



The evolution of waving displays in fiddler crabs (*Uca* spp., Crustacea: Ocypodidae)

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Male fiddler crabs are commonly recognized by the presence of a single massive claw used in a variety of contexts, including territorial defence, agonistic interactions, and courtship behaviour. The most common behavioural context involving these enlarged chelipeds is their use in waving displays, which are remarkably diverse among species. Although the waving display is one of the most obvious behavioural features of male fiddler crabs, little is known about their main evolutionary trends during the diversification of the genus. The present study employed phylogenetic comparative methods to investigate the evolution of waving behaviour in a sample of 19 species of *Uca* from Central and North America. Digital recordings were used to quantify the temporal dynamics of waving behaviour in each species. Multivariate ordination methods were used to assess whether different elements of the display showed distinct evolutionary dynamics, particularly with respect to body size and the environment where species are most commonly found. Most of the interspecific variation in displays involves differences in the overall waving velocity, with no correspondence to their local environments, nor their body size. Interestingly, despite the strong concentration of variance in the first two ordination axes, there was no statistically significant evidence for phylogenetic signals in their respective scores. These results suggest that the overall structure of waving displays is evolutionarily labile, at the same time as being concentrated in a few particular axes of variation, possibly indicating evolution along lines of least resistance. The approach employed in the present study highlights the utility of phylogenetic comparative methods for elucidating the evolution of complex behavioural characteristics, such as the waving display in male fiddler crabs. © 2012 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2012, **106**, 307–315.

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INTRODUCTION

The diversity of signalling systems found among animal taxa is the complex outcome of a variety of mechanisms operating at ecological and evolutionary time scales, including sexual selection (Andersson, 1994; Zahavi & Zahavi, 1997), natural selection (Edmunds, 1974; Caro, 2005), and the physical properties of the signalling environment (Endler & Basolo, 1998; Maan *et al.*, 2006). The complex interaction of these mechanisms makes an understanding signal

evolution difficult. Many important advances have been achieved in recent times, such as the evolution of honest/deceptive signalling and its interplay with sexual and kin selection (Searcy & Nowicki, 2005). However, little is known about the evolutionary mechanisms driving the diversification of signalling systems at macro-evolutionary scales, particularly because the analytical tools to address this question have only become available in the past few decades (Felsenstein, 1985; Martins, 1996; Martins & Hansen, 1997). The advent of increasingly powerful statistical techniques, including explicit modelling of the evolution of complex traits, can serve as a valuable tool to

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understand signalling systems. For example, in a study of the visual displays of anole lizards, Ord & Martins (2006) demonstrated that evolutionary changes in display duration appear to be linked to sexual size dimorphism, whereas measures of display complexity (number and uniformity of display components) were more tightly associated with species recognition and the type of light environment in which the display is typically performed. The extent to which these patterns extend to other visual displays is still unknown.

Fiddler crabs (*Uca* spp., Ocypodidae) are an ideal taxon for investigating the evolution of signalling behaviours in the context of sexual selection. These crabs are best known for their remarkable sexual dimorphism: males have highly asymmetrical claws (chelipeds), with the major claw greatly enlarged (up to five times in length) relative to both the male's own minor claw and the female's two symmetrical minor claws (Rosenberg, 2002). In addition to fighting, males use their major claw in a variety of movements and signalling postures, most conspicuously during claw-waving displays (Christy & Salmon, 1984; Pope, 2005). Although claw waving is a common behaviour among male ocypodid crabs, the level of complexity of waving displays in fiddler crabs is unparalleled among crustaceans (Crane, 1975). In addition to variation in overall tempo and form, claw-waving displays also differ among species with respect to the presence/absence of movements in the minor claw, vertical movements in legs and the entire body, as well as stereotyped walking and running patterns when waving (Crane, 1975). Waving displays appear to play an important role in fiddler crab species recognition, given that each species has a unique wave form and sympatric species tend to employ claw-waving displays that contrast greatly with each other (Salmon & Atsides, 1968; Crane, 1975; Salmon *et al.*, 1978; Doherty, 1982; How, Zeil & Hemmi, 2009).

Although the waving behaviour of male *Uca* has been known for a long time (Crane, 1975), one of the pioneering studies to describe quantitatively the structure of these waving displays in an interspecific context was reported by How *et al.* (2009), in which seven Australian species of fiddler crab were investigated using digital video recordings. In addition to variation between individuals and geographical locations, How *et al.* (2009) also showed evidence for species-specific differences in the structure and timing of the displays, which were suggested to follow phylogenetic relationships. However, that suggestion was based on a visual inspection of different display patterns, and no study to date has used phylogenetic comparative methods to investigate the extent of phylogenetic signals in different components of the fiddler

crab waving displays, nor to model their evolution explicitly. The present study aimed: (1) to describe quantitatively the male waving displays of minor and major chelipeds in a diverse sample of *Uca* spp.; (2) to determine the main ways in which the waving tempo evolved over the course of the evolution of the genus; (3) to investigate the evolution of different temporal features of the waving displays in a phylogenetic context; and (4) to evaluate the existence of the relation between the tempo of waving display with habitat and carapace width.

MATERIAL AND METHODS

Measurements of the waving displays of 19 species of *Uca* (*Uca batuenta*, *Uca beebei*, *Uca deichmanni*, *Uca ecuadoriensis*, *Uca festae*, *Uca herradurensis*, *Uca heteropleura*, *Uca inaequalis*, *Uca intermedia*, *Uca oerstedii*, *Uca ornata*, *Uca panamensis*, *Uca princeps*, *Uca saltitanta*, *Uca stenodactylus*, *Uca stylifera*, *Uca tenuipedis*, and *Uca terpsichores*) were based on footage obtained from September to November 1997 at three sites in Panama: Naos (8°57'50"N, 79°31'53"W), Rodman Naval Base (8°56'58"N, 79°34'30"W), and Diablo Creek (8°57'50"N, 79°34'10"W). Additional recordings of *Uca pugilator* were obtained at Flax Pond, Long Island, New York, in July of 1998. Digital versions of the footage were analyzed frame-by-frame at 0.034-s intervals using the software VIDEOPOINT (Vernier Software). Although the displays performed by male fiddler crabs involve complex three-dimensional movements of the body and chelipeds, the analyses in the present study focused specifically on the most noticeable component of the display: the vertical movement of the major and minor chelipeds (Zeil, Nalbach & Nalbach, 1986; Christy & Salmon, 1991; Land & Layne, 1995; Zeil & Al-Mutairi, 1996; Oliveira & Custódio, 1998; Murai & Backwell, 2006). Two positions were recorded on each frame: the position of the tip of the waving cheliped and an additional landmark on the carapace to serve as a fixed reference point. The difference in the Y-position of these two points was computed to describe the vertical position of the cheliped in each frame. The time-series of this measurement was used to characterize graphically the waving display of each species. To obtain the precise vertical variation of waves, only recordings in which the animal was in full-face view were used, thus excluding *U. ecuadoriensis* from this analysis. Although there is evidence for individual differences in waving displays owing to social context and environmental factors (Hyatt, 1977; Jordão, Curto & Oliveira, 2007), this variation was assumed to be small in relation to interspecific differences, which is a common assumption of comparative studies (Martins, 1996).

Table 1. Measured characteristics of the waving displays of *Uca* spp.

Characteristic	Description
(a) Duration of the upward movement	The duration of the movement of the cheliped from its resting position to the maximum height position
(b) Duration at the peak of the wave	The duration of the time while the cheliped is kept at its maximum height
(c) Duration of the downward movement	The duration of the movement of the cheliped from the maximum height position to its resting position
(d) Complete wave duration	The total duration of the entire display itself.
(e) Interwave interval	The duration of the interval between the end of (c) and the beginning of (a) between successive waving displays

In addition, videos were only recorded when the weather was fairly consistent during the time period of the reproductive season, meaning that environmental factors possibly had little influence on the structure and tempo of the displays. Also, measurements were obtained only from waves that were performed without females in the near vicinity of the displaying male, thus providing a baseline display that is comparable among species. Furthermore, only the most frequent kinds of waving were included in the analysis, leaving aside those that do not have evident reproductive purpose (Muramatsu, 2010).

Additional measurements were taken to characterize the main features in the waving displays for both minor and major claws of different species, namely the duration of the upward movement, the duration at maximum height, the duration of the downward movement, the duration of the complete waving display, and the duration of the interwave interval (Table 1). The main patterns in the waving displays among the studied species were characterized using a phylogenetically-corrected principal component analysis (PPCA) using the mean of each measurement for each species (Revell, 2009) (Table 2). This method has been shown to provide estimates of the eigenstructure of the dataset that have lower variance relative to nonphylogenetic procedures, thus reducing type I error to its nominal level when scores are analyzed using phylogenetic methods. Phylogenetic information was obtained from Rosenberg (2001). The results of the PPCA were visualized in a phylomorphospace (Figure 2), comprising a projection of the phylogenetic relationships among species in the ordination space of the studied variables (Sidlauskas, 2008). These analyses were complemented by simulations to test whether the observed concentration of variance among ordination axes is different from what would be expected by chance. We simulated a 19-taxon phylogeny and evolved five characters with the same rate of evolution to emulate a dataset analogous to the one used in the present study. The

proportion of variance explained by each ordination axis was then calculated for each 5×19 matrix and the entire procedure was replicated 1000 times. Phylogeny simulations were conducted using the GEIGER, version 1.3-1 (Harmon *et al.*, 2008) and trait simulations were conducted using PHYTOOLS, version 0.0-9 (Revell, 2011).

Second, we tested the extent of phylogenetic signals in the evolution along the PPC axes. This was carried out using the approach developed by Pagel (1999) based on an extension of a constant-variance random-walk model (sometimes called Brownian motion). Under those conditions, the degree of similarity in a given trait between two lineages is proportional to the extent of their shared history, as indicated by the phylogeny, such that traits evolve at each instant of 'time' dt with a mean character change of zero and an unknown but constant variance δ^2 . Pagel introduced another parameter, λ , to estimate the extent to which the phylogeny correctly predicts patterns of similarity among species. This parameter can range from 1 (as predicted by the Brownian motion model) to 0 (trait similarity among species is independent of phylogeny). Hypothesis-testing using this approach is based on the likelihood ratio statistic, which compares the goodness of fit of a model to the data with that of a simpler model lacking one or more of the parameters. Analyses using Pagel's method were implemented using GEIGER (Harmon *et al.*, 2008).

Finally, we used the phylogenetic generalized least squares method (PGLS) (Martins & Hansen, 1997) to test how PPCA scores were associated with differences in body size (as indicated by male carapace breadth; Table 3) and the habitats, with contrasting degrees of background noise, where species were found (Rosenberg, 2002) – species living in either open tidal zones (*U. beebei*, *U. deichmanni*, *U. heteropleura*, *U. intermedia*, *U. ornata*, *U. princeps*, *U. saltitanta*, *U. stenodactylus*, *U. stylifera*, and *U. terpsichores*) or mangroves (*U. batuenta*, *U. ecuadoriensis*, *U. herraduraensis*, *U. inaequalis*, *U. oerstedii*, and *U. tenuipe-*

Table 2. Descriptive statistics of the characteristics of the waving displays of *Uca* spp. investigated in the present study

Species	N	Interwave interval (s)	Duration of the upward movement (s)	Duration of the peak of the wave (s)	Duration of the downward movement (s)	Complete wave duration (s)
<i>Uca batuenta</i>	27	1.314 ± 0.62	0.192 ± 0.15	0.15 ± 0.08	0.135 ± 0.09	0.478 ± 0.17
	10	0 ± 0	0.101 ± 0.03	0.2 ± 0.08	0.079 ± 0.03	0.38 ± 0.1
<i>Uca beebei</i>	326	0.429 ± 0.45	0.246 ± 0.07	0 ± 0	0.09 ± 0.04	0.337 ± 0.08
	53	0.326 ± 0.18	0.167 ± 0.06	0.008 ± 0.02	0.104 ± 0.04	0.279 ± 0.07
<i>Uca deichmanni</i>	100	0.466 ± 0.51	0.2 ± 0.05	0.494 ± 0.15	0.153 ± 0.06	0.847 ± 0.16
	16	0.305 ± 0.41	1.222 ± 0.79	0.091 ± 0.09	0.455 ± 0.4	1.767 ± 0.93
<i>Uca ecuadoriensis</i>	4	2.035	0.241 ± 0.12	0.035 ± 0.05	0.233 ± 0.13	0.509 ± 0.11
<i>Uca festae</i>	489	0.105 ± 0.36	1.268 ± 0.61	1.046 ± 0.89	0.437 ± 0.17	2.751 ± 1.07
	22	0.529 ± 0.69	0.718 ± 0.54	0.029 ± 0.09	0.323 ± 0.20	1.07 ± 0.61
<i>Uca herradurensis</i>	6	4.27 ± 2.53	5.732 ± 1.80	0.146 ± 0.14	1.072 ± 0.36	6.95 ± 2.19
	7	8.506 ± 3.13	2.316 ± 0.33	1.024 ± 0.41	0.144 ± 0.02	3.483 ± 0.62
<i>Uca heteropleura</i>	62	1.316 ± 0.71	0.619 ± 0.20	0.002 ± 0.01	0.279 ± 0.18	0.899 ± 0.29
	34	0 ± 0	0.299 ± 0.09	0.003 ± 0.01	0.145 ± 0.06	0.448 ± 0.14
<i>Uca inaequalis</i>	13	2.439 ± 0.31	0.744 ± 0.07	0 ± 0	0.454 ± 0.15	1.198 ± 0.19
	5	0 ± 0	0.207 ± 0.06	0.143 ± 0.06	0.28 ± 0.02	0.631 ± 0.15
<i>Uca intermedia</i>	240	0.47 ± 0.29	0.174 ± 0.04	0.005 ± 0.01	0.089 ± 0.02	0.268 ± 0.05
	59	0.417 ± 0.15	0.15 ± 0.03	0.001 ± 0.01	0.095 ± 0.03	0.246 ± 0.05
<i>Uca oerstedii</i>	106	1.176 ± 0.41	0.884 ± 0.31	0.256 ± 0.13	0.319 ± 0.10	1.459 ± 0.38
	82	1.316 ± 0.54	0.316 ± 0.15	0.417 ± 0.14	0.166 ± 0.07	0.899 ± 0.22
<i>Uca ornata</i>	117	0.01 ± 0.04	0.466 ± 0.25	1.417 ± 0.98	0.363 ± 0.08	2.246 ± 1.01
	64	0.344 ± 0.21	0.583 ± 0.54	1.262 ± 1.63	0.304 ± 0.18	2,149 ± 1.87
<i>Uca panamensis</i>	149	3.914 ± 2.16	0.454 ± 0.11	0.239 ± 0.12	0.404 ± 0.15	1.097 ± 0.20
	52	4.459 ± 2.68	0.328 ± 0.08	0.349 ± 0.11	0.271 ± 0.09	0.948 ± 0.15
<i>Uca princeps</i>	160	2.497 ± 0.99	0.348 ± 0.10	0.08 ± 0.06	0.222 ± 0.09	0.65 ± 0.13
	72	2.488 ± 0.54	0.254 ± 0.09	0.099 ± 0.08	0.199 ± 0.08	0.552 ± 0.12
<i>Uca pugilator</i>	134	0.554 ± 0.55	0.287 ± 0.10	0.235 ± 0.18	0.29 ± 0.14	0.811 ± 0.26
	36	0.662 ± 0.48	0.258 ± 0.31	0.288 ± 0.26	0.191 ± 0.08	0,738 ± 0.38
<i>Uca saltitanta</i>	111	0.813 ± 0.33	0.272 ± 0.09	0.003 ± 0.01	0.116 ± 0.09	0.391 ± 0.13
	49	0 ± 0	0.109 ± 0.04	0.008 ± 0.03	0.081 ± 0.04	0.198 ± 0.06
<i>Uca stenodactylus</i>	251	0.717 ± 0.56	0.567 ± 0.29	0.141 ± 0.15	0.513 ± 0.22	1.22 ± 0.45
	51	0.547 ± 0.29	0.203 ± 0.11	0.268 ± 0.23	0.209 ± 0.15	0.68 ± 0.30
<i>Uca stylifera</i>	194	0.32 ± 0.15	0.418 ± 0.15	0.089 ± 0.07	0.2 ± 0.12	0.706 ± 0.19
	83	0.385 ± 0.15	0.311 ± 0.17	0.138 ± 0.10	0.137 ± 0.05	0.587 ± 0.16
<i>Uca tenuipedis</i>	28	0.924 ± 1.05	0.549 ± 0.16	0.079 ± 0.13	0.385 ± 0.24	1.012 ± 0.26
	9	0.728 ± 0.23	0.406 ± 0.16	0.215 ± 0.25	0.212 ± 0.07	0.833 ± 0.20
<i>Uca terpsichores</i>	181	0.598 ± 0.68	0.569 ± 0.26	0.053 ± 0.20	0.242 ± 0.76	0.864 ± 0.86
	53	0.035 ± 0.07	0.085 ± 0.05	0.04 ± 0.07	0.079 ± 0.05	0.204 ± 0.12

L and S indicate measurements on displays using major and minor claws, respectively. Data are provided as the mean ± SD.

dis). The remaining species were found in specific environments and were not tested (*U. festae* in thick muddy creek beds, *U. panamensis* on and around rocks, and *U. pugilator* in sheltered shores and mud-sand substrates). Body size was included in the analysis as a continuous predictor variable, whereas the environments were scored as separate dummy variables. The PGLS analyses were implemented using the corBrownian function in APE, version 2.3-2 (Paradis, Claude & Strimmer, 2004) and the GLS function in NLME (Pinheiro *et al.*, 2008). Given that the phylogeny of Rosenberg (2001) did not include branch lengths proportional to divergence times among lineages, the abovementioned analyses were performed by setting all branches to 1 or using the branch length transformation *sensu* Grafen (1989). All analyses were carried

out in the R environment (R Development Core Team, 2011).

RESULTS

There was considerable variation in waving displays among the studied fiddler crab species, from the slowly-ascending *U. herradurensis*, to the simple oscillation of *U. stylifera*, to the fast and sporadic *U. princeps* (Fig. 1). Interestingly, the temporal dynamics of the movements in the minor claws reflected that of the major claws to a large extent, despite the obvious differences in amplitude. Only one species (*U. deichmanni*) did not show any evidence of waving displays with its minor claw.

More precise information of the waving displays was obtained from the analyses of almost 3500 individual waving displays (Table 2). Measures of the timing of different display components in each species were used to compute mean values for their main characteristics (Table 2). These means were integrated with their phylogenetic relationships *sensu* Rosenberg (2001) to compute the PPCA using Grafen-transformed branch lengths. Most of the variance in the data set was concentrated on the first PPC (68.5% and 69.2% for the major and minor claws, respectively) and second PPC (21.7% and 21.3%, respectively). The loadings on the first PPC had a similar magnitude and direction both for major and minor claw displays. In general, the first PPC can be interpreted as indicative of the overall velocity of the displays, although the duration at maximum height and the duration of the interwave interval slightly stood out from the other variables in the major and minor claws, respectively (Table 4). The loadings on the second PPC were different for the major and minor claws (Table 4), with a stronger influence of maximum height and interwave interval, respectively. Repeating the analyses with all branch lengths set to 1 provided qualitatively similar results (not shown). Interestingly, the amount of explained variance on the first ordination axis was considerably

Table 3. Body size of the studied fiddler crab species, measured with calipers to the nearest 0.01 mm

Species	N	Mean carapace breadth (mm)
<i>Uca batuenta</i>	21	6.34
<i>Uca beebei</i>	50	7.87
<i>Uca deichmanni</i>	50	6.78
<i>Uca ecuadoriensis</i>	13	9.30
<i>Uca festae</i>	50	9.48
<i>Uca herradurensis</i>	6	13.40
<i>Uca heteropleura</i>	4	18.98
<i>Uca inaequalis</i>	33	6.86
<i>Uca intermedia</i>	1	14.70
<i>Uca oerstedii</i>	6	8.33
<i>Uca ornata</i>	1	36.90
<i>Uca panamensis</i>	10	14.19
<i>Uca princeps</i>	1	21.75
<i>Uca saltitanta</i>	50	5.70
<i>Uca stenodactylus</i>	50	9.48
<i>Uca stylifera</i>	3	25.18
<i>Uca tenuipedis</i>	11	4.94
<i>Uca terpsichores</i>	50	8.54

Table 4. Loadings of the studied variables on the first two phylogenetic principal component analysis

Variable	Major claws		Minor claws	
	PPC1	PPC2	PPC1	PPC2
Interwave interval	0.73	-0.48	0.81	-0.32
Duration of the upward movement	0.95	-0.07	0.95	-0.10
Duration of the peak of the wave	0.19	0.95	0.17	0.97
Duration of the downward movement	0.94	0.04	0.95	0.03
Complete wave duration	0.96	0.20	0.97	0.16
Percent of explained variance	68.5%	21.7%	69.2%	21.3%

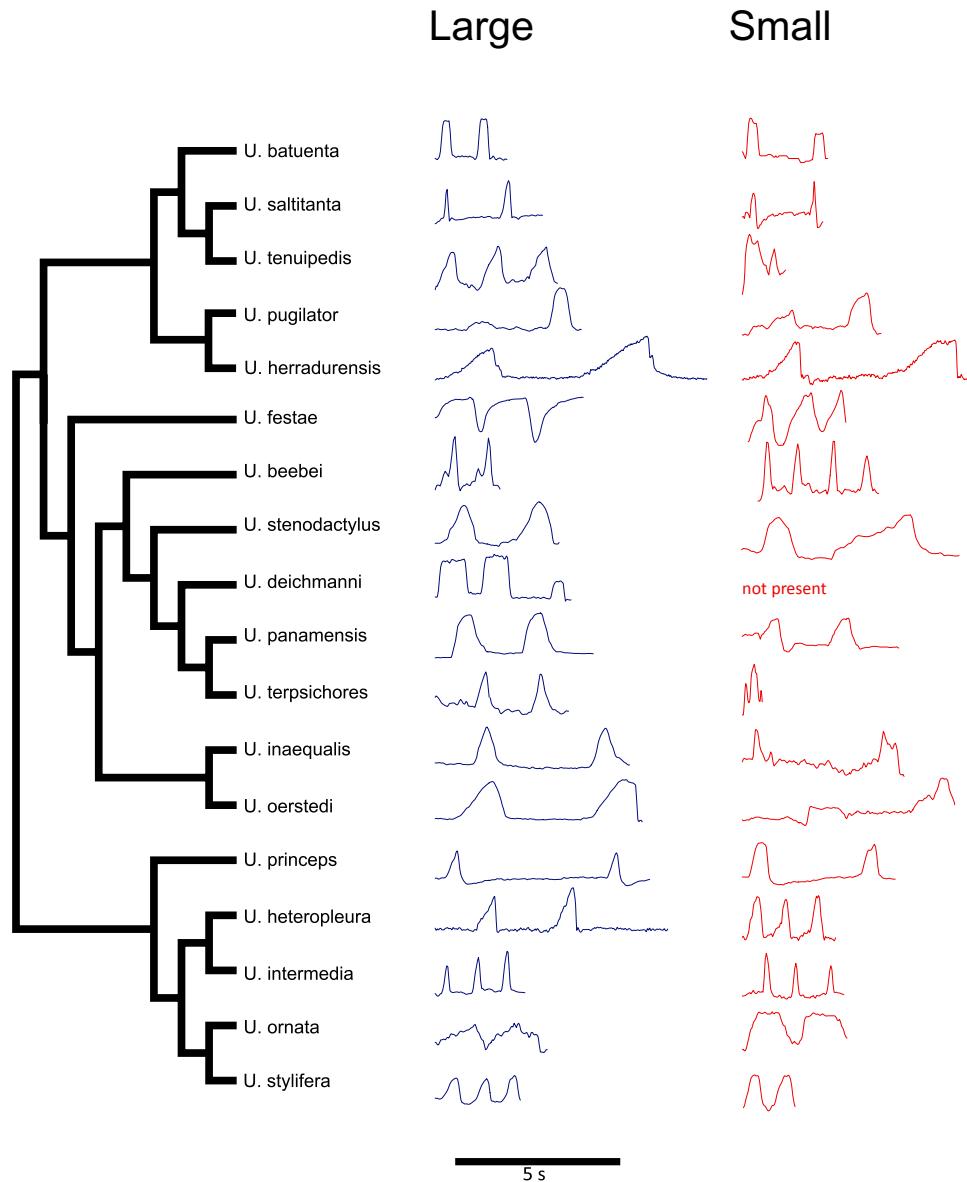


Figure 1. The evolution of the vertical component of minor and major claw waving displays in *Uca* spp. The phylogenetic relationships among the studied species were based on Rosenberg (2001).

higher than in the simulated data set ($52.4 \pm 0.10\%$ and $23.8 \pm 0.06\%$ for the first two ordination axes, respectively).

There was no statistically significant evidence for phylogenetic signals in the scores of each species along PPC1 and 2, both for minor and major claws ($\hat{\lambda} \approx 0$, $P = 1$ in all tests), suggesting a rapid divergence among species to the extent that their phylogenetic history is obscured. This result is in sharp contrast to the high concentration of variance along the first two PPCs and suggests that temporal display evolution has been highly constrained by these two axes. Finally, PGLS analyses did not detect any evi-

dence of a relationship between body size and either tested environment (open tidal zones and mangroves) on PPC scores of the major claw waves [Akaike information criteria (AIC)_{PPC1} = 90.59, $P = 0.23$ – 0.81 , AIC_{PPC2} = 67.22, $P = 0.56$ – 0.02 ; with the latter becoming nonsignificant after a Bonferroni correction for multiple tests].

DISCUSSION

For decades, waving behaviour in fiddler crabs has traditionally been studied in a qualitative way, with pictorial representations of the typical patterns for

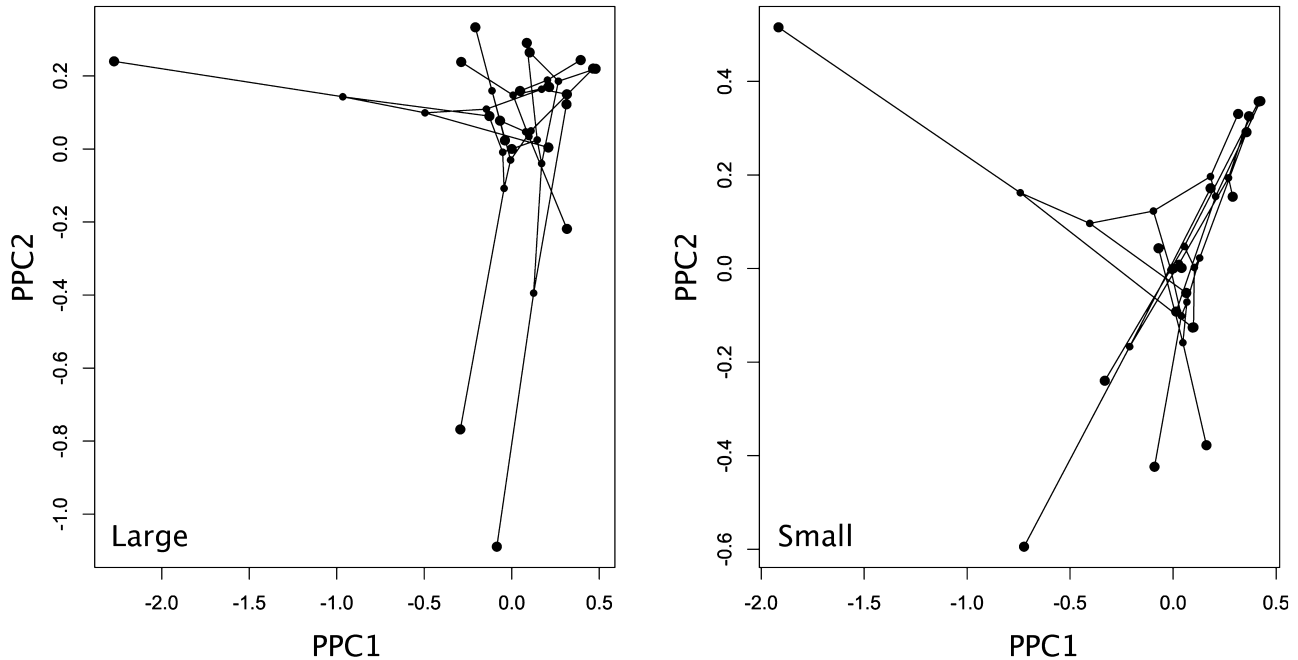


Figure 2. Phylomorphospace based on the first two phylogenetic principal components describing variation in the vertical component of minor and major claw waving displays in *Uca* spp. PPC, principal component.

each species (Crane, 1975; How *et al.*, 2009), leading to a traditional classification of displays that has been hypothesized to progress from the simple vertical wavers to the more complex lateral waving displays (Crane, 1975 but see Salmon & Zucker, 1988; Levinton, Sturmbauer & Christy, 1996). Although all species included in this analysis are considered lateral wavers (Crane, 1975), the quantitative approach employed in the present study allowed for the uncovering of several interesting patterns regarding interspecific waving variation and thus represents a substantial improvement in the investigation of this communication system. For example, despite the considerable interspecific variation in waving displays, almost 70% of these differences predominantly involve changes in overall display velocity, with all elements being correspondingly delayed or advanced (Table 4). This is an interesting pattern given that there was no statistically significant evidence for phylogenetic signals of PPCA scores, suggesting rapid divergence between species that erased the phylogenetic history of the waving display. The absence of phylogenetic signals also disagrees with several studies suggesting that related species have similar waves (Crane, 1975; von Hagen, 1982; How *et al.*, 2009) and supports the idea that waving displays were largely affected by a series of other adaptations, such as conspecific recognition, predation risk and female preference (Doherty, 1982; Christy & Salmon, 1991; Levinton *et al.*, 1996; Sturmbauer, Levinton & Christy, 1996; Jennions & Backwell, 1998; Koga *et al.*,

1998; Oliveira & Custódio, 1998; Pope, 2000; Murai & Backwell, 2006; How *et al.*, 2008). Interestingly, interspecific differences of waving displays do not appear to be affected by either the contrasting signalling environments or body size, despite increasing evidence for an influence of such factors on other signalling systems (Endler & Basolo, 1998; Maan *et al.*, 2006). Nevertheless, the concentration of change along a few axes of variation, although showing great evolutionary lability, could indicate evolution on lines of least resistance upon which unidentified traits are coevolving. This phenomenon is commonly suggested in morphological characteristics (Schluter, 1996; Marroig & Cheverud, 2005) and, to the best of our knowledge, the present study would represent the first evidence of evolution along lines of least resistance in a behavioural phenotype. Detailed studies about the intraspecific covariance of waving are needed to evaluate this hypothesis.

The present study examined one major aspect of waving display, namely the timing of the raising and lowering of the chelipeds. There are many additional differences in waving not captured by these analyses, such as whether the major cheliped is waved vertically in front of the crab (as in *U. heteropleura*), vertically next to the crab (as in *U. stylifera*) or is moved in a more circular 'come-hither' motion (as in *U. beebei*). Nevertheless, vertical displacement is one of the most conspicuous features of wave display, given that it could be noticed regardless the viewer's position, whereas spatial components change with

orientation. However, although this timing of the wave is certainly of critical importance, more detailed video analysis that captures both the horizontal and vertical movement of the cheliped (in two-dimensions, as seen from the front) or the full three-dimensional movement of the wave would aid considerably in understanding interspecific variation and the evolution of wave forms. Unfortunately, these types of studies would require a much better video recording of displays than is readily available at this time.

The contribution of the minor cheliped during waving displays has been largely overlooked in previous work on fiddler crabs. In the present study, minor chelipeds were consistently used during the waving displays of all studied species, except for *U. deichmanni*, showing a strong correspondence between the temporal patterns of movement of minor and major chelipeds, with a few interesting differences (Table 4). This correlation indicates that the minor cheliped waving pattern may simply be a by-product of the major claw waving. Although the role of the minor cheliped during the display is poorly understood, the use of this structure could provide an intriguing trade-off between sexual and natural selection, given that minor chelipeds are important for food acquisition (e.g. Valiela *et al.*, 1974; Crane, 1975; Rosenberg, 2001; Matsumasa & Murai, 2005).

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