A test for resource-defence mating in the fiddler crab *Uca beebei*

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Abstract. Males of the fiddler crab *Uca beebei* defend, court from and attract females to burrows in intertidal mud flats. Females sequentially enter and leave several male burrows before they stay in one, mate and breed. This reproductive pattern is common among fiddler crabs and suggests that males may compete for females by competing for high-quality breeding sites and females may choose mates based on burrow quality. These ideas were tested for *U. beebei* by comparing structural features of (1) male and female burrows and (2) the male burrows females entered and left and those in which they mated. Male burrows had narrower openings and shafts than female burrows, but neither these nor 10 other burrow features differed between the male burrows females left and those in which they mated. Thus, there was no evidence of resource-defence mating in *U. beebei*. This pattern of mating behaviour may be rare in the genus because burrows suitable for breeding generally may be abundant and available to both sexes. Male fiddler crabs may compete for burrows due to their value for post-copulatory mate guarding and females may choose mates on the basis of courtship displays, not the quality of burrows for breeding.

Studies of the ecological correlates of mating patterns suggest that the dispersion of resources crucial to female reproduction largely determines female dispersion, which in turn strongly influences how males compete for mates (Bradbury & Vehrencamp 1977; Emlen & Oring 1977; Wells 1977; Thornhill & Alcock 1983; Davies 1991 for a recent review). When the availability of such resources is limited in space or time, male resource defence is favoured. Selection on female reproductive success leads to female choice of mates and breeding sites based on the quality of male-defended resources (Kirkpatrick 1985).

Male fiddler crabs, genus *Uca*, in the subgenera Celuca and Minuca (about 40 species) typically court from and defend burrows (Crane 1975) to which females come for mating and in which they oviposit and incubate their eggs until they hatch (Christy 1978, 1982, 1987a; Christy & Salmon 1984; Murai et al. 1987; Goshima & Murai 1988). A study of the reproductive ecology and behaviour of the sand fiddler crab, *Uca pugilator* (Celuca) (Christy 1978, 1982, 1983), showed that females can oviposit and incubate successfully only if they gain access to burrows of a minimum

depth with expanded terminal chambers that will not flood and collapse during breeding. Males dig, fight for and court from such burrows in the supratidal zone and females show an active mating preference for them. This study suggested that mating patterns of other fiddler crabs that mate and breed in male-defended burrows also may result from competition among males for high-quality breeding sites, and female choice based on burrow structural features that affect female reproductive success (Christy & Salmon 1984). Here we report the first test of this hypothesis in another fiddler crab, *Uca beebei* (Celuca), that breeds in male-defended burrows.

The Reproductive Behaviour of *U. beebei*

Uca beebei burrows in intertidal mud flats on protected shores of Central and northern South America (Crane 1975). Both sexes occupy and defend burrows at the same locations. Crabs emerge from their burrows during daytime low tides, feed by them and interact socially. Males wave their single enlarged claws and direct other visual displays to females that are moving on the surface away from their own burrows (Christy 1988b). During each low tide activity period some males build mud pillars about 1·5 cm high at their

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burrow entrances ('pillar burrows') while others do not ('no-pillar burrows') (Christy 1988a, b). Pillar building appears to depend on male nutritional state and all males may build pillars at some time (Christy 1988b; P. Backwell, unpublished data). A wandering receptive female typically enters and leaves several (23 is the recorded maximum) male burrows before she stays in one, whereupon the resident male plugs the burrow and the pair presumably mates. From 1·5 h to 3 days later, after the female has oviposited, the male leaves the burrow but the female stays, at least until her eggs hatch about 12 days later (Christy 1987a). This is the most common reproductive pattern in this species. Crabs also copulate on the surface with their neighbours and females that do so breed in their own burrows (Christy 1987a).

Receptive female *U. beebei* approach and enter pillar burrows significantly more often than no-pillar burrows (Christy 1988b). Both behavioural differences between males with and without pillars as well as the presence and absence of pillars themselves contribute to this difference in attractiveness (Christy 1988b; unpublished data). Pillars function as visual guideposts to which wandering females orient (Christy 1988b; Christy & Salmon 1991). There is no significant difference in the frequency with which females stay and mate in pillar and no-pillar burrows (Christy 1988b). Thus, the female preference to approach and enter pillar burrows does not affect whether they leave or stay. Rather, females may leave or stay in male burrows according to preferences based on cues that indicate the quality of these burrows for breeding. For example, females may prefer (1) burrows with larger terminal chambers for oviposition and incubation, (2) relatively moist burrows for irrigation of eggs, (3) longer and deeper burrows that provide more constant thermal environments for incubation, or some combination of burrow features. A previous study (Christy 1987a) indicated that females prefer longer, deeper burrows but measurement methods were imprecise and no other burrow structural features were measured.

Application of the general theory of the ecological determinants of mating patterns (Davies 1991) to the reproductive behaviour of *U. beebei* suggested two specific tests of the hypothesis that males compete for high-quality breeding sites and females choose mates based on burrow quality.

First, we compared the structure of male and female burrows to determine whether they differ in features that may affect female reproductive success. Such differences are expected if burrows that provide the best breeding environments are not generally available to females and males compete for them in order to obtain mates. Second, we compared the same features of the male burrows females entered and left with those in which they stayed to determine whether female choice may be based on these burrow features.

METHODS

Study Site

The study site was an intertidal muddy-sand flat on the west bank of the Pacific entrance to the Panama Canal, about 1 km upstream from the Bridge of the Americas. The flat is well drained by two tidal creeks that delimit its seaward borders, and grades to mud as it rises landward toward a mangrove forest. *Uca beebei* occurs in a nearly monospecific colony occupying about 100 m^2 on the seaward, sandier portion of the flat.

Sampling Methods

We selected female burrows and male pillar and no-pillar burrows for study in two ways. (1) Approximately 1 h before low tide on each of 11 days from 26 May to 21 July 1989, we used twine to delimit a 2-m^2 plot at a location with abundant burrows. No area was sampled more than once. We marked all burrows with numbered wire stakes and 1–1·5 h later, when pillars had been built, we selected randomly (random numbers table or coin toss) 10 or fewer burrows of each category. (2) On 16 days from 7 July to 18 August 1989, we located and followed receptive females as they moved on the surface and interacted with resident crabs. We marked each male burrow the females entered and left ($N=41$) and those in which they stayed for at least 10 min ($N=16$) with numbered blowgun darts. Females spent on average 21·7 s (range=2–178 s) in the male burrows they left. Thus, we assumed that females that spent more than 10 min in male burrows would have stayed and reproduced in them had we not dug them up.

Burrow Features and Crab Size

We made wax casts of burrows from which we measured burrow dimensions (Fig. 1). We assigned subjectively each burrow to one of six shape categories (Fig. 1). We measured burrow volume as the amount of water that burrow casts displaced. We collected samples of sediment from the bottom of each male burrow females entered and placed the samples in air-tight bags. Using indicating paper (E. Merck, colorpHast) we measured the pH of the sediment samples immediately after we collected them in the field. We measured the per cent moisture by weight of this sediment as the per cent weight lost after drying to a constant weight. We measured crab carapace width and length and, for males, the propodus length of the large cheliped to permit analysis of covariance (ANCOVA) of burrow dimensions that might depend on crab size.

Statistical Analyses and Tests of Hypotheses

We tested two null hypotheses: (1) pillar, no-pillar and female burrows do not differ and (2) pillar and no-pillar burrows females leave do not differ from those in which they stay. By treating male pillar and no-pillar burrows separately we were also able to test the inference from previous studies (Christy 1987a, 1988b) that these two classes of male burrows do not differ structurally in ways that may affect breeding decisions once females enter burrows. We used G-tests of independence to compare burrow shapes and one-way analysis of variance (ANOVA) to compare nine burrow dimensions, sediment pH and moisture content. We used the sequential Bonferroni technique (Rice 1989) to set significance levels for the component statistical tests of each null hypothesis based on 'table-wise' α levels of 0·05. The technique sequentially compares P_i values, ranked from smallest to largest, to the values $\alpha/(1+k-i)$ where k is equal to the total number of statistical tests and i is equal to the rank of the P-value. All $P_i \leq \alpha/(1+k-i)$ values were significant.

RESULTS

Female, Pillar and No-pillar Burrows

Burrow shape was independent of burrow category ($G=6·379$, $df=10$, $P>0·50$). Bow, S, and
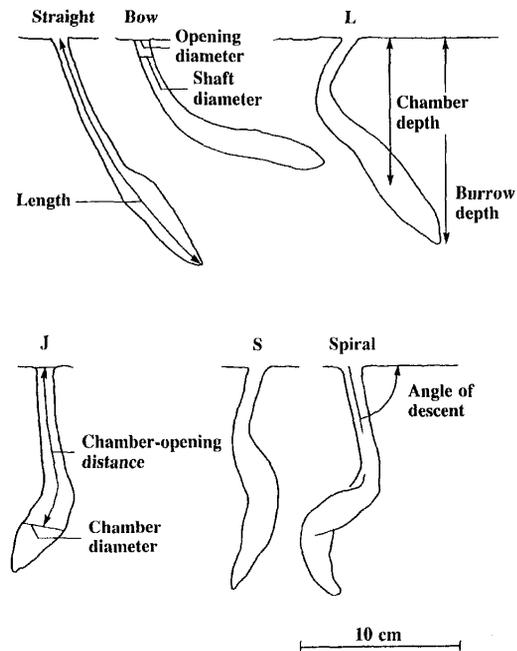

Figure 1. Features of male and female burrows determined from burrow casts. Words and letters above the burrow drawings refer to shape categories. Dimensions in centimetres were measured with a tape rule (1 mm precision), those in millimetres were measured with calipers (0·02 mm precision) and angles were measured with a protractor (1° precision).

spiral shapes were approximately equally common, together accounting for 72% of all burrows.

Only burrow opening and shaft diameter differed significantly between pillar, no-pillar and female burrows (Table I). Results of an ANCOVA revealed that these two burrow dimensions increased at significantly different rates with carapace length among burrow categories (Fig. 2; opening diameters: $F_{2,182}=8·847$, $P<0·001$; shaft diameters: $F_{2,175}=8·712$, $P<0·001$). Pillar male, no-pillar male and female carapace lengths differed significantly (one-way ANOVA: $F_{2,178}=5·551$, $P=0·005$). A comparison of means showed that the two categories of males did not differ in carapace length (pillar: 6·1 ± 0·07 mm; no-pillar: 6·2 ± 0·08 mm; Tukey HSD, $P=0·497$) but both were significantly smaller than females (6·5 ± 0·09 mm; Tukey HSD, $P<0·05$ for both comparisons). Hence, differences in (1) the rate of increase of burrow opening and shaft diameter with carapace length among burrow categories and (2)

Table I. Comparisons of male and female burrows. Entries are means ± SE, (*N*, range)

| Burrow feature | Burrow category | | | ANOVA*, *P*-value |
	Male, pillar	Male, no-pillar	Female	
Length (cm)	16·9 ± 0·26	16·1 ± 0·29	16·5 ± 0·48	0·073
	(87, 11·2–23·7)	(73, 10·8–26·2)	(32, 8·9–21·4)	
Depth (cm)	12·9 ± 0·28	12·5 ± 0·26	13·3 ± 0·36	0·219
	(87, 5·8–20·8)	(73, 8·3–17·8)	(31, 8·6–17·6)	
Opening diameter (mm)	7·4 ± 0·08	8·1 ± 0·17	8·7 ± 0·16	<0·001†
	(92, 5·4–10·3)	(83, 5·4–13·2)	(52, 6·9–12·5)	
Shaft diameter (mm)	7·2 ± 0·07	7·4 ± 0·82	7·8 ± 0·11	<0·001†
	(87, 5·4–10·1)	(81, 5·7–10·9)	(51, 5·6–9·9)	
Chamber diameter (mm)	16·3 ± 0·25	16·7 ± 0·31	16·3 ± 0·58	0·705
	(91, 11·7–23·3)	(77, 10·8–26·7)	(33, 8·0–22·1)	
Volume (ml)	16·3 ± 0·39	15·8 ± 0·50	16·8 ± 0·68	0·478
	(85, 10–31)	(74, 6–34)	(30, 9·5–23·5)	
Chamber-opening	12·9 ± 0·26	11·9 ± 0·29	12·8 ± 0·39	0·056
distance (cm)	(86, 7·4–19·4)	(73, 7·1–23·2)	(31, 8·6–16·4)	
Chamber depth (cm)	10·3 ± 0·25	9·8 ± 0·23	10·8 ± 0·38	0·102
	(87, 4·8–16·3)	(73, 6·1–15·6)	(31, 7·1–15·6)	
Angle of descent (degrees)	73·4 ± 0·19	75·1 ± 1·35	77·0 ± 1·22	0·171
	(89, 38–89)	(77, 35–90)	(50, 50–88)	

*F-tests, one-way ANOVA.
†Significant by the sequential Bonferroni technique (see Methods), *P*-values were <0·006, (α/9).

carapace lengths of pillar males, no-pillar males and females in our samples may both contribute to the observed differences in burrow opening and shaft diameters.

Burrow Features and Mating

Whether females left or stayed in burrows was independent of burrow shape (*G*=9·043, *df*=5, *P*>0·10). Bow, S and spiral were the most common shapes of the burrows females entered (75%), as they were for male and female burrows generally.

None of the ANOVAs testing for differences between the remaining features of pillar and no-pillar burrows from which female left and those in which they stayed approached the level of significance necessary to reject the null hypothesis, based on a table-wise α of 0·05 (Table II). Two of three component tests of burrow-shaft diameter gave individual *P*-values of less than 0·05. This might suggest a female preference for narrower burrows. However, females were most attracted to, and thus prefered, pillar burrows and the shaft diameters of pillar burrows in which females stayed did not differ significantly from the diameters of all burrows females left.

DISCUSSION

Tests of Hypotheses

Male burrows, and especially pillar burrows, tended to be narrower than female burrows. We found no evidence, however, of a female preference for narrower burrows suggesting that they are not better for breeding. Indeed, one might expect females to prefer wider burrows so that they could move freely while incubating their eggs beneath their abdomens and emerge unhindered to release their larvae. Males may dig narrower burrows because they are better able to defend them when fights for burrows continue underground. No other burrow feature we measured differed between male and female burrows and we found no evidence of female preferences based on burrow features. Although pillars and the courtship displays of the males that build them are highly attractive to females, they do not provide cues of high-quality breeding sites.

In retrospect, it is not surprising that we found few differences between male and female burrows. Males leave their burrows to their mates after oviposition, non-breeding burrow residents may lose their burrows in fights with crabs of the
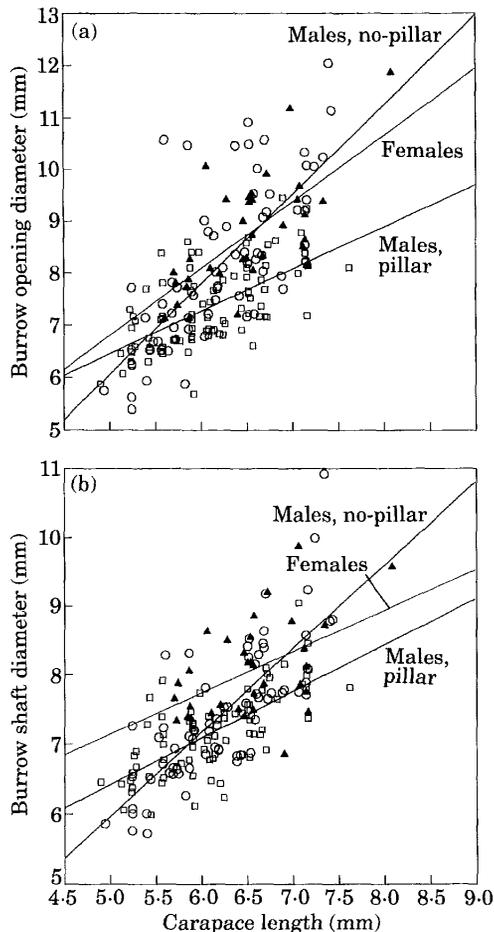
Figure 2. Relationships between (a) opening diameters and (b) shaft diameters of female (▲), pillar (□) and no-pillar (○) burrows and the carapace lengths of crabs resident in these burrows. Lines fitted by least-squares regression.

opposite sex, and burrows in muddy-sand sediments where this species lives probably change little over relatively long periods of time (Frey & Mayou 1971; Allen & Curran 1974; Basan & Frey 1977). Hence, the dynamics of burrow exchange and burrow structural stability may explain why male and female burrows are so similar.

The Status of Resource-defence Mating in Fiddler Crabs

Resource-defence mating may be exceptional among fiddler crabs that mate in male burrows.

Uca pugilator is the only species for which there is a strong case for this mating pattern, and then only for a single population that lives on pure sand beaches (Christy 1978, 1982, 1983; contrast Salmon & Hyatt 1983), a habitat that is unusual for fiddler crabs (Crane 1975). In this habitat, non-breeding females occupy intertidal burrows that collapse when they are flooded by the tide and thus are unsuitable for breeding. Males compete for and females prefer stable burrows in a narrow region in the supratidal zone. Most fiddler crabs live in stable intertidal burrows in mud or muddy-sand, or in sediments supported by roots (Crane 1975; Reingold 1979; Montague 1980; Bertness & Miller 1984). Hence, burrows that are suitable for breeding generally may be available to both sexes, a condition that does not favour resource-defence mating.

An Alternative to Resource-defence Mating

We suggest that males of fiddler crab species that breed in male-defended burrows may be competing for females directly (Christy 1987b) and that male reproductive behaviour may be best understood in the context of sperm competition (Murai et al. 1987; Goshima & Murai 1988). Male *U. pugilator* (Christy 1978, 1982), *U. beebei* (Christy 1987a), *U. lactea* (Murai et al. 1987; Goshima & Murai 1988; Severinghaus & Lin 1990) and probably other species that breed in male-defended burrows (Greenspan 1980, 1982) stay underground with their mates until they have oviposited. In *U. lactea* (Murai et al. 1987), sperm from the last male to mate with a female have precedence in fertilization. A last male advantage in sperm competition is also known for *Scopimera globosa* (Koga et al. 1993), a related species in the same family (Ocypodidae) that has similar reproductive behaviour, and may be common among brachyuran crabs (Diesel 1991). Hence, male fiddler crabs may defend burrows, not because they are important resources for females, but because they provide protected sites where males can guard their mates successfully until they oviposit and thus be assured that their sperm are used in fertilization (Murai et al. 1987; Goshima & Murai 1988).

Wandering by receptive females on the surface away from their own burrows apparently has led to 'attract and defend' (e.g. *U. beebei*) and 'capture and defend' (e.g. *Uca deichmanni*: Zucker

Table II. Comparisons of the male-defended burrows in which females mated and those they entered and left. Entries are means ± SE (N, range)

Burrow feature	Mated			Entered and left			ANOVA: mated/left*		
	All	Pillar	No-pillar	All	Pillar	No-pillar	All/all	Pillar/all	No-pillar/all
Length (cm)	16·8 ± 0·50 (15, 14·2–20·6)	17·7 ± 0·61 (9, 15·8–20·6)	15·4 ± 0·46 (6, 14·2–17·1)	17·4 ± 0·48 (40, 11·8–26·2)	17·3 ± 0·53 (22, 13·0–23·7)	17·5 ± 0·86 (18, 11·8–26·2)	0·481	0·752	0·120
Depth (cm)	13·2 ± 0·57 (14, 10·2–18·5)	14·3 ± 10·73 (8, 11·7–18·5)	11·7 ± 0·47 (6, 10·2–13·4)	12·9 ± 0·45 (40, 5·8–17·9)	12·9 ± 0·60 (22, 5·8–17·9)	12·9 ± 0·70 (18, 8·5–17·8)	0·792	0·222	0·302
Opening diameter (mm)	7·3 ± 0·18 (14, 6·3–8·7)	7·0 ± 0·38 (8, 6·3–7·9)	7·7 ± 0·29 (6, 6·9–8·7)	7·8 ± 0·02 (40, 5·8–17·9)	7·5 ± 0·16 (23, 6·6–9·2)	8·1 ± 0·33 (18, 5·4–11·1)	0·173	0·085	0·879
Shaft diameter (mm)	6·8 ± 0·10 (14, 6·0–7·5)	6·9 ± 0·14 (8, 6·3–7·5)	6·7 ± 0·14 (6, 6·0–6·9)	7·3 ± 0·12 (41, 5·4–11·1)	7·2 ± 0·15 (23, 6·6–9·2)	7·5 ± 0·18 (18, 5·4–11·1)	0·020	0·157	0·043
Chamber diameter (mm)	15·4 ± 0·53 (15, 11·8–18·8)	15·3 ± 0·69 (9, 11·8–17·9)	15·5 ± 0·91 (6, 12·2–18·8)	16·5 ± 0·34 (41, 13·2–22·8)	16·6 ± 0·52 (23, 13·2–22·8)	16·4 ± 0·42 (18, 13·5–21·2)	0·082	0·131	0·283
Volume (ml)	15·3 ± 0·84 (13, 10·5–21·0)	16·3 ± 1·30 (7, 11·0–21·0)	14·2 ± 0·90 (6, 10·5–17·0)	17·5 ± 0·84 (40, 10·0–34·0)	16·7 ± 0·97 (22, 10·0–31·0)	18·5 ± 1·43 (18, 10·0–34·0)	0·157	0·547	0·136
Chamber-opening distance (cm)	12·7 ± 0·53 (14, 9·3–16·9)	13·8 ± 0·53 (8, 12·0–16·9)	11·2 ± 0·64 (6, 9·3–13·7)	12·7 ± 0·52 (40, 6·3–23·2)	12·7 ± 0·63 (22, 8·2–19·4)	12·6 ± 0·93 (18, 6·3–23·2)	0·977	0·365	0·315
Chamber depth (cm)	10·5 ± 0·68 (14, 6·2–16·3)	11·8 ± 0·75 (8, 10·0–16·3)	8·7 ± 0·81 (6, 6·2–11·6)	9·9 ± 0·38 (40, 5·7–15·6)	9·9 ± 0·47 (22, 5·7–13·0)	9·9 ± 0·62 (18, 6·1–15·6)	0·486	0·844	0·220
Angle of descent (degrees)	74·8 ± 3·64 (14, 40–89)	76·5 ± 3·61 (8, 61–89)	72·5 ± 8·06 (6, 40–88)	73·0 ± 1·82 (41, 50–88)	73·2 ± 2·31 (23, 50–87)	72·8 ± 2·98 (18, 50–88)	0·646	0·439	0·920
Moisture (%)	27·8 ± 1·41 (11, 20·6–35·5)	28·6 ± 2·17 (5, 21·9–35·5)	27·2 ± 1·78 (6, 20·6–33·0)	29·3 ± 0·99 (32, 13·0–39·6)	29·8 ± 1·35 (15, 19·6–39·3)	28·8 ± 1·47 (17, 13·0–39·6)	0·442	0·797	0·392
pH	6·9 ± 0·07 (16, 6·5–7·5)	6·8 ± 0·08 (9, 6·5–7·0)	6·9 ± 0·13 (7, 6·5–7·5)	6·8 ± 0·05 (41, 6·0–7·5)	6·9 ± 0·05 (23, 6·5–7·5)	6·8 ± 0·08 (18, 6·0–7·5)	0·611	0·971	0·442

*F-tests, one-way ANOVA; entries are *P*-values.

1983; *U. stenodactylus*: Zucker & Denny 1979; Christy & Salmon 1991) modes of competition among males for mates (Christy 1987b). To understand how sexual selection may be operating in these species, it is necessary to know why females leave their own burrows.

The present study suggests that females do not leave their burrows because they are poor breeding sites. Indeed, females mate on the surface and breed in their own burrows in *U. beebei* (Christy 1987a), *U. lactea* (Yamaguchi 1971; Murai et al. 1987; Goshima & Murai 1988) and perhaps many other species that also mate and breed in male-defended burrows (Crane 1975). The causes of female wandering have been studied in detail only in *U. lactea* (Murai et al. 1987; Goshima & Murai 1988). Aggressive interactions with males, often following courtship refusals, cause females to leave their burrows. Those with mature ovaries end wandering by mating in male burrows, while those with immature ovaries take new burrows by themselves (Murai et al. 1987; Goshima & Murai 1988). It is unclear why some females refuse to mate on the surface. By mating, they could stay and breed in their own burrows and avoid the risk of predation and expense of fighting for a burrow, digging a new one or searching for an empty burrow (Murai et al. 1987; Severinghaus & Lin 1990). Nevertheless, aggressive displacement of females from their burrows may be a common cause of female wandering in fiddler crabs (Crane 1975; Zucker 1977).

In summary, burrow loss through aggression, rather than the dispersion of resources crucial to female reproduction, may determine the dispersion of wandering receptive females. Males compete for these females either by attracting them into their burrows with courtship displays, or by physically capturing and forcing them into their burrows where they then guard them until females oviposit to assure their paternity. By mating with males in their burrows females would gain breeding sites but in most species of fiddler crabs females probably do not discriminate among males and burrows on the basis of the quality of burrows for breeding.

ACKNOWLEDGMENTS

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