THE DESIGN OF A BEAUTIFUL WEAPON: COMPENSATION FOR OPPOSING SEXUAL SELECTION ON A TRAIT WITH TWO FUNCTIONS

Stefan Dennenmoser$^1$ and John H. Christy$^{2,3}$

$^1$Department of Biological Sciences, University of Calgary, Calgary, T2N 1N4, Alberta, Canada
$^2$Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Ancón, Republic of Panama
$^3$E-mail: christyj@si.edu

Received June 11, 2012
Accepted November 8, 2012
Data Archived: Dryad doi:10.5061/dryad.2m65j

Male fiddler crabs, genus Uca, have one greatly enlarged claw with which they court females and threaten and fight other males. Longer claws are more effective signals but are thought to be less effective weapons because the relative closing force at the tip of the claw decreases with claw length. We studied claw morphology and fighting in Uca terpsichores and Uca beebei and found a mechanism that may resolve opposing selection for signaling and fighting ability. When males fought they delivered gripping forces not at the tips but at the tubercles on the inner margins of their claws’ fingers. As claws grow, these tubercles remain relatively close to the apex of the gape. Consequently, the mechanical advantage that governs the forces that can be delivered at these tubercles decreases only slightly with increasing claw length allowing the claw to be an effective signal and a powerful weapon. Animal weapons are exceptionally diverse in form and detail of armature and the causes of this diversity are poorly understood. We suggest that the designs of weapons may often reflect compensatory patterns of growth and placement of armature that enhances the weapon’s overall utility for multiple uses in competition for mates.

**KEY WORDS:** Biomechanics, claw, fiddler crab, secondary sexual trait compensation, sexual selection.

Males of many animals have traits that they use to threaten and fight other males and attract females for mating (Berglund et al. 1996). Selection arising from weapon and signal functions may be aligned, favoring the same design, or opposed, favoring different features for the two functions (e.g., Andersson 1994; Jones and Hunter 1999; Candolin 2004; Hunt et al. 2009). If opposed, then evolution may favor traits that compensate for the functional compromises imposed by design features that increase the performance of one function at the expense of the other (Møller 1996; Tomkins et al. 2005; Husak and Swallow 2011) and thus support the simultaneous dual functions of the character. Traits that compensate for the effects of exaggeration of signals on locomotion, flight and other aspects of performance have been found in several species (Husak and Swallow 2011). However, traits that compensate for the effects of opposing sexual selection on weapons used both for signaling and for fighting have not, to our knowledge, been described. Here we show how fighting tactics coupled with a morphological feature of fiddler crab claws compensate for a negative effect of exaggeration for signal function on claw closing force, allowing claws to be both beautiful and powerful weapons. Male fiddler crabs of the genus Uca (Decapoda, Ocypodidae) use their single greatly enlarged major claw (Fig. 1) as a visual signal (the claw waving display) to attract females and threaten males, and as a weapon. As expected of a signaling structure, longer claws are more attractive to females and repellant to males (Backwell and Passmore 1996; Jennions and Backwell 1996; Oliveira and Custódio 1998; Backwell et al. 2000; McLain and Pratt 2007; Milner et al. 2010; Callander et al. 2012; but see also Pope 2000a,b). However, long claws are not hollow semaphores; as expected of a weapon, the claw closer muscle is full-sized making claws strong (Levinton and Judge 1993; Levinton et al. 1995; Levinton and Allen 2005).
Males with larger claws usually win fights (e.g., Jennions and Backwell 1996) suggesting that claw closing force affects the outcome of combats (Sneddon et al. 2000). Claw closing force is determined by the mechanical advantage of the claw’s dactyl (movable finger) and by the cross-sectional area, sarcomere length, and angle of pinnation of the closing muscle. This muscle is attached to the flat cuticular apodeme that originates on the proximal ventral floor of the dactyl and longitudinally bisects the space inside the manus of the claw (Alexander 1968; Warner and Jones 1976). The force that the closing muscle can apply to the apodeme is directly proportional to the apodeme area, which correlates tightly with the muscle cross-sectional area (MCA; Warner and Jones 1976). Mechanical advantage is a characteristic of the simple lever system of the claw (Fig. 1). Contraction of the closing muscle rotates the dactyl around a pivot (fulcrum) against the pollex (fixed finger; e.g., Levinton and Allen 2005). Under the assumption of a frictionless pivot, $F_1 L_1 = F_2 L_2$ where $F_1$ is the muscular force applied to the in-lever of length $L_1$ and $F_2$ is the closing force produced at the end of the out-lever of length $L_2$. Mechanical advantage (MA) is the ratio of the in-lever to the out-lever $L_1 / L_2$ (Warner and Jones 1976). The product of MCA and MA gives an index of closing force (ICF) that correlates well with the measured forces male fiddler crabs produce when they contract their large claws (Levinton et al. 1995).

The use of the claw as a weapon should favor a relatively large manus and closer muscle and short fingers to achieve a large mechanical advantage. In contrast, the use of the claw as a signal, especially in the repetitive claw waving display to attract females, should favor relatively long fingers and a small manus to reduce muscle and exoskeletal mass (Taylor 2001). By lengthening the dactyl and pollex disproportionately relative to the size of the manus males produce a visually conspicuous signal at relatively low cost. However, following this design for signal function, as claws grow, dactyl length (out-lever) increases more than does dactyl height (in-lever) and the relative mechanical advantage of the claw decreases (Levinton and Allen 2005). Thus, sexual selection for signal function results in claws that become relatively weaker as they become longer compared to claws designed to maintain a constant mechanical advantage. Levinton and Allen (2005) described this relationship as the “paradox of the weakening combatant”—beauty begets weakness.

This paradox assumes that males grip their opponent’s claw with the tip of their own claw, and that this grip delivers the critical force that determines the outcomes of fights. Although the tip of the claw can become engaged with an opponent, this is unusual. Typically, males forcefully contract their claws only when they are interlaced (Crane 1975; Hyatt and Salmon 1978). In this position, the force is applied by tubercles located along the ventral inner margin of the dactyl and the dorsal inner margin of the pollex (Fig. 1). The mechanical advantage at these tubercles is greater than at the claw tip because of the shorter out-levers to these contact points. If, as claws grow, these tubercles stay relatively close to the pivot of the dactyl, then the mechanical advantage at these tubercles may stay constant or decline more slowly than the decline in mechanical advantage at the claw tip. There may be little or no relative loss in closing force with increasing claw length when the force is measured at the point where it is delivered. If true, there is no paradox; males may make long claws that are both effective signals and effective weapons by preserving the mechanical advantage of shorter claws as they grow.

Here we determine whether the loss of mechanical advantage at claw tips is compensated by changing tubercle positions on the dactyl and pollex in two species of fiddler crabs, Uca terpsichores (Crane) and Uca beebei (Crane). These two species provide two possible examples of compensation. Given the limitations on inferring adaptation from two-species comparisons (Garland and Adolph 1994), we defer interpretation of differences between the species in degree of compensation to a subsequent, broadly comparative paper.
Methods
The study was conducted in the Republic of Panama during November 2005 to February 2006. Male *U. terpsichores* (*n* = 94) and *U. beebei* (*n* = 121) were collected on the west bank of the Pacific entrance to the Panama Canal approximately 1 km upstream from the Bridge of the Americas, and on the beach at Culebra Point about 5 km to the southeast along the Amador Causeway.

We used a dial caliper to measure to the nearest 0.02 mm the carapace width and length of all males. We caused the males to autotomize (shed without damage) their major claws and immediately released the males in the field. The autotomized claws were taken to the laboratory where we measured and dissected them. Using a dial caliper we measured on each claw propodus length (hereafter, claw length), dactyl length, and dactyl height. We measured the out-lever distances from the fulcrum to the dactyl tip, to the tubercle on the dactyl and to the point where the dactyl applies force against the opposing pollex tubercle (Fig. 1). Smaller claws were measured under a stereo-microscope so that the jaws of the caliper could be precisely positioned. We dissected the claw closer muscle apodeme from the manus, removed the muscle, and photographed the apodeme against a grid. ImageJ (v. 1.34s; freeware, National Institute of Health) was used to calculate the area of the apodeme which we took as a measure of the cross-sectional area (MCA) of the claw closer muscle.

We calculated the MA at the claw tip and at the tubercles on the dactyl and pollex (Fig. 1). Videos of fighting crabs showed that males most often gripped their opponent’s relatively smooth outer manus with their dactyl tubercle. As a measure of MA compensation at the dactyl tubercle, we used ratio of the MA at the dactyl tubercle to the MA at the dactyl tip.

We made video recordings of fights in the field to determine how crabs fought and where they gripped their opponent’s claw. We also noted the locations of small puncture wounds (usually marked by darkened indentations) on all the claws we collected. We video recorded 22 fights between *U. terpsichores* males, all induced, and 24 fights between *U. beebei* males, 16 induced and 8 natural. We induced fights by placing males in shallow artificial burrows (made with a stick) close to resident males of about the same size. We enclosed the males with a circular plastic fence 30 cm in diameter so that the introduced males would not leave without fighting. We considered only fights in which the opponents fully interlocked their major claws (Crane 1975; Hyatt and Salmon 1978).

**Statistical Analyses**
Pearson’s χ² goodness-of-fit tests were used to compare frequencies with which the dactyl and pollex tubercles contacted the opponent’s manus when males contracted their claws during fights. Eight claw length outliers (possibly regenerating claws), six in *U. beebei*, two in *U. terpsichores* were identified using Cook’s distance plots and Bonferroni outlier tests and were excluded from the analyses. We used generalized linear models (GLMs) with a γ distribution and a log-link function to evaluate relationships between MA and claw length. The GLM model with the lowest Akaike’s information criterion (AIC) value was chosen as the best-fit model (Akaike 1973; Burnham and Anderson 2002). We used log-likelihood ratio tests to test whether MA-slopes differ significantly from 0. We did not log-transform the raw data and thereby avoided biased slope parameters caused by back-transformation (Packard 2011). For each species, the slopes of mechanical advantage at the claw tip, and the dactyl and pollex tubercles were compared by an analysis of covariance (ANCOVA) with claw length as the covariate, followed by Bonferroni-adjusted post hoc tests.

ICF were log-transformed to achieve homogenous variances and normality of residuals. For *U. terpsichores*, we performed GLMs with a Gaussian distribution and an identity-link function, whereas ICF data for *U. beebei* were better fitted by orthogonal polynomial regressions (Narula 1979). For comparing ICF slopes at the claw tip with the two tubercules we performed an ANCOVA, with Bonferroni-adjusted post hoc tests. One outlier identified in the *U. terpsichores* ICF pollex tubercle dataset was excluded from regression analyses because of its high leverage effect. We regressed our measure of degree of compensation at the dactyl tubercle (MA dactyl / MA tip) against claw length using orthogonal polynomial regressions. Residuals from all regression models were tested for normality using Shapiro–Wilk tests and quantile plots, and for homogeneity of variances using residual plots and Breusch–Pagan tests. Nonsignificant ($P < 0.05$) factor × covariate interactions were removed from ANCOVA models. All statistical analyses were performed in R version 2.14 (R Development Core Team 2011).

**Results**
Fights escalated to forceful combat following a patterned sequence of threats and pushes as is typical of fiddler crabs (Crane 1975; Hyatt and Salmon 1978; Dryad, Video 1, 2 doi:10.5061/dryad.2m65)). Males did not grip each other with the tips of their claws; they waited to contract their claws until they were at least partially interlaced. Moments before they contracted their claws both males typically worked the dactyls of their walking legs deeper into the sediment. The gripping contraction of the manus evidently was accompanied by contractions in the muscles of the carpus and merus producing a lifting force that was resisted by the opponent’s leg grip into the sediment. If the leg grip failed the intruder sometimes was flipped upside down and thrown to the side or the resident was lifted out of the entrance of his burrow.
Claw length plotted against carapace width for *U. terpsichores* (filled circles) and *U. beebei* (open circles).

In 22 fights between *U. terpsichores* males, the closing force was delivered to the outer manus 18 times by the dactyl tubercle and 4 times by the pollex tubercle ($\chi^2$ goodness-of-fit, $p = q = 0.5$, $\chi^2 = 8.909$, df = 1, $P = 0.003$; Fig. S1). In 24 fights between *U. beebei* males, the closing force was delivered 21 times by the dactyl tubercle and 3 times by the pollex tubercle to this area on the opponent’s claw ($\chi^2 = 13.5$, df = 1, $P < 0.001$). It was difficult to see exactly how opponent’s claws contacted each other on the inside of the manus (the palm). The inner margins of the pollex (usually) or dactyl (rarely) undoubtedly contact the elevated oblique ridge of tubercles and other armature present on the palms of each species giving purchase when males contract their interlaced claws (Crane 1975).

Males delivered the force of a contraction with the pollex tubercle to the opponent’s outer manus only when they were of opposite handedness (claws line up manus-to-tip when males face each other) and in either of two situations. First, when both males were on the surface and one rotated his claw outward, the tubercle on the pollex of his opponent would contact his manus. Second, when a resident withdrew into his burrow and left his claw flat on the surface blocking the entrance he would grip the outer manus of the claw of the intruder with the his pollex tubercle.

Puncture wounds on the claws we collected also showed that males forcefully grip opponents’ claws when they fight. A total of 20 of 121 (16.5%) claws of *U. beebei* and 36 of 94 (38.3%) claws of *U. terpsichores* had puncture wounds on the outer manus (Fig. S1).

**Claw Measures**

*U. terpsichores* had longer claws in relation to carapace width than did *U. beebei* (Fig. 2; Data File S1) However, claw lengths of lager males of the two species were similar because relative claw length declined with increasing body size more rapidly in *U. terpsichores* than in *U. beebei*.

MA at the claw tip and the pollex tubercles decreased with increasing claw length in both species (Fig. 3). The slope of MA at the dactyl tubercle against claw length did not differ significantly from zero in *U. terpsichores* ($F(1,89) = 1.55$, $P = 0.217$; slope $= -0.005$ [95% CI: $-0.012$, $-0.002$]), suggesting that there is no significant loss of MA at the dactyl tubercle with increasing claw length. *U. beebei* showed a slight but significant decrease of MA at the dactyl tubercle ($F(1,107) = 7.74$, $P < 0.01$; slope $= -0.009$ [95% CI: $-0.016$, $-0.003$]). For both species, the relative loss of MA was significantly less pronounced at both tubercles than at the claw tip indicating that tubercles stay relatively close to the pivot as the claw grows longer (ANCOVA, *U. terpsichores*: claw length $\times$ tubercle location interaction: $F(2,266) = 8.94$, $P < 0.001$; Bonferroni corrected post hoc tests: tip $\times$ dactyl-tubercle: $t = 4.169$, $P < 0.001$; tip $\times$ pollex-tubercle: $t = 2.317$, $P < 0.0426$; *U. beebei*: claw length $\times$ tubercle location interaction: $F(2,328) = 15.88$, $P < 0.001$; Bonferroni corrected post hoc tests: tip $\times$ dactyl-tubercle: $t = 5.46$, $P < 0.001$; tip $\times$ pollex-tubercle: $t = 4.01$, $P < 0.001$).
Compensation of MA at the dactyl tubercle increased with increasing claw length in both species (Fig. 3). The dactyl tubercle is positioned closer to the hinge in *U. terpsichores* than in *U. beebei* (Fig. 1) and the average MA compensation was much higher in this species.

Muscle cross-sectional area (MCA, measured as apodeme area) showed lower values in *U. terpsichores* than in *U. beebei* over the whole range of claw lengths as expected from the apparently smaller manus of *U. terpsichores* (Figs. 1, S2). The relative ICF with increasing claw length was less pronounced at the dactyl tubercle than at the claw tip in both *U. terpsichores* and *U. beebei* (Fig. 4). In contrast, the relative loss of ICF at the pollex tubercle did not differ significantly from the loss at the claw tip, either in *U. terpsichores*, or in *U. beebei* (ANCOVA, *U. terpsichores*: claw length × tubercle location interaction: $F_{(2,254)} = 3.469, P = 0.0326$; Bonferroni corrected post hoc tests: tip × dactyl-tubercle: $t = 2.633, P = 0.018$; tip × pollex-tubercle: $t = 1.363, P = 0.348$; *U. beebei*: claw length × tubercle location interaction: $F_{(2,313)} = 3.472, P = 0.032$; Bonferroni corrected post hoc tests: tip × dactyl-tubercle: $t = 2.496, P = 0.026$; tip × pollex-tubercle: $1.936, P = 0.107$).

**Figure 4.** Index of closing force (ICF) in *U. terpsichores* (A) and *U. beebei* (B) at the dactyl tubercle (black circles), the pollex tubercle (grey circles), and the claw tip (open circles).

**Discussion**

We have identified a two-part compensatory mechanism that allows the large claws of two species of fiddler crabs to be both effective semaphores and effective weapons, resolving the “paradox of the weakening combatant” (Levinton and Allen 2005). First, fighting male *U. beebei* and *U. terpsichores* delivered claw closing forces to opponents’ claws at the tubercles on the dactyl and pollex of their claws, not at the tips. Second, as males’ claws grow, the tubercles of their dactyl and pollex remain relatively close to the pivot (fulcrum) of the claw’s lever system. Consequently, the loss of mechanical advantage with increasing claw length was much less pronounced at the tubercles than at the tips of the claws of both species.

The morphological element of this compensatory mechanism could result from three nonexclusive processes (see also Pomfret and Knell 2006). First, selection for signal function might favor a gradient of responsiveness of claw tissue to growth factors (Hopkins 2001; Emlen 2012) leading to greater distal compared to proximal elongation of the dactyl and pollex at each molt. Second, the establishment of such a gradient could reflect selection against pleiotropic effects of elongation along the entire claw as a consequence of selection for longer claws that are better signals. Compensation for negative pleiotropic effects should be common (Pavlicev and Wagner 2012), and may be expected to relax pleiotropic constraints over evolutionary time. Males of some species of fiddler crabs, and predominantly those in the basal clade (eight species; Rosenberg 2001), exhibit marked asymmetrical inflation of the carapace and legs and elongation of the eyestalk on the side of the major claw, the later reaching an extreme in *Uca stylifera*, the males of which have a long terminal ocular style with no known function (Crane 1975). Although some of these effects may be beneficial (e.g., enlarged leg segments; Takeda and Murai 1993) others, such as unequal eye heights and visual fields may be detrimental favoring developmental mechanisms that control these apparently pleiotropic costs. Indeed, asymmetry of body parts is substantially reduced in species of the other two derived clades of the genus *Uca* (Rosenberg 2001). Finally, as for the horns of some dung beetles (Emlen 2001) differential growth along the axis of the dactyl and pollex may be a consequence of competition between regions for resources. When males of the *Uca lactea* species group (four species) lose their large claw, they grow a new one that is an effective signal because it is long and light, but is a poor weapon (Backwell et al. 2000; Reaney et al. 2008) because the manus and closer muscle are relatively small as are the forces these claws can deliver (Lailvau et al. 2008; see also McLain et al. 2010). These new regenerated claws also lack tubercles in the gape. Hence, when resources are limited, males invest in terminal rather than proximal growth along the axis of the claw. During normal claw growth, such a pattern of differential investment might leave the tubercles of the gape relatively close to the pivot and fortuitously maintain weapon function. A trade-off (corrected for crab size and phylogeny) between signal and weapon function also is evident among 21 species of *Uca* in the Americas (B. Swanson, unpubl. data).

Compensation is widespread in nature and is a consequence of diverse mechanisms ranging from phenotypic accommodation (e.g., the two-legged goat effect; West-Eberhard 2003, p 51) to selection favoring secondary genetic modification of detrimental pleiotropic effects (Pavlicev and Wagner 2012). In evolutionary time, compensatory mechanisms govern changes that reduce the negative effects of selection for one function on performance of another and thereby increase the adaptive integration of the phenotype (Murren 2012). Since the publication of the “handicap
principle," (Zahavi 1975), students of signal evolution have paid far more attention to the costs of exaggerated sexually selected traits (e.g., Searcy and Nowicki 2005) than to mechanisms that may reduce costs. Yet recent theoretical corrections to the handicap principle (Getty 2006) have made it clear that such mechanisms should be common and, predictably, some have been described (Husak and Swallow 2011).

Sexually selected ornaments often impede movement and most examples of compensation in response to the effects of sexual selection are of traits that reduce the costs of ornaments on locomotion or flight (Outiiero and Garland 2007; Husak and Swallow 2011). In most known cases, the compensatory trait is separate from the exaggerated trait. For example, stalk-eyed flies compensate for reduced flight performance caused by their long eyestalks by increasing the sizes of their wings and thorax (Husak et al. 2011). More recently, Worthington et al. (2012) described how the shape of eyestalks reduces aerodynamic costs of flight providing a rare example of a compensatory trait that is part of the exaggerated trait. Another example is found in the elongated tails of barn swallows. Long tails are more attractive to females than are short tails. However, males with longer tails exhibit reduced flight performance (maneuverability, velocity, acceleration), foraging success and ability to escape hawks (Møller et al. 1998). These costs are compensated by a decrease in the asymmetry of long tail feathers and by a reduction in the width of the outermost tail feathers (Møller 1991, 1995, 1998; see also Matyjasiak et al. 2009 for the House Martin). These examples show how sexually selected traits may negatively affect performance in relation to naturally selected tasks favoring compensatory traits that reduce costs and increase survival.

The mechanism of compensation in the claws of fiddler crabs we discovered does not reduce mortality but rather the negative effects of exaggeration of claws for one sexually selected function, signaling, on another, fighting. Hunt et al. (2009) compiled 51 examples of male traits that are the target of both female preference and selection for fighting ability and found that these two modes of sexual selection usually are linear, positive, and aligned and that body size was the targeted trait in 31 (61%) of the examples. Most of the other examples are of structures used to signal. An example of a dual-function aggressive structure under opposing selection from female choice and male–male competition was reported for the pala (expanded terminal leg segment) of a waterboatman (Candolin 2004). Males display their palae to females and females mate more readily with males with larger palae, but males with relatively large palae do less well in competitive contexts. Hence, as for fiddler crab claws, sexual selection for large palae for signaling opposes sexual selection that arises in competition. Unfortunately, it is not known why males with large palae are poor competitors and hence whether or how they compensate for these costs. Similarly, in the carrion fly Prochyl-

iza xanthostoma males with long heads are more attractive to females but males with short heads tend to win single (but not multiple) aggressive interactions between males (Bonduriansky and Rowe 2003). Thus, male head length in this fly may be a compromise between opposing sexual selection with no apparent compensatory mechanism.

Female preferences and the use of weapons in combat have long been thought to jointly affect weapon design (Berglund et al. 1996). Weapons also often are used to threaten and fight in different ways. For example, earwigs display their terminal abdominal cerci visually as a threat, and use them to strike, slam and grip opponents (Briceño and Eberhard 1995). Each use may favor different morphological features best at different defensive or offensive tactics. Horned beetles provide another compelling example of functional diversity of weapons (Emlen et al. 2005). Species that exclusively lever opponents lack features on their horns useful for gripping (e.g., Golofa porteri; Eberhard 1977), whereas species that clamp their opponents between two horns often bear small bumps on one of the horns that enhance gripping (e.g., Podischnus agenor; Eberhard 1979). Weapons are exceptionally diverse and divergent in both general design and detail (Emlen 2008), as expected of sexually selected traits (Eberhard 1985). The dearth of examples of how the different modes of sexual selection affect the designs of weapons, and whether compensation is common in weapon design is, therefore, surprising.

Based on our study of fiddler crab claws, we speculate that selection for weapon size for signaling or for tactics such as leveraging may often run counter to selection for pinching or gripping, and that gripping surfaces should be positioned to maintain a mechanical advantage with increasing weapon size. This may be common feature of the cerci of earwigs (Briceño and Eberhard 1995), and the horns and mandibles of beetles that males use to grip, rip, lever, lift, and toss opponents from defended burrows or perches (Eberhard 1979; Emlen 2008). We emphasize that studies of the functions and compensatory features of weapons require an integrated approach that links description of how weapons are used for display and combat with detailed knowledge of how weapon morphology affects performance because of responses of receivers and because of the mechanical relationships between parts of weapons and the muscles that move them.

ACKNOWLEDGMENTS

We thank the Smithsonian Tropical Research Institute for financial and logistical support, Taewon Kim for field assistance, and Brook Swanson for comments on an earlier version of this paper. We also thank the Unidad Administrativa de Bienes Revertidos of the Ministerio de Economía y Finanzas, the Servicio Nacional Aeronaval, and the Autoridad del Canal de Panama, Republic of Panama, for permission to access to the old Rodman Naval Base and its adjacent tidal flats on the west bank of the Panama Canal.
Literature Cited


Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher’s web site:

Appendix S1. Morphological measurements of *Uca terpsichores* and *Uca beebei* used in this study.

Figure S1. Outer surface of the major claws of male *U. terpsichores* (left) and *U. beebei* (right) showing (A, B) the locations of puncture wounds on the claws we collected from males in the field and (C, D) the approximate points of contact of the dactyl tubercle (light circles) and pollex tubercle (dark circles) when fighting males forcefully contracted their interlaced claws (as seen in video recorded fights).

Figure S2. Apodeme area, a measure of closer muscle cross-sectional area (MCA), in relation to claw length of male *U. terpsichores* (dark circles) and *U. beebei* (open circles)

This material is available as part of the online article form:
http://www.blackwell-synergy.com/doi/abs/XXXXX (This link will take you to the article abstract).