

Patricia R.Y. Backwell · Neville I. Passmore

Time constraints and multiple choice criteria in the sampling behaviour and mate choice of the fiddler crab, *Uca annulipes*

Received: 23 March 1995/Accepted after revision: 14 January 1996

Abstract Active female sampling occurs in the fiddler crab *Uca annulipes*. Females sample the burrows of several males before remaining to mate in the burrow of the chosen partner. Females time larval release to coincide with the following nocturnal spring tide and must therefore leave sufficient time for embryonic development after mating. Here we show how this temporal constraint on search time affects female choosiness. We found that, at the start of the sampling period (when time constraints are minimal), females selectively sample the larger males in the population. Towards the end of the sampling period (when the temporal constraints increase the costs of sampling), females are less selective. Furthermore, we suggest that the number of males sampled (and other indices of “sampling effort”) may not be reliable indicators of female choosiness and may not reflect the strength of female mating preferences under certain conditions. Burrow quality also emerged as an important criterion in final mate choice. Burrow structure potentially influences reproductive success, and mate acceptance based on burrow structure appears to involve a relatively invariant threshold criterion. Since there is no relationship between male size and burrow quality, females are using at least two independent criteria when choosing potential mates. We envisage mate choice as a two-stage process. First, females select which males to sample based on male size. They then decide whether or not to mate with a male based on burrow features. This sampling process

explains how two unrelated variables can both predict male mating success.

Key words Fiddler crab · Multiple mate choice criteria · Mate sampling behavior · Search time constraints

Introduction

Many studies have reported non-random mating due to female choice (Harvey and Bradbury 1991). Females make complex decisions about mate suitability (Thornhill 1984; Engelhard et al. 1989; Trail and Adams 1989; Milinski and Bakker 1991; Petrie et al. 1991; Gibson and Bachman 1992). Costs associated with sampling have emerged as an important constraint on mate choice that influence the expression of female mating preferences (Alatalo et al. 1988; Houde 1993). Examples of such costs are energy expenditure, predation risk and risk of disease/parasite transfer, which reduce components of female fitness as females sample successive potential mates.

The trade-off between the costs of sampling and the benefits of mate choice effects both the pattern of sampling as well as final mate choice. In sticklebacks (*Gasterosteus aculeatus*) mate acceptance criteria in relation to male pigment brightness are reduced when females are forced to swim against stronger water currents in order to sample additional males (Milinski and Bakker 1991, 1992). Increased risk of predation is another cost that has been shown to reduce female choosiness. In the presence of predators females often choose less attractive males compared to those they choose under predator-free conditions, (guppies, *Poecilia reticulata*: Houde 1993).

Search time also should influence mate choice (Janetos 1980; Parker 1983; Real 1990; Dombrowsky and Perrin 1994), but there is little evidence that it does.

P.R.Y. Backwell (✉)¹
Department of Biology, University of Natal, King George V
Avenue, Durban 4000, South Africa

N.J. Passmore
Department of Zoology, University of the Witwatersrand,
Private Bag 3, WITS 2050, Johannesburg, South Africa

Present address:

¹Smithsonian Tropical Research Institute, APDO 2072, Balboa,
Ancón, Republica de Panama

Many animals breed cyclically at specific times of the year, lunar cycle or even day (Real 1990) because the reproductive fitness is strongly correlated with when mating occurs. For example, in many temperate-breeding birds females that mate earlier in the season are more likely to rear their first clutch successfully, and to initiate a second clutch (Kirkpatrick et al. 1990). In various frogs, there may be physiological thresholds which constrain the time females have available to sample before spontaneous oviposition, and total loss of the egg clutch if a male is not found (Salthe and Mecham 1974). Under these circumstances, excessive choosiness will increase the risk of sub-optimal mating, or possibly even lead to reproductive failure. Females should therefore adjust their behaviour according to the time available for mate choice.

Several theoretical models outlining the rules females could use to find the best mate under different constraints have been developed (see Janetos 1980; Parker 1983; Wittenberger 1983; Real 1990; Dombrovsky and Perrin 1994). The difficulty of investigating female behaviour has hampered tests of these models. With a few notable exceptions (e.g. Fredrick 1987; Trail and Adams 1989; Engelhard et al. 1989), most studies to date have been on captive populations. In fiddler crabs (genus *Uca*), however, female sampling and mate choice occur within a matter of hours, making them ideal species for such studies.

Although most studies have focused on a single criterion of choice, such as tail length, there is now growing evidence that multiple criteria are often employed during mate assessment (Burley 1981; Thornhill 1983; Balmford et al. 1992; Møller 1992; Zuk et al. 1992; Pomiankowski and Iwasa 1993). The best known cases of multiple choice criteria occur when females select mates on the basis of both male phenotype and the quality of defended resources (e.g. scorpionflies, *Hylobittacus apicalis*: Thornhill 1983; Lifjeld and Slagsvold 1988; mottled sculpin, *Forsterygion varium*: Thompson 1986; topi, *Damaliscus lanatus*, and puku, *Kobus vardonii*: Balmford et al. 1992). However, in many of these studies the independent effects of morphology and resource quality on female choice are only revealed by multivariate statistical analyses. For example, larger males tend to possess higher-quality resources, making it difficult to assess the importance of male phenotype and resource quality as independent predictors of female choice (Balmford et al. 1992).

In the absence of paternal care, direct benefits of female choice for defended resources are generally likely to outweigh any indirect "genetic" benefits of choice based on male phenotype (Halliday 1983; but see Iwasa et al. 1991). Choice based on male phenotype may have direct fitness benefits, however, such as decreased risk of acquiring sexually transmitted diseases, or avoidance of harassment (Reynolds and Gross 1990). Even so, these benefits are likely to be small relative to those attributable to variation in resource

quality. Thus, when choice is based on male phenotype and resource quality, females will presumably give primary consideration to resource quality. By selectively weighting the two factors and combining them into a single index of male suitability, females could use a "threshold criterion" tactic of choice (Wittenberger 1983). In such cases, females should mate with the first male encountered who meets a minimum acceptance criterion of male suitability.

We studied a population of fiddler crabs (*Uca annulipes*) in order to determine (1) whether the increasing risk of suboptimal mating due to temporal constraints caused female choosiness to decline over the brief period of mating activity each semi-lunar cycle; (2) whether male size and burrow quality are independent predictors of female choice; and (3) the relative importance of each of these factors in female mating decisions.

Active sampling has been recorded in many fiddler crab species, including *Uca annulipes* (Crane 1975). Receptive females wander through a population of displaying males. They enter and leave the burrows of several males before remaining to mate in the burrow of the chosen partner (Christy 1980, 1983, 1987; Greenspan 1980). The male emerges about 10 min later to block the burrow entrance with a sand plug, sealing himself and the female in the burrow. When receptive females leave the burrows of sampled but rejected males, the males emerge and continue to court the leaving females, indicating that it is the female (rather than the male) that makes the decision to accept or reject the mate.

Mating takes place in the terminal chamber of the burrow and, after oviposition, the male leaves the burrow which is then used by the mated female during incubation and embryonic development (Christy 1987; Christy and Salmon 1991). The burrows of chosen males are therefore an important resource for gravid females (Christy 1983, 1987). In *U. pugillator*, the quality of the mated male's burrow influences reproductive success and females preferentially mate in stable burrows – those least likely to flood or collapse causing females to lose eggs during oviposition and incubation (Christy 1987). In *U. beebei* females also prefer long, deep burrows which may provide a better thermal environment for incubation than short, shallow ones (Christy 1987). Given the similarity in *Uca* reproductive physiology, it is likely that burrow quality has similar effects on breeding success in *U. annulipes*. We therefore tested whether burrow features can be used to predict male mating success.

Sampling time is likely to be a strong constraint on female choice in most fiddler species. Their intertidal habitat restricts activity to the 4–6 h period centred around the diurnal low tide. Since crabs are generally inactive when low tide falls at dawn or dusk, activity is limited to a period of about 11 days each semi-lunar cycle (Crane 1975). Females time larval release to

coincide with the following high-amplitude nocturnal spring tide (Christy 1982, 1983; Morgan and Christy 1995) and must therefore allow sufficient time for embryonic development after mating. Thus, within these 11-day periods, mating activity is largely restricted to 5 or 6 consecutive days since mating during this period will allow sufficient time for embryonic development. Fiddler crab females are therefore time-limited both in the short term (by the rising tide each day) and in the long term (by the time to the following nocturnal spring tide which is the optimal time for larval release). We studied a population of *U. annulipes* in order to determine whether the increasing risk of sub-optimal mating due to temporal constraints caused female choosiness to decline over the brief period of mating activity each semilunar cycle.

The existence of mate suitability thresholds based on assessment of male phenotype and resources may allow us to directly demonstrate the independent effects of these two factors. Constraints on sampling behaviour, such as limited time or increased risk of predation, may cause females to lower their mate acceptance criteria, either by discarding or lowering their acceptance levels for one of the contributing factors (Wittenberger 1983). In species without male parental care where male phenotype and resource quality are both assessed, it is likely that the acceptance threshold for phenotypic traits will be lowered, or even discarded, before that for resource quality. The decrease in fitness arising from the choice of a mate with inferior resources is likely to far exceed that from choosing an inferior male.

Methods

We studied a population of *Uca annulipes* in the mangrove swamp conservation area of Durban Harbour, South Africa during October 1992–April 1993 and November 1993–January 1994. All work was carried out on a 60 × 40 m intertidal mud flat. We estimated the size distribution and density of the male population by measuring all males within a demarcated 3-m² area of mud flat. Mating behaviour was observed throughout the study period and wandering females ($n = 55$) were individually tracked. We operationally defined sampling as a behavioural sequence in which a female directly approaches a displaying male, the male descends into his burrow once the female is within 10 cm of the entrance, and the female follows. The female either emerges in a few seconds, leaves and responds to other males, or she stays below, in which case the male emerges approximately 10 min later and blocks the burrow entrance with a sand plug, sealing himself and the female into the burrow. When females emerge from a sampled burrow and begin responding to other displaying males, the previously sampled male usually emerges and recourts the leaving female. This indicates that it is the female (rather than the male) who is selective.

The burrows of sampled and mated males were marked with coloured metal pins and the males later captured. Carapace width and major cheliped (hereafter “claw”) length were measured using vernier callipers. We checked the repeatability of our measurements by measuring each dimension twice. Both carapace width ($F_{14,15} = 652.5$, $P < 0.0001$) and claw size ($F_{14,15} = 2809.5$, $P < 0.0001$) showed high repeatability. We made casts of males’

burrows using diphenylmethane-diisocyanate foam (Sista foam manufactured by Henkel (Pty) Ltd). The foam, once sprayed into the burrow, expands to 3 times its volume filling the burrow cavity. The excess is extruded through the burrow entrance. The foam is fast-drying and casts could be dug up after approximately 1 h. It was not always possible to make casts of the burrows of all males sampled, in which case we made burrow casts of the last one to four sampled males of the sequence ($n = 41$ sampled males’ burrows, 23 mated males’ burrows). The distances between successively sampled burrows were measured in 35 of the sampling sequences and the time of mating noted. Females were captured and measured (carapace width) after final mate choice in 27 of the sampling sequences (16 of which were sequences in which burrow casts were made).

Females searching for mates are only identifiable by their sampling behaviour, and it was not always possible to track them from the start of a sampling bout. The observed number of males sampled is therefore imprecise. “Mating time” was calculated as the number of minutes before (–) or after (+) low tide that the female entered the burrow of her mate. “Time of cycle” was calculated as the number of days before spring tide that mating occurred. Relative size difference between mated and sampled males was calculated as the mated male claw length minus the mean claw length of the sampled males in the sequence, divided by the mean claw length of all males in the sequence. Analyses using carapace width, claw length, and the ratio of the carapace to claw size produced almost identical results. However, since the claw is used in mate attraction and claw length is a better predictor of mating success than the other

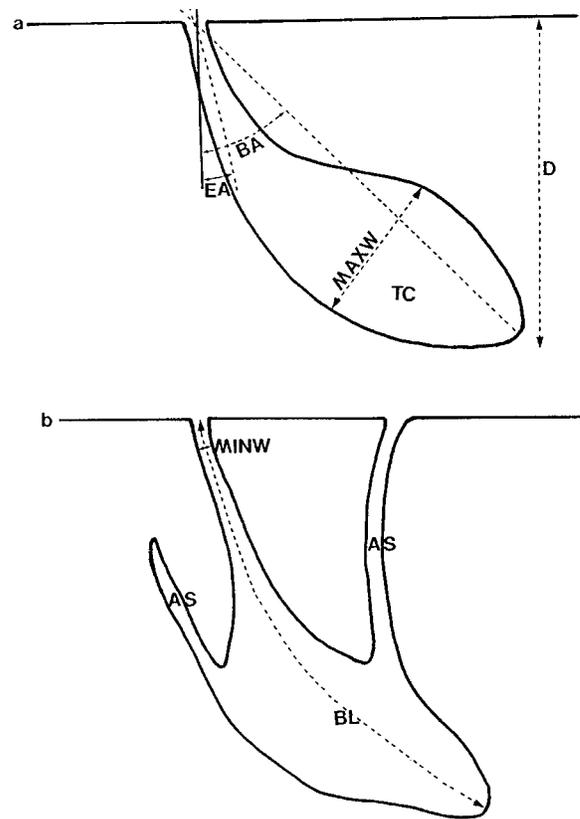


Fig. 1 Drawings of burrow casts of male *Uca annulipes*. Most burrows had the simple structure depicted in **a**. **b** Illustrates the additional shafts branching off the terminal chamber that were present on some burrows. A description of the measured variables is given in Methods. *EA* entrance angle, *BA* burrow angle, *MAXW* maximum width, *MINW* minimum width, *BL* burrow length, *D* burrow depth, *TC* terminal chamber, *AS* additional shafts

two measures (Mann-Whitney U -tests comparing mated males to the population: claw: $P = 4.55 \times 10^{-14}$; carapace: $P = 1.29 \times 10^{-11}$; ratio: $P = 1.86 \times 10^{-9}$), it is the measure of male size used in this paper.

To test whether the size of active males decreased across the duration of the tidal cycle, we used data from a separate study involving individually marked males housed in seven 2 m² enclosures on the mudflat (M. Jennions and P. Backwell, unpublished work). There were 24 marked males per enclosure. We noted the size of all males on the surface for 5–8 days across the tidal cycle.

Cast identities were coded to avoid observer bias during measurement. We measured ten variables for each cast (Fig. 1). "Entrance angle" was defined as the angular deviation (from vertical) of the first 5 cm of the burrow shaft. "Burrow angle" was measured as the angular deviation (from vertical) of a line connecting the burrow entrance and the furthestmost point of the terminal chamber. "Depth" was measured as the distance from the sediment surface to the deepest point of the burrow. "Maximum and minimum widths" were measured as the distances between opposite walls at the narrowest and widest parts of the burrow. "Burrow length" was determined as the shortest internal distance between the burrow entrance and the furthestmost point of the terminal chamber. "Volume" was measured as the amount of water displaced when the cast was submerged in a graduated glass container. Most burrows had the simple structure depicted in Fig. 1a. Some burrows, however, had additional shafts branching off the terminal chamber (Fig. 1b). These shafts occasionally extended to the sediment surface, thus forming additional burrow entrances. The number of "burrow entrances" was noted, as was the number of "branches" off the terminal chamber that did not extend to the surface. Additional entrances were distinguishable from the primary burrow shafts (Fig. 1b), and measurements of entrance angle, burrow angle, minimum width and burrow length were made on the primary shaft only. The tenth burrow variable was an index of sediment density around the burrow chamber. The pressure of the expanding foam caused fine fissures in the surrounding sediment, resulting in casts having delicate fin-like "frills" radiating from the chambers. The number and size of these frills was variable and appeared to indicate the level of sediment compression around the burrow. The presence and extent of frills was scored on a scale of 1–5. Burrows were only measured after the frills had been removed.

Results

Natural history

Females entered the burrows of up to 24 males before selecting a mate ($\bar{x} = 7.46 \pm 5.95$, $n = 50$). Females travelled up to 28 m ($\bar{x} = 6.87 \pm 6.54$, $n = 35$), usually in a slightly curved path, but did not return to previously sampled males. Although females occasionally stopped moving in order to forage, it was far more common for females to move continuously from one male to the next during a sampling sequence. The density of males (all size classes) was 49 males/m², however, less than half of those males waved at any time (Backwell, unpublished data: seven plots of 1 m² observed over an entire tidal cycle: $\bar{x} = 19.6$ waving males, $n = 81$). The number of waving males in the population was large (approximately 50 000 waving males), and the chance of different females sampling overlapping sets of males was therefore very low.

Mated male size

We compared the claw size of sampled males and mated males with those from the population sample ($n = 147$). Females preferentially sampled (Mann-Whitney U -test: $Z = -6.77$, $P < 0.001$, $n = 427,147$) and mated with (Mann-Whitney U -test: $Z = -5.31$, $P < 0.001$, $n = 55,147$) the larger clawed males in the population. In a separate (unpublished) study, we found that small males (claw > 0.34 cm) courted females and were reproductively active. This suggests that the differences in claw size of mated/sampled males and the population mean is due to females selectively approaching large males. Females may selectively approach large males because of some characteristic that correlates with male size rather than selecting male size per se (e.g. it is possible that large males behave in ways that are more noticeable/detectable to females). Whatever reason lies behind the females' selection of large males, the process ultimately results in a large male mating advantage. The claw size of males who were sampled and then rejected did not differ significantly from that of mated males (Mann-Whitney U -test, $Z = 1.84$, $P = 0.174$, $n = 55,372$). This result was robust and held when we compared the mean size of previously sampled males within each sequence with that of the mated male (Wilcoxon test: $Z = 1.43$, $P = 0.153$, $n = 45$). There was also no difference in the relative claw size (= residuals from Model I regression of claw length on carapace width) of sampled but rejected males and mated males (Mann-Whitney U -test, $Z = 0.02$, $P = 0.89$, $n = 55,372$).

Some females consistently sampled larger males than others (Kruskal-Wallis: $H = 119.53$; $df = 49$; $P < 0.001$). This consistent pattern of sampling was related to female size. There was a positive relationship between female carapace size and the size of the sampled males ($r_s = 0.47$, $P = 0.02$, $n = 24$).

Time of cycle and mated male size

There was no correlation between the time of the semi-lunar tidal cycle and the size of the females we monitored (Table 1). We therefore investigated variation in sampled and mated male size over the breeding cycle. The later in the cycle that sampling occurred the smaller the mated male, the smaller the mean size of the males sampled, and the smaller the relative size difference between mated and sampled males (Table 1). There was also a significant relationship between time of cycle and the time relative to low tide at which females finally chose a mate. The later in the cycle, the earlier in the daily activity period final mate choice occurred (Table 1). Direct relationships between the other measured variables are presented in Table 1. All relationships where $P < 0.001$ are significant at the $P = 0.05$ level after correction for table-wide probability using

Table 1 Spearman's correlation coefficients (sample sizes) and two-tailed probability values

	Time of cycle	Claw length of mate	Number of males sampled	Mating time	Relative size difference	Distance travelled	Female carapace width
Mean claw length of sampled males	-0.36 (45) 0.018	0.63 (45) < 0.001*	0.07 (45) 0.65	-0.07 (45) 0.65	-0.07 (45) 0.63	0.21 (30) 0.25	0.46 (24) 0.026
Female carapace width	-0.05 (27) 0.81	0.31 (27) 0.12	-0.04 (27) 0.83	0.09 (27) 0.85	-0.04 (24) 0.85	0.02 (27) 0.93	
Distance travelled	0.18 (35) 0.30	-0.34 (35) 0.05	0.90 (35) < 0.001*	-0.10 (35) 0.57	-0.33 (30) 0.08		
Relative size difference between mated and sampled males	-0.46 (45) < 0.001*	0.79 (45) < 0.001*	-0.14 (45) 0.34	0.36 (45) 0.019			
Mating time	-0.55 (50) < 0.001*	0.29 (50) 0.04	0.04 (50) 0.78				
Number of males sampled	-0.08 (50) 0.56	-0.27 (50) 0.058					
Claw length of mate	-0.50 (50) < 0.001*						

(* $P < 0.05$ Bonferroni correction, $n = 28$ correlations tested)

Table 2 Kendal's partial rank-order correlation coefficients with the effect of "time of cycle" partialled out. Sample size in parenthesis

	Time of day	Distance travelled by female	Number of males sampled	Mean claw length of sampled males
Mated male claw length	0.09 (50) NS	-0.21 (35) < 0.05	-0.19 (50) < 0.05	0.40 (45) < 0.05
Relative size difference between mated and sampled males	0.16 (45) NS	-0.22 (30) < 0.05	-	-
Female Carapace Size	-	-	-	0.41 (24) < 0.05

Two-tailed probabilities where NS indicates that $P > 0.05$. * $P < 0.05$ Bonferroni correction, $n = 7$ correlations tested

the sequential Bonferroni procedure (corrected $P = 0.05/28 = 0.00179$).

It is possible that the size of courting males decreases over the tidal cycle, and that this could account for the decrease in the size of mated males. However, data from marked males in enclosures did not indicate a significant decrease in the size of waving males across the cycles in any of the seven enclosures. The mean Spearman regression coefficient actually indicated a slight increase in size across the cycle, but did not differ significantly from zero (mean $r_s = 0.33$, one-sample test, $t = 1.75$, $P = 0.13$, $n = 7$).

Since there was an *a priori* prediction that time of cycle will influence sampling behaviour, Kendal's partial rank-order correlations were used to remove the

effect of time of cycle when it was correlated with either, or both, of the variables in each of the correlations presented below (Siegel and Castellan 1988) (Table 2). Apart from the rather obvious relationship between the number of males sampled and total distance travelled, five other significant relationships emerged (Table 2). The size of the mated male correlated with both (1) the number of males sampled, and (2) the cumulative distance travelled by the female [the greater the number of males sampled (and hence the longer the total distance travelled), the smaller the mated male]. (3) The relative size difference between mated and sampled males correlated with the distance travelled by the female (the greater the distance travelled, the smaller the relative size difference between mated and sampled

Table 3 Comparisons between mated and sampled male burrows (Mann-Whitney *U*-tests), and Spearman's correlations between male claw length and burrow features

	Mated (<i>n</i> = 23) \bar{x} (SD)	Sampled (<i>n</i> = 41) \bar{x} (SD)	<i>Z</i>	<i>P</i>	Correlation with male claw size (<i>n</i> = 64)	
					<i>r_s</i>	<i>P</i>
Frills	1.13 (0.92)	2.88 (1.21)	4.84	< 0.001*	0.13	0.31
Burrow angle	20.00 (8.53)	28.29 (9.40)	3.69	< 0.001*	-0.01	0.96
Maximum width (cm)	3.28 (0.65)	4.55 (1.42)	3.74	< 0.001*	0.15	0.25
Volume (cm ³)	60.65 (24.23)	109.51 (73.43)	3.63	< 0.001*	0.35	0.01*
Branches (number)	1.04 (0.21)	1.90 (1.20)	3.60	< 0.001*	-0.01	0.93
Minimum width (cm)	1.52 (0.28)	1.83 (0.45)	2.84	< 0.01*	0.13	0.29
Length (cm)	18.52 (5.58)	22.76 (8.57)	1.79	0.07	0.23	0.07
Entrances (number)	1.04 (0.21)	1.29 (0.68)	1.68	0.09	0.13	0.32
Entrance angle	2.83 (4.73)	3.90 (6.47)	0.66	0.51	0.01	0.95
Depth (cm)	15.83 (3.73)	16.61 (2.71)	0.56	0.58	0.19	0.13

**P* < 0.05 Bonferroni correction, *n* = 20 tests

Table 4 Comparisons between mated and sampled male burrows (Mann-Whitney *U*-tests), and Spearman's correlations between male claw length, female carapace width and time of cycle at which mating occurred against the principle components (PC)

	Mated (<i>n</i> = 23) \bar{x} (SE)	Sampled (<i>n</i> = 42) \bar{x} (SE)	χ^2	<i>P</i>	Correlation with male claw size		Correlation with female carapace size		Correlation with time of cycle at mating	
					<i>r_s</i>	<i>P</i>	<i>r_s</i>	<i>P</i>	<i>r_s</i>	<i>P</i>
PC1	-1.26 (0.23)	0.92 (0.36)	20.74	< 0.001*	0.21	0.10	0.02	0.92	0.23	0.23
PC2	0.03 (0.16)	-0.27 (0.22)	0.011	0.92	0.12	0.33	0.26	0.32	-0.17	0.42
PC3	-0.49 (0.19)	0.27 (0.15)	7.48	0.006*	-0.16	0.36	-0.35	0.18	0.26	0.22

**P* < 0.05 Bonferroni correction

males). Finally, the mean size of the sampled males correlated with both (4) female carapace width, and (5) the size of the mated male (larger females sampled larger males, and the larger the sampled males, the larger the mated male).

Burrow quality

Univariate analysis showed that the burrows of mated (*n* = 23) and sampled (*n* = 41) males differed for six of the 10 measured variables, even after the sequential Bonferroni procedure was applied (Table 3). The burrows of mated males were smaller both in terms of volume as well as maximum and minimum width. They had fewer branches off the terminal chamber and were more vertical than sampled male burrows. They were also located in areas with more compact sediment (based on frills). Because there is some criticism of the use of multiple univariate measures, we also applied principal component (PC) analysis. Principal components were obtained using all ten measured variables which were first standardized so that they had equal influence on the principle components. The first three PCs all had eigenvalues greater than 1 indicating that they explain more of the variance in burrows than any of the original variables. Together they explain 69% of the variance (45% + 13.7% + 10.3%). PC1 and PC3 differed significantly between mated and sampled burrows (Mann-Whitney *U*-tests, with Bonferroni correction; see Table 4).

Table 5 Trait loadings (weightings), associated eigen values and the percentage of total variance accounted for by the eigenvalues of three principal components (PC) in the analysis of the relationships between burrow features

Burrow feature	Trait loadings		
	PC1	PC2	PC3
Volume	0.419	0.115	-0.153
Depth	0.244	0.391	-0.486
Max. width	0.376	0.061	0.051
Min. width	0.289	0.250	0.340
Entrances (no.)	0.316	-0.430	-0.240
Branches (no.)	0.361	-0.353	-0.008
Frills	0.242	-0.044	0.564
Entrance angle	0.114	0.652	-0.059
Burrow angle	0.264	0.090	0.428
Length	0.408	-0.155	-0.242
Eigenvalue	4.504	1.367	1.030
% Variance	45.03	13.67	10.34

Only four sampled males (9.8%) had a burrow PC1 lower than that of the mated male in the same sampling sequence. The mated male had the lowest value for PC1 in 14 of the 17 sequences (82.4%). Use of this component therefore provides a highly accurate way to predict which male in a given sequence will mate. The trait loadings of the three PCs are given in Table 5.

None of the principal components was significantly correlated with male claw length (Table 4). In the univariate analysis only burrow volume was correlated with

male claw size (Table 3). None of the principal components correlated with the size of the female that chose the male's burrow (Table 4), or the time of cycle at which mating occurred (Table 4). Hence there is no evidence for a time-dependent change in the features of burrows that females choose to breed in.

Discussion

This study clearly demonstrates female selectivity for both mate size and burrow quality in *Uca annulipes*. Previous studies of fiddler crabs have not demonstrated such choices. In *U. rapax*, females do behave selectively with respect to male size, but this is due to size-assortative mating which results in medium sized males having a mating advantage (Greenspan 1980). The study of Christy (1983) demonstrates that *U. pugilator* females are selective in their choice of burrows. Although large males had a definite mating advantage, female choice based on burrow quality alone could account for the increased frequency of mating by large males.

In both *U. annulipes* and *U. pugilator*, the movement of receptive females among males and burrow provides the opportunity for choice based on both male and burrow characteristics. Why then do female *U. annulipes* select larger males while *U. pugilator* do not? Christy (1983) suggests that the high level of predation on *U. pugilator* coupled with the relatively low probability of finding a suitable burrow may be excessively costly to females. In contrast, there is a remarkably low level of predation on the population of *U. annulipes* studied here. There is also an extremely large number of potential mates and burrows from which to choose. It is possible that these ecological factors account for the observed difference between the two fiddler crab species.

Temporal variation in female choosiness

Due to the large male mating advantage found in this species, we are able to use mated male size as an index of temporal variation in female mate acceptance criterion. The smaller the mated male, the lower the female's acceptance criterion. The relative size difference between mated and sampled males can also be used as an index of female choosiness. If a female is not selective with respect to male size the mated male should generally be the same size as the average sampled males. The larger the mated male relative to the sampled males, the higher the females mate acceptance criteria and the more choosy the female. A third indicator of female choosiness is the mean size of the sampled males. Since females are selective in terms of who they choose to sample from the total male population, choosier

females should sample larger males. Although females show positive assortative sampling on the basis of size, there was no relationship between the size of the monitored sampling females and time of cycle. Therefore temporal changes in the size of mated and sampled males do not result from temporal changes in the size of sampling females.

Time of cycle had significant effects on female mate acceptance criteria with respect to all three measures of female choosiness. The later in the cycle that mating occurred, the smaller the mated male, the smaller the mean size of the sampled males and the smaller the relative size difference between mated and sampled males. In *U. annulipes* and other fiddler species, successful mating is restricted to the last 5 or 6 days of each semilunar cycle due to temporal restriction on optimal spawning time (Christy 1980). Females must allow sufficient time between mating and the release of larvae at the next nocturnal spring tide for embryonic development. Excessive female choosiness at the end of the cycle increases the female's risk of either not finding a suitable mate, or of sub-optimal mating due to delayed larval release, or the release of underdeveloped larvae. The evidence presented here suggests that females decrease their acceptance criteria, in terms of whom they chose to sample and mate with, as the time before the next larval release date decreases. At the start of the cycle, when time constraints are minimal, females sample larger males and, of those sampled, select the larger males as mates. When the costs of delaying mating increase, females are less selective and no longer choose the larger of the sampled males as mates. This temporal decrease in choosiness is further supported by the relationship between the time of mating in the cycle and the time of mating in the day. Mating occurs earlier in the daily activity period (relative to low tide) later in the cycle. However, this trend is partially confounded by the fact that the diurnal low tides occur later in the day towards the end of a cycle so that there is sometimes less time available for sampling before light levels drop. Overall, however, the evidence strongly suggests that females are less choosy, at least in terms of the size of their mate's claw and carapace, as the likelihood of sub-optimal timing of mating increases.

The temporal decrease in female choosiness suggests that females are, in fact, behaving selectively with respect to male size, and that the non-random mating is not merely due to the increased detectability of large males. The extremely large number of courting males and burrows suggest that females would have a full range of male sizes and burrow qualities from which to choose at all times of the semilunar cycle. It is unlikely that female choosiness decreases because males and/or burrows are "removed" from the potential sampling pool by previously mated females. Females pass numerous males at all times of the cycle.

Does sampling effort indicate female choosiness?

After removing the effect of time of cycle, three significantly negative relationships between variables that are considered indicators of female choosiness emerged. The size of the mated male was negatively related both to the number of males sampled and the cumulative distance travelled by the female. The more males sampled and the greater the distance travelled, the *smaller* the mated male. An alternative measure of female choosiness, namely the relative size difference between the mated and sampled males, was also negatively correlated with the distance travelled. These three relationships seem to indicate that female choosiness decreases as her "sampling effort" increases. Again, these results can not be attributed to variation in female size, as there is no relationship between female size and distance travelled or number of males sampled.

The direction of these three relationships is counter-intuitive since the number of sampled males, and other indices of sampling effort (such as distance travelled), are generally assumed to be good indicators of female choosiness (see Real 1990). How then can we explain our results? We suggest that the number of males sampled (and distance travelled) need not reflect the strength of a female's mating preference. Choosiness may decline if a female is unsuccessful at finding a suitable mate after some initial sampling period (Wittenberger 1983; Real 1990). Since potential mates are encountered at random, a run of "bad luck" may lower a female's mate acceptance criterion. A small difference between the sizes of sampled and mated males may indicate a low acceptance criterion, but the reason for having sampled many males to begin with was due to a high initial acceptance criterion. Another possible explanation is that the "experience" of individual females may play a role: experienced females may be more discriminate in their sampling behaviour.

Females can only assess burrow quality by entering burrows as there is no relationship between male size and burrow quality. At the start of a sampling sequence, females may choose to sample the burrows of larger males, thereby increasing their chances of finding a large male with a suitable burrow. However, after they have sampled a number of males (without successfully finding a burrow that exceeds the acceptance threshold), females may show less choosiness in terms of the size of males whom they approach and sample. This scenario can account for the observed negative relationship between the number of males sampled and the final size of the mated male, as well as the size difference between mated and sampled males.

Burrow quality

The burrows of mated males were clearly distinguishable from the burrows of sampled and rejected males.

This provides strong evidence that females directly assess burrow quality when selecting a mate. The accuracy with which we can statistically separate mated and sampled male burrows is impressive, particularly since we are unlikely to have used the same criteria females employ when determining burrow quality. Female *U. annulipes* seldom mate in a burrow that is "less suitable" than those previously sampled, and they do not return to the burrows of previously sampled males. It therefore appears that females have a fixed threshold for mate acceptance based on burrow quality, selecting the first male whose burrow surpasses a critical threshold value (see Wittenberger 1983). The selected burrow features in *U. annulipes* are likely to affect incubation and larval survival and, as in *U. pugillator*, burrow quality is probably an important determinant of female reproductive success (Christy 1983). It is therefore not surprising that the female threshold for burrow quality does not decrease with increased temporal constraints.

Multiple criteria of choice

Females are using at least two criteria, namely male phenotype (size) and resource quality (burrow features) when choosing potential mates. Mated male size changes over the course of the semi-lunar breeding cycle. There is no relationship between the burrow quality of mated males and the time in the semi-lunar cycle at which mating occurs. As the semi-lunar cycle progresses, females decrease their selectivity in relation to the size of males they choose to sample. However, selectivity on the basis of burrow quality remains constant. The difference in the relationships between time of cycle and male size and the burrow index graphically illustrates the fact that male phenotype and resource quality are independent predictors of female mate choice. It also supports theoretical predictions that, when the costs of sampling increase, females should be less selective for those factors where variation in female fitness due to reduced choosiness is relatively small (Halliday 1983). Burrow quality is likely to have large effects on the direct fitness of females, while the benefits of choosing larger males are probably indirect due to "good genes" (Iwasa et al. 1991), or possibly small direct benefits if male size is an indicator of risks such as the likelihood of disease transfer. It is therefore not surprising that females are always choosy about the type of burrow they mate in, while becoming less choosy about male phenotype later in the semi-lunar cycle.

In many species, it is often difficult to separate the effects of male phenotype and resource quality because the two factors are confounded (Balmford et al. 1992). Multivariate statistical techniques must therefore be used to estimate the independent effect of these two factors. This is not a problem in our study. In

U. annulipes both male size and burrow features are good independent predictors of male mating success. Rather, our dilemma is to explain how two factors (male size and burrow type) can both predict mating success given that (1) females do not return to the burrows of previously sampled males; (2) the mated male burrow had the lowest primary principal component value in 82% of the observed cases; and (3) male size and burrow index are unrelated variables. The data suggest that females have a fixed threshold for mate acceptance based on burrow type. Given that females do not return to previously sampled burrows, and that they pick the “best” burrow of those sampled, how then can male size also predict mating success? The answer appears to be related to how females initiate sampling. We envisage mate choice in *U. annulipes* as a two-stage process. First, females decide which males they will sample. They tend to approach and investigate the burrows of larger males. Second, they then decide whether or not to mate with a male based on burrow features. This sampling process explains the large male mating advantage as females choose to sample the larger males in the population. The ability of the primary principal component to separate mated and unmated males is then attributable to females mating with the first male they choose to sample whose burrow index exceeds a threshold value.

Conclusions

This study demonstrates that an increased cost of sampling may result in a decreased acceptance threshold value. This scenario is similar to the theoretical model of Real (1990) of a one-step decision tactic with a decreasing acceptance threshold (however, in Real's model, females often return to mate with a previously visited male). Furthermore, this study indicates that females apparently select the first male whose burrow surpasses some critical threshold value (see Wittenberger 1983), and they are therefore using a fixed threshold for mate acceptance based on burrow quality. This complex choice strategy (a changing threshold value for one character and a fixed threshold for another) may not be unique to this species. The results of other work on female sampling behaviour suggest that females in many species make complex economic decisions about mate suitability. Although it is possible that vertebrates may be better able to “remember” previously visited males and that they may have a more flexible reaction system, there are probably not very large differences between fiddler crabs and e.g. birds for carrying out complex mate choice behaviours (see Steger and Caldwell 1983).

Recent theoretical work has begun to address issues such as female choice based on multiple criteria (Pomiankowski and Iwasa 1993). However, less atten-

tion has been paid to understanding how this occurs at the proximate level. How do females choose males based on assessment of two or more factors, especially when these factors do not covary? Answers will need to be framed in terms of knowledge of female sampling tactics, and information on the differences in the value of preferred traits for sampled and mated males. Experimental studies in which the costs of female sampling are manipulated may allow workers to rank the relative importance of different factors for females (see Kirkpatrick and Ryan 1991). Less important factors are more likely to be discarded as the costs of sampling rise. As a general prediction we suggest that increased costs to sampling are more likely to reduce female choosiness based on male phenotype than that based on resource quality (see Halliday 1983, Kirkpatrick and Ryan 1991). Further empirical testing remains crucial to painting a more realistic picture of how females choose males, and what limits the expression of mating preferences.

Acknowledgements We thank Michael Jennions, Rob Brookes and John Christy for commenting on the manuscript and Mandy Dyson for help in the field. Permission for P.R.Y.B. to work in Durban Harbour was provided by the Port Captain and Portnet. P.R.Y.B. was funded by a Natal University Post-doctoral award. N.I.P. and P.R.Y.B. were funded by the Communication Biology Research Group (Wits University).

References

- Alatalo RV, Carlson A, Lundberg A (1988) The search cost in mate choice of the pied flycatcher. *Anim Behav* 36:289–291
- Balmford A, Rosser AM, Albon SD (1992) Correlates of female choice in resource-defending antelope. *Behav Ecol Sociobiol* 31:107–114
- Burley N (1981) Mate choice by multiple criteria in a monogamous species. *Am Nat* 117:515–528
- Christy JH (1980) The mating system of the sand fiddler crab, *Uca pugilator*. PhD dissertation, Cornell University
- Christy JH (1983) Female choice in the resource-defence mating system of the fiddler crab *Uca pugilator*. *Behav Ecol Sociobiol* 12:169–180
- Christy JH (1987) Female choice and the breeding behaviour of the fiddler crab *Uca beebei*. *J Crustacean Bio* 7:624–635
- Christy JH, Salmon M (1991) Comparative studies of reproductive behaviour in mantid shrimps and fiddler crabs. *Am Zool* 31:329–337
- Crane J (1975) Fiddler crabs of the world, Ocypodidae: Genus *Uca*. Princeton University Press, Princeton
- Dombrowsky Y, Perrin N (1994) On adaptive search and optimal stopping in sequential mate choice. *Am Nat* 144:355–361
- Engelhard G, Foster SP, Day TH (1989) Genetic differences in mating success and female choice in seaweed flies (*Coelopa frigida*). *Heredity* 62:123–131
- Frederick P (1987) Extrapair copulations in the mating system of white ibises (*Eudocimus albus*). *Behaviour* 100:170–201
- Gibson RM, Bachman GC (1992) The costs of female choice in a lekking bird. *Behav Ecol* 3:300–309
- Greenspan BN (1980) Male size and reproductive success in the communal courtship system of the fiddler crab *Uca rapax*. *Anim Behav* 28:387–392
- Halliday TR (1983). The study of mate choice. In: Bateson PPG (ed) *Mate choice*. Cambridge University Press, Cambridge

- Harvey PH, Bradbury JW (1991) Sexual selection. In: JR Krebs, Davies NB (eds) Behavioural ecology, an evolutionary approach. Blackwell, Oxford, pp 203–233
- Houde AE (1993) Evolution by sexual selection: what can population comparisons tell us? *Am Naturalist* 141: 796–803
- Iwasa Y, Pomiankowski A, Nee S (1991) The evolution of costly mate preferences. II. The “handicap” principle. *Evolution* 45: 1431–1442
- Janetos AC (1980) Strategies of female mate choice: a theoretical analysis. *Behav Ecol Sociobiol* 7:107–112
- Kirkpatrick M, Ryan MJ (1991) The evolution of mating preferences and the paradox of the lek. *Nature* 350:33–38
- Kirkpatrick M, Price T, Arnold SJ (1990) The Darwin-Fisher theory of sexual selection in monogamous birds. *Evolution* 44: 180–193
- Lifjeld JT, Slagsvold T (1988) Female pied flycatchers, *Ficedula hypoleuca*, choose male characteristics in homogenous environments. *Behav Ecol Sociobiol* 22:27–36
- Milinski M, Bakker TCM (1991) Sequential female choice and the previous male effect in sticklebacks. *Behav Ecol Sociobiol* 29:205–210
- Milinski M, Bakker TCM (1992) Costs influence sequential mate choice in sticklebacks, *Gasterosteus aculeatus*. *Proc R Soc Lond B* 250:229–233
- Møller AP (1992). Female swallow preference for symmetric male ornaments. *Nature* 357:238–240
- Morgan SG, Christy JH (1995) Adaptive significance of the timing of larval release by crabs. *Am Nat* 145:457–479
- Parker GA (1983) Mate quality and mating decisions. In: Bateson P (ed) *Mate choice*. Cambridge University Press, Cambridge, pp 141–161
- Petrie M, Halliday T, Sanders C (1991) Peahens prefer peacocks with elaborate trains. *Anim Behav* 41:323–331
- Pomiankowski A, Iwasa Y (1993) Evolution of multiple sexual preferences by Fisher’s runaway process of sexual selection. *Proc R Soc Lond B* 253:173–181
- Real L. (1990) Search theory and mate choice. I. Models of single-sex discrimination. *Am Nat* 136:376–405
- Reynolds JD, Gross MR (1990) Costs and benefits of female mate choice: is there a lek paradox? *Am Nat* 136:239–243
- Salthe SW, Mecham JS (1974) Reproductive courtship patterns. In: Lofts B (ed) *Physiology of the Amphibia*. vol II. Academic Press, New York, pp 209–251
- Siegel S, Castellan NJ Jr (1988) *Nonparametric statistics for the behavioral sciences*. McGraw-Hill, New York
- Steger R, Caldwell RC (1983) Intraspecific deception by bluffing: a defence strategy adopted by newly moulted stomatopods (Arthropoda: Crustacea). *Science* 221:558–560
- Thompson S (1986) Male spawning success and female mate choice in the mottled sculpin, *Forsterygion varium* (Pisces: Tripterygiidae). *Anim Behav* 34:580–589
- Thornhill R (1983) Cryptic female choice and its implications in the scorpionfly *Harpobittacus nigriceps*. *Am Nat* 122:765–788
- Thornhill R (1984) Alternative female choice tactics in the scorpionfly *Hylobittacus apicalis* (Mecoptera) and their implications. *Am Zool* 24:367–383
- Trail PW, Adams ES (1989) Active mate choice at cock-of-the-rock leks: tactics of sampling and comparison. *Behav Ecol Sociobiol* 25:283–292
- Wittenberger JF (1983) Tactics of mate choice. In: Bateson P (ed) *Mate choice*. Cambridge University Press, Cambridge, pp 435–447
- Zuk M, Ligton JD, Thornhill R (1992) Effects of experimental manipulation of male secondary sex characters on female preferences in red jungle fowl. *Anim Behav* 44:999–1006

Communicated by R. Gibson