Variation in courtship rate in the fiddler crab *Uca annulipes:* is it related to male attractiveness?

Michael D. Jennions[a] **and Patricia R. Y. Backwell**[a,b]
[a]Smithsonian Tropical Research Institute, Republic of Panama, and [b]Communication Biology Research Group, Department of Zoology, University of the Witwatersrand, Private Bag 3, WITS 2050, Johannesburg, South Africa

We investigated among-male variation in courtship waving in the fiddler crab *Uca annulipes*. Wave rate is positively correlated with both male carapace size and relative claw size (controlled for body size), and relative claw size is positively correlated with an index of body condition. An experimental reduction in the availability of food decreased male wave rate. These data suggest that some of the variation in wave rate among males is due to variation in male condition combined with energetic costs to waving (differential costs). However, we also found that the correlation between male size and wave rate decreased over the semilunar cycle. Later in the cycle, smaller males increase their wave rate relative to that of larger males. Previous work has shown that females are more likely to accept a smaller male as a mate later in the cycle. We suggest that smaller males invest disproportionately more in courtship later in the cycle because the potential benefits are greater due to their increased attractiveness to females (differential benefits). Alternative explanations for the observed temporal trend are also discussed. *Key words:* courtship, female choice, fiddler crabs, male choice, ornaments, sexual selection, *Uca annulipes.* *[Behav Ecol 9:605–611 (1998)]*

Despite directional female choice, there is often considerable phenotypic variation among males for sexually selected traits like ornaments or courtship (Pomiankowski and Møller, 1995). This is usually explained in terms of variation among males in their ability to pay advertisement costs like greater energetic expenditure or higher predation risk that are associated with increased ornamentation (for review, see Andersson, 1994). Consequently, the expression of these sexual traits is often condition dependent because males in better condition pay smaller costs for a given marginal increase in investment (Grafen, 1990; Kodric-Brown and Brown, 1984; Zahavi, 1977). As recently noted, "the condition-dependent theory [for variation in sexually selected attributes] has been constructed solely on the basis of differential costs. This ignores potential differences among individuals in the benefits of courtship due to other sexually selected traits" (Reynolds, 1993: 914).

Although rarely invoked, courtship rates may vary among males when the benefits of courtship depend on their investment in other sexually selected characters ("differential benefits hypothesis"). For example, even when the cost of courtship is identical for all males, the function relating courtship to mating success may reach its asymptote sooner for morphologically more attractive males. This will lead to a lower optimum for investment in courtship by more attractive males and thereby generate population variation in courtship (Reynolds, 1993). Is there evidence for this differential benefits model whereby courtship varies in relation to male "attractiveness"? First, if males generally adjust courtship in relation to its benefits, they should more vigorously court females who yield higher benefits, phenomena that can be termed male mate choice (Houde, 1997). Indeed, males do preferentially court females that have higher fecundity (Sargent et al., 1986), are more sexually receptive (Sumner et al., 1994), or are likely to yield higher paternity following sperm competition (Schwagmeyer and Parker, 1990). Second, to relate these results to courtship variation among individual males, however, the potential benefits of courting different types of females must also vary among males. Only recently have researchers begun to investigate among-female variation in mate choice (for review, see Jennions and Petrie, 1997). Unsurprisingly then, given that male mate choice is less well studied, there are few examples of among-male variation in choosiness, and there are almost no studies where variation in choosiness is related to male attractiveness. One instructive exception is size-dependent variation in male choosiness in the sailfin molly (*Poecilia latipinna*). Larger males are more discriminating when distinguishing between sexually receptive and unreceptive females (Sumner et al., 1994). Smaller males primarily obtain matings after forced copulations ("gonopodial thrusting"), whereas larger males actively court females and rely more heavily on female cooperation to copulate successfully (Travis, 1994). The benefits of courting receptive females may therefore be greater for larger, more attractive males who are strongly preferred by females (Ptacek and Travis, 1997).

Third, in some species the average female preference for particular male sexual traits changes temporally or spatially in response to external cues (for review, see Jennions and Petrie, 1997). If males fine tune their courtship by adjusting to these changes in their sexual attractiveness to females, the phenotypic relationship between the sexually selected traits conferring attractiveness and courtship should vary depending on where or when it is measured. Unfortunately, there are few species in which predictable effects of environmental or temporal features on female preferences have been reported. Moreover, most of these cases are associated with female mating responses to elevated predation risk (e.g., Forsgren, 1992; Gong and Gibson, 1996; Godin and Briggs, 1996; Hedrick and Dill, 1993; Houde, 1997). This makes it difficult to distinguish between changes in male courtship due to changes in their relative attractiveness (differential benefits) or changes in the

---

relative costs of courtship (differential costs), given that more attractive males tend to be more conspicuous to predators (Andersson, 1994). Reynolds (1993) carried out an elegant laboratory study on guppies, *Poecilia reticulata,* that allowed him to distinguish between the two hypotheses. He showed that differential costs were probably responsible for the change in the relationship between male size and courtship under two light intensities. Given the general paucity of data, the hypothesis that differential benefits generate among-male variation in courtship is largely unsupported, and those studies that have examined variation in courtship tend to focus on differential costs to males in the face of predation (Houde, 1997).

Aims of the study

In this study we investigated temporal changes in the correlation between male phenotype (body and claw size) and courtship in a fiddler crab, *Uca annulipes,* which shows a predictable decline in a large-male mating advantage over each semilunar cycle. This appears to be related to a decreased female preference for male size because of temporal constraints on the timing of fertilization by females (Backwell and Passmore, 1996; see below for details). A male's risk of predation is unlikely to vary over the semilunar cycle because avian predation on courting males did not occur at our study site (Jennions and Backwell, personal observations). These phenomena would seem to select for a change in courtship over time consistent with differential benefits for different-sized males (but see Discussion for an alternate explanations for such a trend). We asked two main questions: (1) Do condition-dependent differences among males in the costs of courtship influence their display rate, as predicted by the handicap principle? Specifically, does variation in food availability influence courtship? (2) Does the relationship between male size and courtship change over the semilunar cycle?

Study species

Uca annulipes is a small fiddler crab (1–2 g) found in mixed-sex colonies on intertidal mudflats (Crane, 1975). Our study was conducted in Durban Harbour, South Africa, from 1992 to 1994. Both sexes defend burrows used as refugia during tidal inundation. In some *Uca* males wave their major claws primarily at other males (e.g., *U. vocans*; Backwell PRY, unpublished data). In *U. annulipes,* however, $97 \pm 6\%$ SD of waves are directed at females (Backwell et al., 1998). Males court females from their burrow entrance by waving the enlarged major claw in a "come hither" display (Christy and Salmon, 1991; Crane, 1975).

Active female mate sampling occurs in the Durban population. Gravid females leave their burrows and sequentially approach and enter males' burrows. Eventually they remain in a burrow and copulate with the resident male. There is considerable variation in the size of sexually mature males (carapace width: 9 mm to >17 mm). Toward the beginning of each 14-day semilunar tidal cycle, females selectively visit the burrows of, and eventually mate with, males larger than the population average. At the end of the cycle, however, females visit and mate randomly with respect to male size. Backwell and Passmore (1996) followed individual females who were mate sampling and found that the significant decline in mated male size is due to changes in female mate-choice decisions rather than to direct male–male competition. This reduction in female choosiness for male size, or a correlate thereof, over the semilunar cycle may be due to temporal constraints on sampling. Females must allow sufficient time after egg fertilization for larval development to occur before the larvae are released on the following nocturnal spring tide (which occurs shortly after the start of the next semilunar cycle) (Morgan and Christy, 1995). Females are therefore under greater pressure to mate later in the cycle. Further information on *U. annulipes* can be found in Backwell and Passmore (1996), Jennions and Backwell (1996) and Backwell et al. (1998).

METHODS

The cost of waving: a feeding experiment

We constructed eighteen 40-cm diam enclosures of plastic netting with a strip of solid plastic surrounding the top to prevent males from escaping. The enclosures were arranged in six blocks with one replicate of each of three treatment per block. The treatments were food addition, food removal, and control. Each day we diluted 8.0 g of Tetramin fish flakes in 1 l of sea water and distributed it across the surface of the six addition enclosures. We removed food from the six removal enclosures by lightly scraping the top layer of sediment off with a builder's trowel. This was done as soon as the tidal water had receded and therefore before male emergence. Previous work on *U. beebei* showed that this method of food addition affects behavior in a manner consistent with greater food availability (Backwell et al., 1995). Scraping off the upper sediment removes the diatoms (the main food of *Uca*; Weissburg, 1993) deposited by inundating tidal water and should therefore reduce food availability. We neither added food to nor scraped sediment off the control enclosures. We doubt that scraping per se affects male behavior. *Uca annulipes* is far less timid than other fiddler species, perhaps because there is no apparent avian predation on adults at the study site (Jennion and Backwell, personal observations). Predation by aquatic predators may occur during tidal inundation. Unlike other species, male *U. annulipes* will emerge from burrows and resume normal behavior within a few centimeters of a stationary observer's feet (Jennion and Backwell, personal observations). Consistent with this, scraping did not decrease male activity on the surface (see Figure 1a). Treatments were carried out daily for one semilunar cycle. For the next cycle, each block was observed daily for 12 days during a 45-min period after low tide (26 November–7 December 1994). The numbers of males waving and present on the surface per enclosure were recorded.

Size and wave rate

We monitored 93 clusters of non-enclosed, waving males in the field. The burrows of 4–11 males per cluster were marked with colored pins for identification ($n = 754$ males). We then recorded the cluster for approximately 10 min using a Panasonic VHS camera. A cluster was simply a set of males in sufficiently close proximity that they appeared on the same video. Video recordings were then transcribed in the laboratory. Each male was observed for the same 5-min period, and the number of waves given counted. After recording, males were captured and major claw length and carapace width measured to the nearest 0.1 mm using dial calipers. We calculated the repeatability of measurements by making each measurement twice for a subset of 15 males. Both measures were significantly and highly repeatable (carapace width: $r_I = 1.00$, $F > 1000$, df $= 14,15$, $p < .0001$; claw length: $r_I = 1.00$, $F > 1000$, df $= 14,15$, $p < .0001$; $r_I = $ intraclass correlation coefficient; Zar, 1984).

We also haphazardly collected a sample of 112 males to obtain data on body condition in relation to morphometrics. We made these males drop ("autotomize") their major claw and then separately weighed major claw mass and the mass of
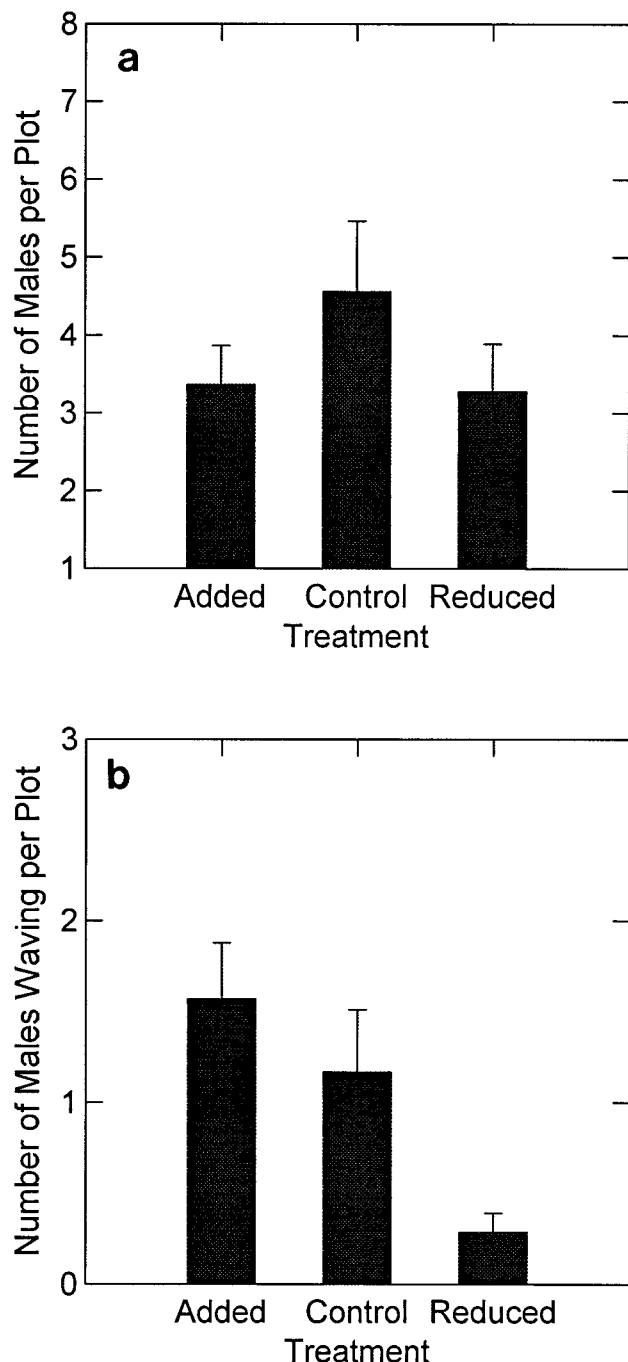
Figure 1
Feeding experiment: (a) the mean ± SE number of males on the surface per enclosure under the three food regimes; (b) the mean ± SE number of males waving per enclosure ($n = 6$ enclosures per treatment).

the rest of the crab ("body mass") to the nearest 0.01 g with a Sartorius balance. Claw removal did not appear to harm males and sometimes occurs naturally during male–male encounters (Jennions and Backwell, 1996). We then calculated relative claw size, defined as the standardized residuals from a least squares regression of major claw length on carapace width (Smith and Palmer, 1994); and body condition, defined as the standardized residuals from a least squares regression of body mass on carapace width. Lengths and masses were log-transformed. Although widely used, body condition indices

defined using wet weight occasionally underestimate variation in true condition due to interindividual variation in water content (e.g., in fish; Fitzgerald et al., 1989; but see Knapp, 1995). This is likely to reduce the likelihood of detecting differences in condition among different classes of males if males in poorer condition replace lost somatic tissue or lipids with water.

Statistical analysis

Costs of waving
Variation among treatments in the mean number of males present or waving per day per enclosure was analyzed using Friedman's randomized block tests. Each enclosure contributed one data point per test, which was the mean value over the 12-day observation period. There was no pseudoreplication. Post-hoc multiple pairwise comparisons were made when Friedman's tests indicated significant variation.

Size and relative wave rate
We calculated the Spearman correlation between male carapace width and wave rate in each cluster, then tested whether the mean coefficient differed from zero with a one-sample t test of Z-transformed values (Sokal and Rohlf, 1995). To determine whether the value of the correlation changed over the semilunar cycle, we then regressed Z-transformed correlation coefficients against day in the cycle in an analysis of covariance. We defined day 1 as the last day of the semilunar cycle. (On Day 0, low tides occurred at dawn and dusk.) We collected data over four semilunar cycles (days per cycle: $n = 12, 6, 3, 3$) and therefore treated "cycle" as the categorical variable. To test for homogeneity of slopes, we included the interaction term in the final model, but first subtracted the mean value of "day" from each "day" value and used this derived term as the covariate (Wilkinson et al., 1996). We treated the coefficients from each cluster as a statistically independent data point. A second analysis using mean daily values of cluster coefficients yielded similar results.

Absolute wave rate
We carried out ANCOVA with cycle identity as a fixed factor and day in cycle, log-transformed carapace width, and relative claw size as covariates. The dependent variable was log-transformed absolute wave rate. The initial model contained all six two-way interactions, but all nonsignificant interaction terms were removed from the final model. We also recalculated the model each time using the outlier function to remove data points whose residuals were in the top or bottom 2.5% of the distribution (Wilkinson et al., 1996). We repeated this procedure four times until the final model had no outliers. A total of 32 outliers were removed.

The size dependence of waving weakened and absolute wave rate changed over the semilunar cycle (see Results). This could be due to several possible combinations of size-dependent temporal increases or decreases in wave rate. To examine this trend we therefore divided males into three groups based on carapace width such that each group had approximately equal sample sizes ($n = 241, 250, 252$). Small males were <11.1 mm, intermediate males 11.1–12.6 mm, and large males >12.6 mm in carapace width. We then regressed absolute wave rate (standardized for each cycle; mean = 0, SD = 1) on day in cycle for each category of male.

Analyses were carried out using SYSTAT 5.02 for Windows (Wilkinson et al., 1996). In the morphometric regressions, the outlier function was used to remove data points whose residuals were in the top or bottom 2.5% of the distribution. We also excluded 11 of 754 males from the analyses of wave rate. They all had unusually small claws, probably due to incomplete regeneration after claw loss (>2 SD below the regression
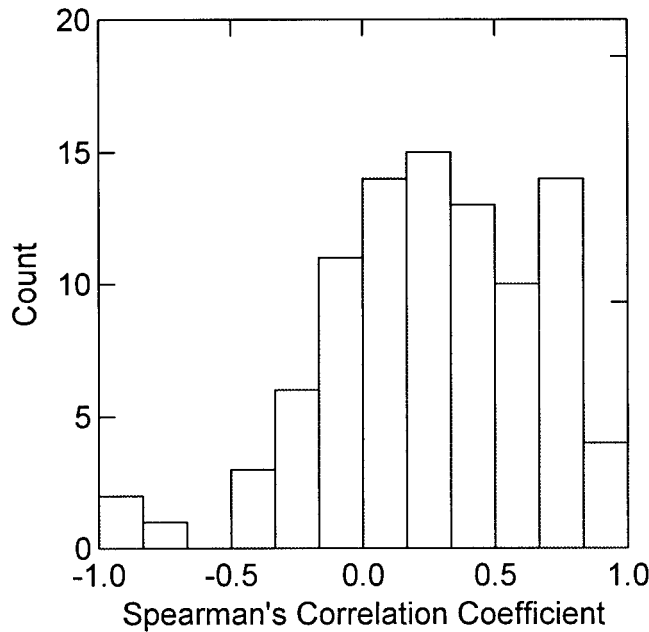
Figure 2
Histogram of the Spearman's correlation coefficients for 93 clusters of males.

Figure 3
The relationship between size-dependence of wave rate and day in the cycle. For legibility daily mean values are shown; the regression lines are from model I regressions of each clusters Z-transformed Spearman's correlations on day in cycle: cycle 1, $Y = -0.015 + 0.180*day$ ($n = 15$, $F = 2.218$, df $= 1,13$, $p = .16$); cycle 2: $Y = 0.092 + 0.033*day$ ($n = 52$, $F = 4.038$, df $= 1,50$, $p = .05$); cycle 3: $Y = 0.068 + 0.094*day$ ($n = 8$, $F = 1.591$, df $= 1,6$, $p = .25$); cycle 4: $Y = -0.304 + 0.044*day$ ($n = 18$, $F = 0.494$, df $= 1,16$, $p = .49$). The lines from top to bottom are for cycles 1, 3, 2, and 4, respectively.

line). Unless otherwise stated, all tests are two-tailed, α was set at 0.05, and summary statistics are presented as means ± SE.

RESULTS

Differential costs

The mean number of males present on the surface did not differ significantly among treatments (Friedman's test, $F = 1.65$, df $= 2,17$, $p = .44$; Figure 1a). However, the mean number of males waving differed significantly among treatments (Friedman's test, $F = 10.33$, df $= 2, 17$, $p = 0.006$; Fig. 1b). There were significantly fewer waving males in the removal treatment compared to the control or addition treatments (both $p < .05$). Although more males waved in the addition than control treatment enclosures, the difference was not significant ($p > .10$). In sum, a reduction in food availability decreased the proportion of males waving, but not the number present on the surface, suggesting that waving is effected by short-term food availability.

Male size and time of cycle

The mean Spearman correlation coefficient per cluster for the relationship between male carapace width and wave rate was 0.258 ± 0.042 ($n = 93$ clusters; with 743 males; Figure 2). This is significantly greater than zero (one-sample t test, $t = 6.14$, $p < .001$), indicating that larger males waved more than smaller males.

The positive relationship between male size and wave rate weakened over the course of all four semilunar cycles. The relationship was only significant ($p < .05$) in the cycle with the largest sample size (Figure 3). Overall, however, the strength of the within-cluster relationship between size and wave rate was significantly related to the day in the cycle (ANCOVA, $F = 6.593$, df $= 1,85$, $p = .012$) and differed among cycles ($F = 7.885$, df $= 3,85$, $p < .001$). There was no significant heterogeneity in slopes, indicating that the temporal relationship did not differ among cycles ($F = 0.819$, df $= 3,85$,
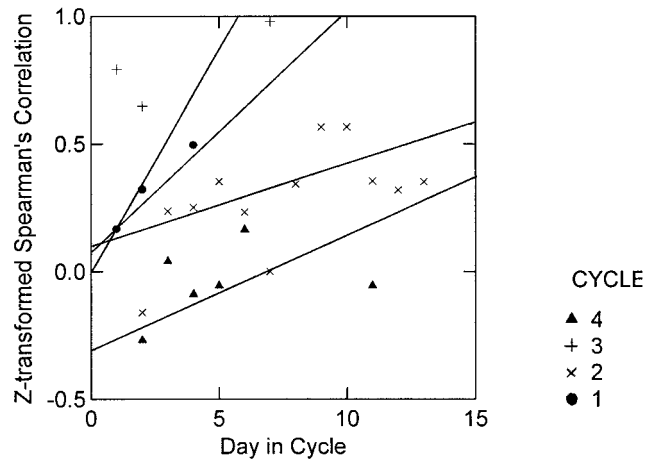
$p = .487$), supporting the general claim that the size-dependent nature of waving is weaker later in the cycle.

Absolute wave rate

Those male characters or temporal factors that explain variation in absolute wave rate are presented in Table 1. The absolute wave rate differed significantly among cycles. There were no significant interactions between relative claw size and carapace width and between day in cycle and relative claw size. To aid our interpretation of these interaction terms, we examined the bivariate model I regressions of log-transformed absolute wave rate on each variable in each cycle. Standardized regression coefficients and associated p values are shown in Table 2. Wave rate increased significantly with carapace width in three cycles and had a standardized regression coefficient of zero in one cycle. Wave rate increased significantly

Table 1

ANCOVA with log-transformed absolute wave rate as the dependent variable

Source of variance	Sum of squares	df	F	p
Log carapace width	77.117	1	48.243	.000
Relative claw size	2.027	1	1.268	.261
Day in cycle	26.790	1	16.759	.000
Cycle	66.392	3	13.845	.000
Cycle × log carapace width	50.724	3	10.577	.000
Cycle × relative claw size	17.370	3	3.622	.013
Cycle × day in cycle	90.277	3	18.825	.000
Day in cycle × log carapace width	21.925	1	13.716	.000
Error	1160.518	726		

The nonsignificant interactions between relative claw size and carapace width and relative claw size and day in the cycle are excluded from the final model, which explains 30.2% of the variance in waving ($n = 743$).

Table 2

Standardized correlation coefficients for bivariate, model I regressions of log-transformed wave rate on log carapace width, relative claw size and day in cycle

	Cycle 1	Cycle 2	Cycle 3	Cycle 4
Log carapace width	0.293 (0.004)	0.137 (0.003)	0.562 (0.000)	−0.004 (0.968)
Relative claw size	0.091 (0.81)	0.117 (0.012)	−0.055 (0.694)	0.163 (0.058)
Day in cycle	−0.403 (0.000)	−0.259 (0.000)	0.047 (0.738)	0.270 (0.002)
N	95	458	54	136

A negative coefficent for day in cycle indicates an increase in wave rate latter in the cycle; p values are given in parentheses.

with relative claw size in one cycles, marginally so in the second ($p = .058$), and had standardized regression coefficients close to zero in two cycles. Wave rate was significantly higher later in the cycle for two cycles, lower for one cycle, and unchanged in the fourth cycle. When the initial ANCOVA model was recalculated after removing outliers, the main effect of relative claw size was significant ($p = .036$); all other variables and interactions remained significant ($p < 0.001$, $n = 711$)

The preceding analyses indicate that (1) wave rates of different sized males are more similar later in the cycle (Figure 3), and (2) the average wave rate changed over the course of a cycle (Table 2). This can only happen if different-sized males show differential changes in their wave rate over the cycle. We therefore examined model I regressions of standardized wave rate on day in the cycle (Table 3). In three cycles, small males showed the greatest increase or smaller reduction in wave rate over the cycle. In cycles 1, 2, and 4 large males showed the smallest increase/greatest reduction in wave rate over the cycle. In sum, smaller males waved disproportionately more later in the cycle once changes in overall wave rate across each cycle were taken into consideration. This is also reflected in the significant interaction between carapace width and day in cycle in the ANCOVA (Table 1).

Relative claw size and wave rate

Relative claw size was a predictor of wave rate in the final ANCOVA model when outliers were excluded. We therefore tested whether it was a condition-dependent character. We first calculated the model I regressions of claw mass (CLM) and carapace mass (CRM), respectively, on carapace width (CW). In each successive equation, three outliers were removed, and variables were log-transformed:

$$CLM = -0.439 + (1.590)CW$$
$$(R^2 = 94.6\%, n = 109, F = 1892, df = 1,107,$$
$$p < .001) \tag{A}$$

$$CRM = -3.675 + (3.073)CW$$
$$(R^2 = 97.7\%, n = 106, F = 4465, df = 1,104,$$
$$p < .001). \tag{B}$$

We then regressed relative claw size (residuals of A) on body condition (residuals of B) (Figure 4). The residuals are independent as A and B are model I regressions. Males with relatively larger claws for their carapace width have greater body weight than expected for their carapace width: Relative claw size = $0.025 + (0.393)$Body condition ($R^2 = 14.8\%$, $n = 106$, $F = 19.28$, df = 1,104, $p < 0.001$).

DISCUSSION

Differential costs as an explanation for variation in wave rate

Fewer male *Uca annulipes* waved when food availability was decreased. This suggests that wave rate is, in part, condition dependent and decreases when food availability is reduced. An effect of food availability on display rate has been shown in several other species (e.g., Alatalo et al., 1990; Mappes et al., 1996), including one other species of fiddler crab (Backwell et al., 1995). Additional support for a role for condition dependence comes from our finding that males with relatively large claws had a higher body condition index and that males with relatively large claws tended to have higher wave rates. Relatively large-clawed males are also more likely to win fights (Jennions and Backwell, 1996). These results are consistent with a differential-cost explanation for variation in wave rate, as predicted by condition-dependent, handicap models of signaling (for review, see Johnstone, 1995). In a separate study, we monitored the actual wave rates of individually marked males subject to food addition, removal, or control treatments (D. Polakow et al., unpublished data). Mean wave rate per individual was significantly higher in the food addition treatment and lower in the food removal treatment relative to the control, consistent with the result obtained here based on

Table 3

Standardized regression coefficients for model I regressions of wave rate on day in the cycle for males of three size classes

Male size	Cycle 1	Cycle 2	Cycle 3	Cycle 4
Small	−0.492 (0.011)	−0.411 (<0.001)	−0.170 (0.46)	0.036 (0.04)
n	26	164	21	39
Medium	−0.497 (0.002)	−0.323 (<0.001)	0.421 (0.20)	0.045 (0.76)
n	35	159	11	47
Large	−0.304 (0.08)	−0.190 (0.03)	0.109 (0.63)	0.167 (0.25)
n	34	135	22	50

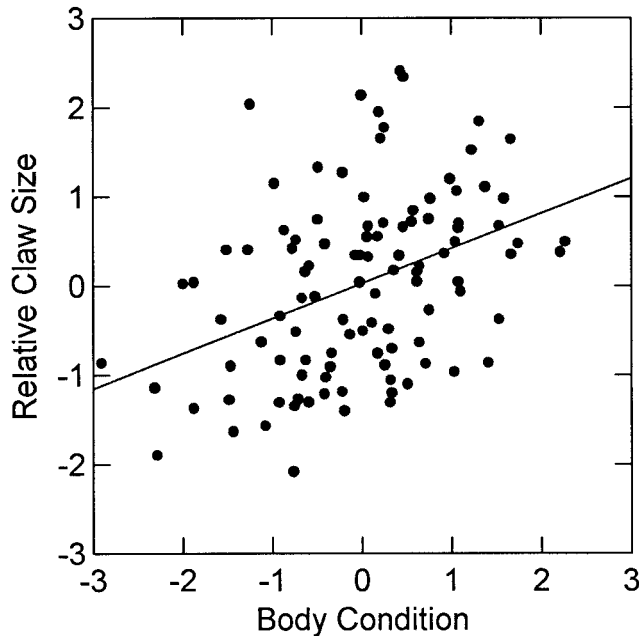p values are given in parentheses.

Figure 4
The relationship between relative claw size and body condition (*n* = 106). For details of the linear equation, see text.

presence or absence of waving. However, we were logistically constrained to one enclosure per treatment, and the observed differences among enclosures therefore cannot be attributed with certainty to the treatments they received.

Size and time of cycle

There was a strong positive relationship between male size and wave rate. This supports the findings from other studies of fiddler crabs (e.g., *U. pugilator*; Hyatt, 1977a,b). This trend is not due to the inclusion of sexually immature males in the sample, as even very small males are capable of mating (Backwell PRY, unpublished data). Unlike previous studies, however, we also documented a temporal pattern to size-based wave rates. Separate analyses for large, medium, and small males indicate that small- and medium-sized males wave proportionately more later in the cycle. The correlation within recorded clusters between male size and wave rate decreased as the semilunar tidal cycle progressed in all four semilunar cycles. Although the overall relationship between the size dependence of waving and time of cycle was significant ($p = .012$), and no significant variation among cycles in this relationship

was detected ($p = .49$), it should be noted that the trend was only significant in cycle 2. The sample size for this cycle was far higher than that for the other cycles ($n = 52$ versus 8–18 clusters), so low power to detect significant trends in the other cycles may partially explain this result.

The changing relationship between wave rate and male size over the cycle could be due to temporal variation in the costs and/or benefits of waving for different-sized males (Reynolds, 1993) (Table 4). There are at least two obvious cost-based explanations. First, size-based predation risk might change over the tidal cycle. At our study site, however, shorebirds are rarely present in areas where fiddlers are waving. Furthermore, we never observed predation on adults during the present study. This was not an artifact of our presence, as we have regularly seen birds prey on fiddler crabs at other sites (Koga et al., submitted). Second, there could be a straightforward, size-based physiological explanation. As the semilunar cycle progresses, low tide occurs approximately 50 min later each day. The temperature when males wave may thus increase slightly each day. If higher temperatures favor greater waving by smaller crabs, this could explain our results. Unfortunately, to our knowledge, differential effects of temperature on wave rate in relation to male size are unstudied in fiddler crabs. It is possible that smaller males, because they have a larger surface-to-volume ratio, are less prone to overheating and can thus wave more later in the cycle. However, this ratio probably also makes them more susceptible to dehydration (crabs often retreat into their burrows to rewet their gills), which would select for less time courting and more time in their burrows later in the cycle.

In contrast to the difficulty of identifying a plausible cost-based explanation for size-dependent changes in wave rate, there is potentially a clear benefit to smaller males that court more later in the cycle. Smaller males are more likely to have their burrows visited by females later in the cycle, which leads to greater mating success for smaller males. We have previously interpreted this as a reduction in female choosiness based on male size (Backwell and Passmore, 1996). If smaller males are relatively more attractive to females later in the cycle, they will obtain greater benefits from courting more at this time. There is one important caveat, though: if female choice of which male to visit is based solely on wave rate, then females may be more likely to visit the burrows of smaller males later in the cycle due to their greater wave rate. Cause and effect are therefore reversed. It should be noted, however, that this explanation still leaves the temporal change in wave rate unexplained. Given the current absence of evidence for temporal variation in the size-based costs of courting, we therefore suggest that differential benefits due to changing female preferences based on male size currently provide the best explanation for our results.

Table 4
Summary of the possible explanations for an increase in wave rate by smaller males relative to larger males over the semilunar cycle

	Comment
Differential costs	
Later in the cycle smaller males suffer lower predation risk than larger males when courting.	Reject because no predators of adult males were observed.
It is less physiologically or energetically costly for smaller males to court more later in the cycle.	No supporting evidence available.
Differential benefits	
Smaller males are more attractive to females later in the cycle.	There is no large-male mating advantage due to female choice later in the cycle.

Future studies

To our knowledge, no field study has conclusively documented short-term temporal changes in female mating preferences. There are field data showing variation in mate choice for male traits over time (e.g., early versus late in the breeding season), but this could be due to factors other than changes in actual mating preferences, such as reduced phenotypic variation in sexually selected traits among potential mates or changes in male behavior. Controlled laboratory studies have, however, demonstrated rapid changes in actual female preferences (for review, see Jennions and Petrie, 1997). If differential benefits select for males that adjust courtship in relation to changes in female mating preferences for morphological traits, it will be difficult to determine whether observed changes in male mating success or female mate choice with respect to male morphology are due to changes in female choosiness or changes in male courtship patterns. This is the major weakness of our study. Ideally, one should control for courtship rate and then look for temporal changes in attractiveness based on other traits. This has been done in the laboratory (e.g., Reynolds, 1993) but remains a challenging task in the field because courtship rate must be continuously monitored and cannot be extrapolated from earlier measurements.

REFERENCES

Alatalo RV, Glynn C, Kundberg A, 1990. Singing rate and female attraction in the pied flycatcher. Anim Behav 39:601–603.

Andersson MB, 1994. Sexual selection. Princeton, New Jersey: Princeton University Press.

Backwell PRY, Jennions MD, Christy JH, Schober U, 1995. Pillar-building in the fiddler crab *Uca beebei*: evidence of a condition-dependent ornament. Behav Ecol Sociobiol 36:185–192.

Backwell, PRY, Jennions MD, Passmore NI, Christy JH, 1998. Synchronised courtship in a fiddler crab. Nature 391:31–32.

Backwell PRY, Passmore NI, 1996. Time constraints and multiple choice criteria in the sampling behaviour and mate choice of the fiddler crab *Uca annulipes*. Behav Ecol Sociobiol 38:407–416.

Christy JH, Salmon M, 1991. Comparative studies of reproductive behaviour in mantis shrimps and fiddler crabs. Am Zool 31:327–339.

Crane J, 1975. Fiddler crabs of the world. Princeton, New Jersey: Princeton University Press.

Fitzgerald G, Guderley H, Picard P, 1989. Hidden reproductive costs in the three-spined stickleback (*Gastrosteus aculeatus*). Exp Biol 48:295–300.

Forsgren E, 1992. Predation risk affects mate choice in a gobid fish. Am Nat 140:1041–1049.

Godin JG, Briggs SE, 1996. Female mate choice under predation risk in the guppy. Anim Behav 51:117–130.

Gong A, Gibson RM, 1996. Reversal of a female preference after visual exposure to a predator in the guppy *Poecilia reticulata*. Anim Behav 52:993–1005.

Grafen A, 1990. Biological signals as handicaps. J Theor Biol 144:517–546.

Hedrick AV, Dill LM, 1993. Mate choice by female crickets is influences by predation risk. Anim Behav 46:193–196.

Houde AE, 1997. Sex, color, and mate choice in guppies. Princeton, New Jersey: Princeton University Press.

Hyatt GW, 1977a. Field studies of size-dependent changes in waving display and other behaviour in the fiddler crab, *Uca pugilator* (Brachyura, Ocypodidae). Mar Behav Physiol 4:283–292.

Hyatt GW, 1977b. Quantitative analysis of size-dependent variation in the fiddler crab wave display (*Uca pugilator*, Brachyura, Ocypodidae). Mar Behav Physiol 5:19–36.

Jennions MD, Backwell PRY, 1996. Residency and size affect fight duration and outcome in the fiddler crab *Uca annulipes*. Biol J Linn Soc 57:292–306.

Jennions MD, Petrie M, 1997. Variation in mate choice and mating preferences: a review of causes and consequences. Biol Rev 72:283–327.

Johnstone RA, 1995. Sexual selection, honest advertising and the handicap principle: reviewing the evidence. Biol Rev 70:1–65.

Knapp RA, 1995. Influence of energy reserves on the expression of a secondary sexual trait in male bicolor damselfish, *Stegastes partitus*. Bull Mar Sci 57:672–681.

Kodric-Brown A, Brown JH, 1984. Truth in advertising: the kinds of traits favored by natural selection. Am Nat 124:309–323.

Mappes J, Alatalo RV, Kotiaho J, Parri S, 1996. Viability costs of condition-dependent sexual male display in a drumming wolf spider. Proc R Soc Lond B 263:785–789.

Morgan SG, Christy JH, 1995. Adaptive significance of the timing of larval release by crabs. Am Nat 145:457–479.

Pomiankowski A, Møller AP. 1995. A resolution of the lek paradox. Proc R Soc Lond B 260:21–29.

Ptacek M, Travis J, 1997. Mate choice in the sailfin molly *Poecilia latipinna*. Evolution 51:1217–1231.

Reynolds JD, 1993. Should attractive individuals court more? Theory and a test. Am Nat 141:914–927.

Sargent RC, Gross MR, van den Berghe EP, 1986. Male mate choice in fishes. Anim Behav 34:545–550.

Schwagmeyer PL, Parker GA, 1990. Male mate choice as predicted by sperm competition in thirteen-lined ground squirrels. Nature 348:62–64.

Smith LD, Palmer AR, 1994. Effects of manipulated diet on size and performance of Brachyuran crab claws. Science 264:710–712.

Sokal RR, Rohlf FJ, 1995. Biometry, 3rd ed. New York: W.W. Freeman.

Sumner IT, Travis J, Wilson CD, 1994. Methods of female fertility advertisement and variation among males in responsiveness in the sailfin molly (*Poecilia latipinna*). Copeia 1994:27–34.

Travis J, 1994. The interplay of life history variation and sexual selection in sailfin mollies In: Ecological genetics (Real LA, ed). Chapel Hill: University of North Carolina Press; 205–232.

Weissburg M, 1993. Sex and the single forager: gender-specific energy maximization strategies in fiddler crabs. Ecology 74:279–291.

Wilkinson L, Blank G, Gruber C, 1996. Desktop data analysis with Systat. Englewood Cliffs, New Jersey: Prentice-Hall.

Zahavi A, 1977. The cost of honesty (further remarks on the handicap principle). J Theor Biol 67:603–605.

Zar JH, 1984. Biostatistical analysis, 2nd ed. Englewood Cliffs, New Jersey: Prentice Hall.