmon, M. (1984) The courtship, aggression and mating system of a 'primitive' fiddler crab (*Uca vocans*: Ocypodidae). *Transactions of the Zoological Society of London* **37**, 1–50.
- Salmon, M. & Hyatt, G.W. (1983) Spatial and temporal aspects of reproduction in North Carolina fiddler crabs (*Uca pugilator* Bosc). *Journal of Experimental Marine Biology and Ecology* **70**, 21–43.
- Schenck, S.C. & Wainwright, P.C. (2001) Dimorphism and the functional basis of claw strength in six brachyuran crabs. *Journal of Zoology London* **255**, 105–119.
- Sokal, R.R. & Rohlf, F.J. (1995) *Biometry*. Freeman, New York.
- Taylor, G.M. (2001) The evolution of armament strength: evidence for a constraint on the biting performance of claws of durophagous decapods. *Evolution* **55**, 550–560.
- Warner, G.F. & Jones, A.R. (1976) Leverage and muscle type in crab chelae (Crustacea: Brachyura). *Journal of Zoology London* **180**, 57–68.
- Weissburg, M.J. (1992) Functional analysis of fiddler crab foraging: sex specific mechanics and constraints. *Journal of Experimental Marine Biology and Ecology* **156**, 105–124.
- Weissburg, M. (1993) Sex and the single forager: gender-specific energy maximizing strategies in the fiddler crab *Uca pugnax*. *Ecology* **74**, 279–291.
- Westneat, M.W. (1990) Feeding mechanics of teleost fishes (Labridae: Perciformes): a test of four-bar linkage models. *Journal of Morphology* **205**, 269–296.
- Westneat, M.W. (1995) Feeding, function, and phylogeny: analysis of historical biomechanics in labrid fishes using comparative methods. *Systematic Biology* **44**, 361–383.
- Westneat, M.W. (1996) Functional morphology of aquatic flight in fishes: kinematics, electromyography, and mechanical modeling of labriform locomotion. *American Zoologist* **36**, 582–598.
- Yparraguirre, C.A. (1981) *Sexual selection in the fiddler crab Uca vocans* (Linnaeus). PhD Thesis, State University of New York at Stony Brook, NY.
- Zahavi, A. (1975) Mate selection – a selection for a handicap. *Journal of Theoretical Biology* **53**, 205–214.
- Zahavi, A. (1977) The cost of honesty (further remarks on the handicap principle). *Journal of Theoretical Biology* **67**, 603–605.
- Zucker, N. (1986) On courtship patterns and the size at which male fiddler crabs (Genus *Uca*) begin to court. *Bulletin of Marine Science* **38**, 384–388.

Received 11 June 2004; accepted 30 July 2004