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Female Choice in the Resource-Defense Mating System of the Sand Fiddler Crab, *Uca pugilator*

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Summary. Mating preferences of individual females and mating patterns among marked crabs were studied during the summers of 1973–1976 on sand beaches in mangrove habitat on the west coast of Florida in order to determine if females choose mates indirectly on the basis of the quality of a resource males defend and females use during breeding, directly on the basis of male size, or both.

Twice each lunar month for periods of 6–8 days when females are sexually receptive, mature males of all sizes fight for, court from and defend supratidal burrows in which females mate, oviposit and reside for about 2 weeks while incubating their eggs. Large males win fights with small males, tend to court from burrows located higher on the beach than the burrows of small males and mate more often than small males. Males are sequentially polygynous and may mate with up to 3 females at a single burrow during each semilunar breeding period.

Male and female sizes were positively correlated in 85 mated pairs because large females can not enter the burrows of small males. However, there were no significant differences among the sizes of the females who mated with males in 5 size classes (13.0–15.5 mm carapace length).

Receptive females spent about 9.5 min sampling 1–12 males and burrows before choosing their mates. Most females began sampling soon after high tide, though some fed first in the lower intertidal zone. Individual females neither chose larger males or higher burrows among those they sampled nor did they move so as to encounter sequentially larger males or higher burrows.

During periods with low tides, males of all sizes courted from burrows located at all positions on the elevation gradient and females chose neither significantly higher burrows nor significantly larger males. During periods with high tides, large males courted from, and females mated in high burrows. Choice of high burrows did not, however, result in choice of larger males considering either all those on the beach or only those at preferred up-beach locations.

Most females mated in burrows that were high enough to escape structural collapse due to tidal inundation or flooding by a tidally driven rise in groundwater. The effects of burrow flooding and collapse on female breeding success may select for choice of stable burrows. Females probably choose stable burrows by assessing directly features of burrows themselves. Burrows appear to be a resource for females and their quality as breeding sites probably is determined largely by their structural integrity.

Costs associated with the sampling behavior necessary for females to choose both a stable burrow and a large male may be sufficiently great to limit choice to burrow quality alone.

Introduction

Differences in choices females make when they select a mate and a time and place to breed are thought to contribute fundamentally to differences in female fitness (see Borgia 1979; Wittenberger 1979 for recent reviews). When males control access to resources that females require for reproduction (resource-defense mating systems, Bradbury and Vehrencamp 1977; Emlen and Oring 1977), females ought to choose mates indirectly

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by mating with males who defend the highest quality resources. Since potential mates can be expected to differ genetically, females also ought to choose males who will make the greatest genetic contribution to the fitness of their offspring. Female choice based on resource quality has been reported for a few species with resource-defense mating systems (e.g., Wells 1977; Howard 1978; Pleszczynska 1978; Jones 1981). Since male and resource quality often are correlated, however, it has been difficult to separate the effects of each on female choice and to demonstrate convincingly choice based directly on morphological or behavioral characters known or presumed to be correlated with male quality (Wittenberger 1981).

In this paper I describe female choice in the sand fiddler crab, *Uca pugilator*, with respect to male size, a character strongly correlated with intrasexual competitive ability, mating success, and, by inference, age and general fitness, and with respect to a primary determinant of the quality of a resource that males defend and females use during breeding. Due to temporal variation in how resources that differ in quality are distributed among males that differ in size, I have been able to separate analytically choice based on resource quality and choice based on male size. I also discuss selective factors that may influence the evolution of both types of choice in this species.

Background on the Mating System

Uca pugilator occurs on protected sandy substrates in estuaries, bays and sounds along the Atlantic and Gulf Coasts of the United States (Crane 1975, p 226). Its courtship and aggressive behavior have been well described (e.g., Crane 1943; Salmon 1965; Hyatt 1977a, b; Hyatt and Salmon 1978), but its mating system is known only from a single study in mangrove habitat on the west coast of Florida (Christy 1978, 1980, 1982). The following summary is based on that study.

Male *U. pugilator* compete for, court from and defend burrows used for breeding (breeding burrows, Christy 1982) in sandy supratidal substrates for 6 to 8 days twice each lunar month when females are sexually receptive and choose mates. Males without burrows (wanderers) fight courting males (residents, terminology from Hyatt and Salmon 1978) for breeding burrows. When a combat results in a change in burrow ownership, the challenging wanderer usually is larger than the defending resident (Hyatt and Salmon 1978; Christy 1980). Large males commonly defend burrows located higher on the beach than the burrows of small males. When prevented experimentally from competing with larger males, however, mature males of all sizes dig and court from burrows at the same locations high on the beach. In addition, small males that are placed experimentally in high burrows accept them as courtship sites but are removed rapidly by larger wanderers. Hence mature males of all sizes compete for high burrows and the correlation between male size and burrow elevation results from the competitive dominance of large males. Male mating frequency is strongly correlated with male size; large males may be sequentially polygynous, mating with up to 3 females at a single burrow during each semilunar period of reproductive activity.

Males court by waving their single enlarged chelae when females are distant and by rapping them against the ground at their burrow entrances when females are near (Crane 1943; Burkenroad 1947; Salmon 1965). Rapping produces substrate vibrations to which females are sensitive (Salmon and Horch 1972). Wandering females approach and briefly enter the burrows of one or more courting males before choosing a mate by remaining in a breeding burrow, whereupon the chosen male seals the burrow with a plug of sand. Mating and ovipositiong take 1 to 3 days and occur in the expanded terminal chambers of breeding burrows. After oviposition, the male opens the burrow and returns to the surface but the female remains in the terminal chamber to incubate her eggs. If the male stays at the burrow, he isolates the female from the burrow shaft with a loose sand plug, digs a new terminal chamber, resumes courtship, and may attract another female. About 14.5 days after females choose their mates, they emerge near dusk from their underground incubation sites (Hyman 1922; Christy 1980) and relase their planktonic larvae into the water at night during high tide (DeCoursey 1979; Bergin 1981).

About half of the females in a local population do not choose mates during each semilunar courtship period and some males court only for 1 or 2 days or not at all. Such nonbreeding crabs occupy relatively shallow, simple burrows (temporary burrows, Christy 1982) in the upper intertidal and supratidal zones during high tides. As the tide ebbs, they leave their burrows and feed in the lower intertidal zone. During flood tide they ascend the beach and enter and plug a temporary burrow where they spend the next high tide period.

Movement of receptive females among males and burrows provides the opportunity for choice based on both burrow and male characteristics. The use of burrows for mating, oviposition and

incubation suggests burrows may be a resource for breeding females. Competition among males for high burrows indicates the value of a burrow as a breeding site may be correlated with burrow elevation. If true, females may choose mates indirectly by preferring to breed in burrows located high on the beach. Although males may differ in many respects, differences in male size may be expecially apparent to females since components of the wave display and the intensity of the substrate vibrations produced during rapping differ among large and small males (Salmon and Horch 1972; Hyatt 1977b). Females may also receive information about the sizes of courting males when they descend their burrows since crab size (carapace length) and burrow diameter are strongly correlated (Christy 1982). I have examined mating preferences of individual females and mating patterns among marked crabs in an enclosed protion of a natural population to determine how female *U. pugilator* choose mates.

Materials and Methods

Study Site. The breeding ecology and mating behavior of *Uca pugilator* were studied during the summers of 1973–1976 on Cayo Pelau, a mangrove island located in Gasparilla Sound, 2.4 km northeast of Boca Grande, Lee County, Florida. Observations were made on several small (5–10 m wide), open sand beaches separated by mixed stands of red (*Rhizophora mangle*) and black (*Avicennia germinans*) mangroves.

Size Relationships. Size relationships between mated males and females were studied to determine if burrow diameter limits the sizes of males females of different sizes can choose as mates. Sizes (carapace length) of males and females in 85 mated pairs were obtained by measuring with a vernier caliper rule (0.02 mm accuracy) crabs dug from plugged burrows or by observing successful courtship sequences among marked and measured individuals.

Behavior of Females. A receptive female is here defined as one who ends a period of surface activity by remaining with a resident in a plugged breeding burrow. An unreceptive female is one who ends a period of activity by remaining in a temporary burrow. Since receptive and unreceptive females can not otherwise be distinguished without handling (Christy 1982), I observed the behavior or both classes of females. Females were selected arbitrarily for observation. Two types of observational records were obtained for receptive females. Complete records began when I observed females leave temporary burrows after high tide and begin responding to courting males or when I saw them move up the beach after feeding, enter the zone with breeding burrows, and approach courting residents. Partial records began when I first observed females already moving in the burrow zone and responding to residents. Only complete records have been used to detect mating preferences and to compute both the time females spent moving on the surface before they chose a mate and the number of males and burrows they sampled.

In addition to their final choice of burrows, I recorded the number of times each wandering female partially entered (checked) or descended breeding and temporary burrows and, if the burrow was a breeding burrow, whether or not the resident courted the female.

Temporal Distribution of Receptive Females. On 20 August 1975, I recorded the number of receptive females that moved through or chose a mate in a 3 by 1.5 m area located just below the upper limit of the distribution of breeding burrows on a small sand beach. Counts were made for the first 10 min of each quarter-hour from 900 h to 2000 h. From 62 to 69 residents courted in the area during peaks of activity. Females were judged receptive if they chose a mate or if they followed courting residents down their burrows three times in sequence and did not descend a temporary burrow.

Mating Patterns. Mating patterns with respect to male size and burrow elevation were studied in a portion of a natural population within a 3 by 6.5 m retangular area of beach positoned with the long axis perpendicular to the water's edge. A fence (0.5 m high) built of galvanized hardware cloth and aluminum sheeting prevented crabs from entering or leaving the area (see Christy 1978, 1980 for construction details). The enclosed area ranged in elevation from 0 to 60.8 cm above mean water level and extended approximately 1.5 m beyond the upper and the lower limits of the distribution of burrows. From 29 June to 13 July 1976, 300 females and 209 males were captured from inside the enclosed area, measured (carapace width (CW) and length (CL) on both sexes, length of the propodus (LP) of the enlarged chela on males only), marked by gluing a numbered plastic tag to the carapace, and returned. About 80% of the females and 90% of the males inside the fenced area were marked. From 15 July to 21 August, marked crabs were observed for an average of 5 h each day. All breeding burrows were flagged with numbered wooden stakes, their elevations were measured and their locations on the beach were mapped. I recorded daily which crabs fed, which males courted at which breeding burrows, which males attracted mates, and which females mated.

Matings were recorded either when (1) a female descended and remained in a breeding burrow, the resident plugged the burrow and it was closed for at least 1 day, or when (2) a resident, who had been courting, remained in a plugged burrow for at least 1 day, then opened the burrow and resumed courtship and defense. Two observations indicate the second sequence is a valid mating criterion. First, 27 breeding burrows were dug up 15 to 20 h after they had been plugged by residents. Females were not seen entering these burrows but all contained a male and female pair. Females in 8 burrows were ovipositing or carried recently laid eggs and the gonopores of all other females were open, providing anatomical evidence of sexual receptivity (Hartnoll 1968; Christy 1982). Second, residents who had not attracted females but had plugged their burrows (usually during high tide) always opened their burrows and resumed courtship within about 3 h. Matings judged by the first criterion will be called class 1 matings; matings judged by the second criterion will be called class 2 matings.

Two questions were asked concerning the location of matings. First, given the distribution of breeding burrows along the elevation gradient, did females mate in relatively high burrows? Second, where along the elevation gradient did matings occur? The location of matings relative to the location of breeding burrows was determined by dividing the area of the enclosed beach containing breeding burrows into 7 contiguous zones, each 3 m wide by 0.5 m deep, and comparing daily the relative frequency distributions of matings and breeding burrows over the 7 zones (Kolmogorov-Smirnov test, $\alpha = 0.05$).

When the distributions differed, the distances from the mean water mark of the burrows at which matings occurred were compared with the distances of the burrows at which residents failed to attract mates to determine if females mated in higher burrows (Mann-Whitney U-test, $\alpha=0.05$).

To determine if females preferred large males, the sizes of the males who mated each day were compared to the sizes of the males who courted but did not mate (Mann-Whitney U-test, $\alpha=0.05$). To control for the possible effects of burrow elevation on choice of large males, only those residents who courted from burrows in the zones in which females preferred to mate were included in the comparisons. When the distribution of matings did not differ significantly from the distribution of residents over the 7 zones of elevation the sizes of the successful males were compared to the sizes of all unsuccessful residents. For each day that the distributions of matings and residents differed, the zones in which females preferred to mate were identified by progressively truncating, from low to high, the distribution of breeding burrows until there was no significant difference between the two distributions (Kolmogorov-Smirnov test, $\alpha=0.05$). The sizes of the males who mated were then compared to the sizes of the males who failed to attract mates but who courted from burrows located at the preferred elevations.

Peaks of courtship and mating in the enclosed area occurred on 21 to 23 July and on 3 to 5 August (Christy 1978). For convenience, I have divided the observation period into two semilunar mating periods: the first beginning 15 July and ending 28 July, the second beginning 29 July and ending 11 August.

Physical Measurements. Tide heights were recorded by a gauge located near the shore of Cayo Pelau, 0.5 km or less from the study beaches. Mean water level is the arithmetic mean of hourly tide heights.

Burrow elevations were measured with a surveyor's transit-level to the nearest mm and are expressed relative to mean water level. Burrow locations are distances up the beach from the position of the water line at mean water level.

Analysis of mating patterns suggested female choice of breeding burrows may be related to maximum groundwater levels. Groundwater levels were measured in 4 standpipes (PVC plastic, 60 by 3.8 cm) located in the upper intertidal and supratidal zones at 2.2, 2.7, 3.2 and 3.7 m above the mean water mark on the beach with the enclosure. Maximum groundwater levels were determined for three high tides by measuring the height of the water in each pipe at 0.5 h intervals for 3 h periods beginning approximately 0.5 h before high tide.

Results

Size Relationships

Male and female sizes were correlated in 85 mated pairs (Fig. 1, $r=0.39$, $P<0.01$). Males up to 1.5 mm smaller than females of a given CL construct breeding burrows as wide or wider than temporary burrows occupied by females of that size (Christy 1982). Although some females mated with males smaller than themselves, none chose males too small to construct burrows wide enough for them to descend (Fig. 1). To determine if crabs paired by size, the sizes of females that mated with

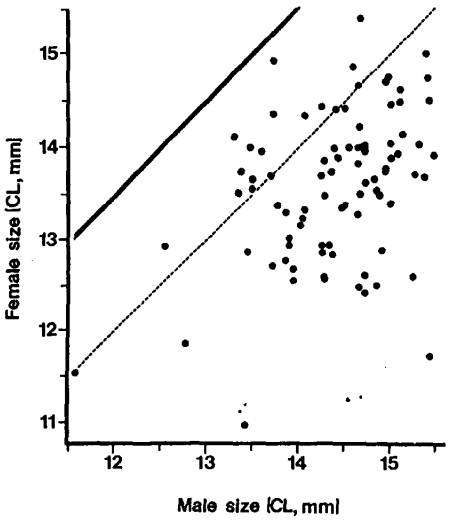

Fig. 1. Sizes of females and males (CL) in 85 mated pairs. *Broken line:* female and male sizes equal. *Solid line:* sizes of the largest females (male CL+1.5 mm) that can descend the burrows of males of given sizes

males in each of 5 size classes (interval widths of 0.5 mm CL) were compared by an ANOVA. There were no significant differences in the sizes of the females who mated with males rainging from 13.00 to 15.48 mm in CL ($F_{(4,78)}=2.04$, $P>0.05$).

The limit set by burrow diameter on the range in the sizes of males with which females of a given size can mate has been taken into account in the analysis of the preferences of individual females by eliminating males that were approached but were too small to defend burrows wide enough for the females to descend. Among the marked crabs in the enclosed population, I often knew neither exactly which females mated each day nor the sizes of the males each female approached before choosing a mate. Approximately 98% (155 out of 158) of the marked females that mated were 15.00 mm in CL or smaller. Since such females can descend the burrows of all males 13.50 mm in CL or larger, I have assumed that all residents that were at least 13.50 mm in CL could have mated with any female.

Behavior of Females

The responses of wandering females toward males and burrows depended on whether or not females were receptive (Table 1; G-test of independence, Sokal and Rohlf 1969, $G=194.58$, $P<0.005$). Receptive females tended to investigate breeding burrows more often (75% of all responses) than did unreceptive females (31% of all responses) ($G=73.12$, $P\ll0.005$). Receptive females also

Table 1. Burrow investigations by 30 receptive and 33 unreceptive females

State of receptivity	Type of burrow investigated						
	Temporary burrow		Breeding burrow				Totals
	Check	Descend	Male in burrow		Male courting		
			Check	Descend	Check	Descend	
Receptive	34	6	6	1	42	64	153
Unreceptive	88	84	30	13	21	12	248
Totals	122	90	36	14	63	76	401

checked or descended breeding burrows significantly more often when residents were courting (95% of all responses at breeding burrows) than when residents were in their burrows ($\chi^2=86.37$, $P<0.005$). In contrast, courtship had no apparent effect on the frequency with which unreceptive females investigated breeding burrows ($\chi^2=1.32$, $P>0.10$). Once a female approached a breeding burrow while a male was courting, her tendency to check or descend the burrow depended on her state of receptivity ($G=5.12$, $P<0.025$); receptive females followed courting males down their burrows approximately 60% of the time, whereas unreceptive females did so about 36% of the time. The frequency with which females checked or descended temporary burrows also depend on whether or not they were receptive ($G=15.24$, $P<0.005$); receptive females checked temporary burrows significantly more often (85% of the time) than they descended them ($\chi^2=19.60$, $P<0.005$), while unreceptive females checked or descended temporary burrows with approximately equal frequency ($\chi^2=0.09$, $P>0.50$).

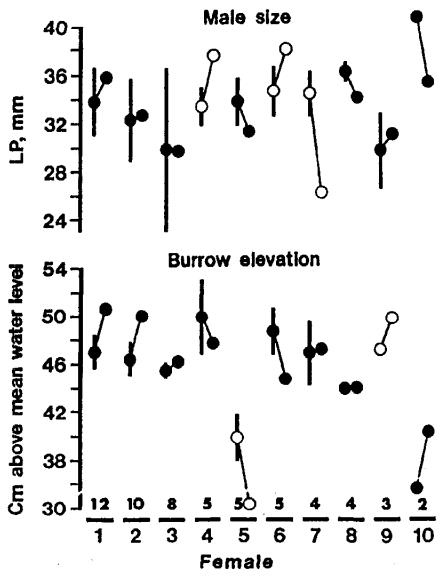

Fig. 2. Mating preferences of 10 females with respect to male size and breeding burrow elevation. *Lefthand symbol* of each pair: mean size (±SE, LP) of the males or mean elevation (±SE) of the burrows each female sampled and rejected; *right-hand symbol:* size of the male or elevation of the burrow each female chose. *Open circles:* sizes of chosen males or elevations of chosen burrows differ significantly from those rejected (*t*-tests, $\alpha=0.05$). Numbers above the x-axis indicate the number of males and burrows sampled

Temporal Distribution of Receptive Females

Eighteen receptive females were seen during the 11 h observation period on 20 August 1975, three of which chose mates from among the males courting in the 4.5 m^2 observation area. The temporal distribution of receptive females was bimodal: 5 were observed from 900 to 1130 h (one each 0.5 h interval) during flood tide, none were observed from 1130 to 1430 h, a period spanning high tide which occurred at approximately 1400 h, 12 were seen from 1430 to 1800 h during ebb tide, and one female was observed sampling males and burrows at dusk as she ascended the beach after feeding. Significantly more receptive females (72%) were seen during the 5 h interval after the mid-day high tide than during the 5 h interval before high tide (binomial test, Zar 1974, $P=0.048$).

Mating Preferences of Individual Females

Six females who responded to courting males soon after emerging during an ebb tide, sampled significantly fewer males and burrows (mean=3.2, range=1–9) than did 8 females who began sampling after feeding (mean=9.4, range=3–18) (Mann-Whitney *U*-test, $U=42$, $P<0.02$). The two

Table 2. Correlations between the sizes (LP, mm) of residents and the distances of their breeding burrows above the mean water mark in the enclosure containing marked crabs. *Asterisks* identify *P* values <0.05

First mating period				Second mating period			
Date	Number of residents	Correlation		Date	Number of residents	Correlation	
		r	*P*			*r*	*P*
July 15	7	0.41	>0.40	July 29	9	0.54	>0.10
16	5	0.23	>0.50	30	15	0.22	>0.40
17	8	0.44	>0.40	31	20	0.31	>0.10
18	10	0.02	>0.90	August 1	33	0.36	<0.05*
19	22	0.04	>0.50	2	30	0.24	>0.20
20	25	0.25	>0.40	3	41	0.36	<0.02*
21	32	0.03	>0.50	4	43	0.35	<0.05*
22	28	0.07	>0.50	5	42	0.53	<0.001*
23	34	0.09	>0.50	6	40	0.27	>0.10
24	26	0.13	>0.50	7	24	0.43	<0.05*
25	24	0.16	>0.40	8	20	0.44	<0.05*
26	14	0.26	>0.20	9	5	0.37	>0.50
27	18	0.32	>0.10	10	7	0.25	>0.50
28	10	0.50	>0.10	11	4	0.43	>0.50

groups of females spent about the same amount of time sampling (mean=9.5 min, $U=32.5$, $P>0.10$).

Mating preferences were determined by comparing the sizes (LP) of the males females chose as mates with the sizes of the males they sampled and rejected, and the elevations of the burrows they chose with the elevations of the burrows they rejected. Comparisons were made for 10 complete records of the behavior of receptive females that sampled 2 or more males and burrows. Females showed no consistent preferences for mating with larger males or in higher burrows among those they sampled (Fig. 2). Movements of females between pairs of burrows and pairs of males were analyzed to determine if females tended to move from lower to higher burrows, from smaller to larger males, or both. No receptive female moved so as to encounter sequentially larger males or higher burrows (binomial test, $\alpha=0.05$). Females neither chose large males directly nor indirectly by choosing relatively high burrows. Three females chose the first male they approached and 1 the second, suggesting choice based on absolute criteria.

Mating Patterns

Correlations Between Male Size and Burrow Elevation. The mating patterns that are expected under the operation of female choice based on male size or burrow elevation depend on whether or not these factors are correlated. To be able to reliably infer mating preferences from mating patterns in the encolsed area, correlations between the sizes of residents and the locations of their burrows on the elevation gradient were determined for each day of both mating periods. Male size (LP) was correlated significantly with burrow location only on 6 days during the second mating period (Table 2).

The Location of Matings. Twelve class 1 and 15 class 2 matings were recorded during the first mating period in July. Eighteen class 1 and 22 class 2 matings occurred in early August during the second mating period. The distribution of matings differed significantly from the distribution of breeding burrows only on 2, 3, 4, and 6 August when the burrows females chose were located significantly higher on the beach than the burrows of males who courted but did not attract mates (Fig. 3).

The distances above the mean water mark of the burrows females chose depended on the heights of the higher semidiurnal high tides (Fig. 3). During the first mating period, tide heights increased from 3 to 30 cm above mean water level and females tended to mate in higher burrows later in the period. During the second mating period, tides were high initially, declined for 3 days, then rose to relatively high levels (20 to 25 cm above mean water level) on 2 to 7 August when most (80%) matings occurred. The locations of matings varied little during this 6 d period; females mated in high burrows on all days and significantly higher burrows on 2, 3, 4, and 6 August. If burrows are a resource for breeding females, choice of high

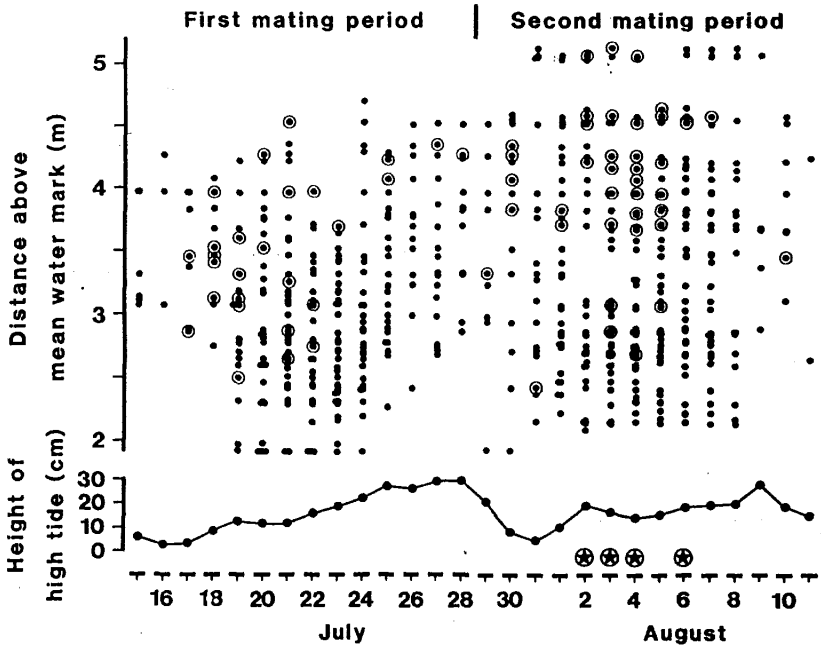

Fig. 3. Distances above the mean water mark in the enclosed area of all courting residents (*dots*) and recorded matings (*circled dots*) on each day of both mating periods. *Circled stars:* dates on which the distributions of matings differed significantly from the distribution of breeding burrows over 7 zones of elevation and females chose significantly higher burrows among all those available. Heights of the higher semidiurnal high tides are also shown

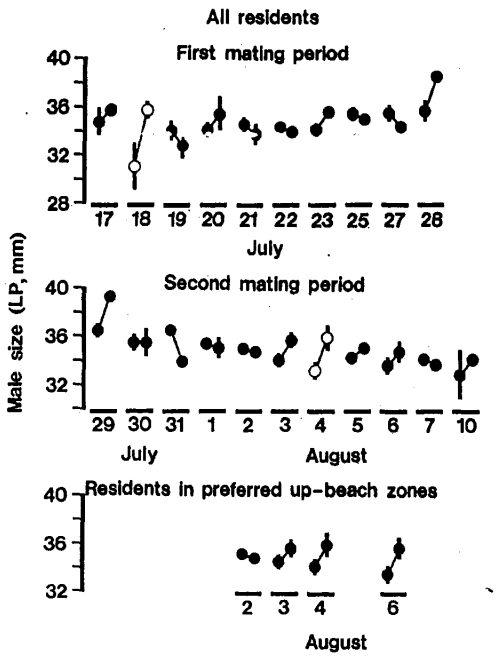

Fig. 4. Mean sizes (±SE, LP) of mated and unmated males in the enclosed area on each day of both mating periods. *Left-hand symbol* of each pair: mean size of the males who courted but did not mate; *righthand symbol:* mean size of the males who mated. *Open circles:* sizes of the males who mated differ significantly from those who did not mate (Mann-Whitney *U*-tests, $\alpha = 0.05$)

burrows during periods with high tides suggests that burrow quality may be correlated with distance above the water mark at high tide.

Female Choice Based on Male Size. Females tended to mate high on the beach when resident size and burrow elevation were correlated significantly (Fig. 3 and Table 2), suggesting females may have preferred large males. Females showed no consistent preference, however, for mating with large males (Fig. 4). The males who mated were larger than those who did not mate on 11 out of 21 days, but females chose significantly larger males only on 18 July and 4 August. In addition, females did not choose significantly larger males considering only these courting from burrows in the preferred zones on 2, 3 and 6 August (top 5 zones) and on 4 August (top 4 zones). Choice of large males on 3 to 6 August, and significantly larger males on 4 August probably reflects a tendency for females to mate in relatively high burrows on these days, not a preference for large males. Females mated with males smaller or larger than those available with approximately equal frequency on the remaining 17 days (binomial test, $P = 0.48$).

Female Choice of Structurally Stable Burrows. Breeding burrows in the relatively homogeneous sand beaches on Cayo Pelau collapsed when they were covered by the tide or flooded by groundwater (Christy 1980). Twenty-five of the 200 breeding burrows in the enclosed area were covered by the tide at least once within 2 weeks after they were last occupied by residents. However, only 1 of the 67 females who mated chose a burrow that was inundated during her 12–14 d breeding period, suggesting choice of supratidal burrows may reflect a preference for breeding in burrows that will not collapse due to tidal flooding.

Choice of burrows located high in the supratidal zone during periods with high tides suggests females also may have preferred burrows that were high enough to escape collapse due to flooding by groundwater, at least during the initial stages of breeding. To evaluate this possibility, I have determined whether daily changes in the lower limit of the distribution of matings corresponded to changes in the position on the beach above which the terminal chambers of breeding burrows would not be flooded by groundwater for at least 4 tidal cycles. Since females usually mate and complete oviposition within about 1.8 d after they choose a mate (Christy 1978), 4 tidal cycles would provide sufficient time for most females to begin incuation. Breeding burrows on the beaches of cayo Pelau had a minimum depth of about 16 cm (Christy 1980). Hence the position on the beach above which breeding burrows would escape flooding (the flooding threshold) while a female mated and laid her eggs would correspond to the position at which the highest groundwater level during the 4 tidal cycles following mate choice would just reach 16 cm below the beach surface. To locate the position of the flooding threshold for burrows of different depths on each day of both mating periods it was necessary to determine how maximum groundwater levels changed in relation to tide height.

Maximum groundwater levels in the 4 standpipes in the supratidal zone were directly related to high tide heigths (regression equations: pipe 1, $y=1.021x+1.165$ cm; pipe 2, $y=0.875x+4.085$ cm; pipe 3, $y=0.785x+5.444$ cm; pipe 4, $y=0.652x+7.182$ cm where y = maximum groundwater level and x = high tide height). Predicted maximum groundwater levels in each pipe for high tide heights ranging in 1 cm increments from 0 to 35 cm above mean water level were plotted against pipe location. Curves were fitted by eye between these values producing profiles of maximum groundwater levels at locations between the pipes for each high tide height. This graphical model was used to determine the locations of the flooding thresholds for burrows of different depths.

The locations of the lowest burrows females chose correspond closely to the positions of the flooding thresholds for burrows 14 to 16 cm deep (Fig. 5). By choosing high burrows during periods with high tides, 62 out of 67 females (93%) chose burrows that escaped flooding by groundwater during mating and oviposition. However, 24 females chose burrows that were flooded sometime during their incubation periods (assuming a burrow depth of 16 cm). Either burrow flooding

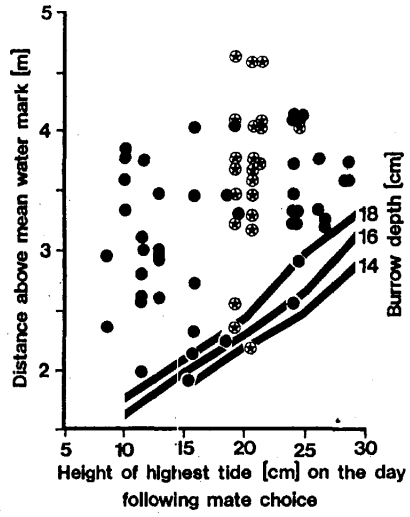

Fig. 5. Distances above the mean water mark of matings recorded in the enclosed area in relation to the heights of the highest high tides on the days following mate choice. *Circled stars:* as in Fig. 3 *Heavy lines:* positions of the flooding thresholds on the days following mate choice for burrows 14, 16 and 18 cm deep

and collapse are unimportant to females who have completed oviposition, or females are unable to judge accurately which burrows will escape flooding beyond 1 or 2 d. The behavior of females who chose relatively low burrows indicates the latter alternative is most reasonable. Two unmarked and 3 marked ovigerous females who mated on 17, 21 and 22 July, emerged from low supratidal burrows on 26 July shortly after the mid-day high tide which reached 24.5 cm above mean water level. An additional unmarked female emerged after the tide peaked at 28.5 cm above mean water level on 27 July. The burrows these females left were about 0.5 m above the water mark at high tide but all probably were flooded by groundwater and had collapsed. Each female moved 1 to 1.5 m up-beach to a new burrow. I did not see the marked females on the surface again until after they released their larvae. Burrows that flood and collapse probably are unacceptable for both oviposition and incubation.

Discussion

The Mating System

The spatial and temporal distributions of female *U. pugilator* and sites suitable for breeding appear to have strongly influenced how males compete for females and how females select mates. Nonbreeding females were mobile, moving each tidal cycle between temporary burrows located approxi-

mately 35 to 45 cm above mean water level and areas in the lower intertidal zone where they fed. Field experiments on Cayo Pelau demonstrated that substrates adjacent to supratidal burrows lacked sufficient food to stimulate feeding, explaining why non-breeding crabs migrated daily to feed in low, moist, food-rich areas (Christy 1980). Similar movements of nonbreeding crabs have been reported for this species in other habitats (e.g., Herrnkind 1968; Robertson et al. 1980) and may result from rapid depletion of food near burrows soon after crabs emerge and feed (Robertson et al. 1980).

Female *U. pugilator* bred in burrows that were at least 16 cm deep and that escaped flooding and collapse during mating and oviposition, if not the entire breeding period. The locations of such burrows changed daily but never overlaped with where females fed. There appears to be little opportunity for females to defend, or even to remain near good breeding sites; females who have fed long enough to produce a clutch (probably about two weeks, Christy 1980) must locate both a mate and a place to breed. I suggest that breeding burrows with stable terminal chambers are a resource required by females for successful reproduction. Feeding females are highly mobile, do not form stable groups and probably are not directly defensible by males. Burrows, however, are point resources and males compete for and defend them as a way of obtaining mates. Since females permit sexual access to males who defend suitable breeding burrows, males can extract the benefits of resource defense (Christy 1980). *U. pugilator*'s mating system may be classified as resource-defense polygyny.

Female Behavior

With few exceptions, females responded to males and burrows as expected given their states of sexual receptivity (Table 1). Unreceptive females sometimes (31%) investigated breeding burrows, even when courted by residents. Non-breeding crabs occasionally entered and plugged breeding burrows when residents were below (most were quickly evicted), suggesting unreceptive females either can not distinguish breeding from temporary burrows, or they find both suitable (if unoccupied) as refuges during high tide. Some females, who were classified unreceptive, approached courting males and checked or descended their burrows. Perhaps such females do not encounter suitable males or breeding sites when they first sample and, therefore, they sample males and burrows during more than one period of wandering.

Receptive females spent little time sampling, moving rapidly from one burrow to the next, but they often paused at and checked (but rarely descended) temporary burrows. Predators of crabs were abundant on Cayo Pelau and I observed predation frequently (Christy 1980). Most crabs were taken when they were on the surface away from burrows. White ibis (*Eudocimus albus*), a common predator, preferred females; a differential escape response between the sexes indicates other avian predators may share this preference. *Uca* sp. use a kinesthetic sense to locate nearby burrows quickly when disturbed (Altevogt and von Hagen 1964). Receptive females who stop frequently at temporary burrows may minimize their risk of being eaten by always being able to retreat quickly to a burrow when threatened.

Some females mated in the first or second burrow they descended, suggesting females may choose stable burrows by assessing directly cues associated with burrows themselves. Most females sampled males and burrows from 0.5 to 3.5 h after high tide, the period when groundwater levels were highest in the supratidal zone. By sampling during this interval, females may have avoided burrows that were certain to flood simply by rejecting those that already were flooded. Since tide heights increased during most of both mating periods, discrimination of collapsed and intact burrows would not necessarily lead to choice of burrows that would remain stable throughout a female's breeding period. Females also may use cues such as the moisture content of sand in terminal chambers to select burrows that remain intact for several days. Nevertheless, neither criterion would be useful to females who sample late in a tidal cycle, and neither would be a good predictor of burrow flooding late in a female's breeding period. Cues that are good predictors of long-term burrow stability simply may not be present or perceptible to females, which may explain why some females chose burrows that collapsed during incubation.

Choice of Breeding Sites

The effects on female reproductive success of burrow flooding and collapse during breeding may produce selection for the preference females exhibited for stable burrows. Female brachyuran crabs appear especially susceptible to egg loss if disturbed during oviposition. Events during oviposition include, in sequence, extrusion of fertilized eggs from paired openings on the 6th thoracic ster-

nites, retention of the semifluid mass of newly laid eggs in the space between the sternum and the deflexed abdomen, and gradual attachment of eggs to seatae on the endopodites of the abdominal appendages (Cheung 1966; Hartnoll 1968, and references therein). Females of several semiterrestrial (Henning 1975; Klaassen 1975) and aquatic (Broekhyusen 1936; Cheung 1966; Norse and Fox-Norse 1977) species select sites for oviposition and othewise behave in ways that minimize their exposure to disturbances that cause loss of unattached eggs.

Flooding and collapse of low burrows may be a potential cause of egg loss by ovipositing female *U. pugilator*. On three occasions I encountered ovipositing females while excavating breeding burrows. Collapse of these burrows caused each female to loose nearly all unattached eggs. Three other females were experimentally disturbed during oviposition: two were covered with saturated sand, one about 1 h and the other about 6 h after onset of oviposition, the third was placed in a dish and covered with seawater at an unknown time after she began to lay eggs. All treatments resulted in extensive egg loss. By selecting supratidal burrows that will not be flooded by groundwater during the first few days of breeding, female *U. pugilator* may minimize loss of reproductive success due to egg loss during oviposition. Although females probably also require burrows with terminal chambers that remain intact and, perhaps, free of groundwater in which to tend their developing eggs, they apparently are not able to choose such burrows with certainty. The structural stability of a breeding burrow appears to be a primary determinant of its quality as a site both for oviposition and for incubation.

Females may have discriminated among burrows located above the flooding threshold on the basis of other unknown factors that affected their quality as breeding sites. This seems unlikely, however, because the larger the number of factors that affect burrow quality, the lower the abundance of high quality burrows and the greater the probability that large males would exclude small males from the best breeding sites. Hence female choice based on resource quality alone probably would have resulted in choice of large males.

Choice Based on Male Size

I found no evidence that female *U. pugilator* preferred larger males among those defending burrows of equal quality as measured by their stability during mating and oviposition. In contrast Hyatt concluded that "... larger high-beach males are preferred by females ..." at a site in North Carolina (Hyatt and Salmon 1978). Hyatt's conclusion was based on an apparent tendency for females to more frequently, approach, pause by, check, descend or remain in the burrows of large rather than small males (Hyatt 1977a, only one probable mating was observed). There are at least three reasons why Hyatt's and my conclusions differ. First, since Hyatt did not distinguish receptive and unreceptive females, an unknown proportion of the responses he scored was probably made by females who were not seeking mates. Second, Hyatt may actually have recorded a tendency for females to sample and reject males of different sizes, since only one of the responses he scored leads to mating. Third, Hyatt failed to control for the possible effects of burrow location on the responsiveness of females to residents. Large males at the North Carolina site were found higher on the beach than small males, presumably because stable burrows could be constructed in such areas. Hence, Hyatt may have recorded a tendency for females to sample males and burrows in areas likely to contain suitable breeding sites, not a tendency for females to respond preferentially to large males. At present, there is no convincing evidence that female *U. pugilator* prefer to mate with large males. What has prevented the evolution of a female preference for large males?

Conditions Favoring Choice of Large Males. The failure of female *U. pugilator* to prefer large males does not appear to be a consequence of a lack of the opportunity to do so. Field experiments demonstrated that the highest level at which males could dig and maintain breeding burrows was determined directly by the moisture content of surface sand and varied little, averaging about 5 m above the mean water mark (Christy 1980). In contrast, the position of the flooding threshold changed daily, moving up-beach as tide heights increased during each mating period. Males at low burrows responded to the rise in the position of the flooding threshold by reducing the depths of their burrows (Christy 1982) or by abandoning them. The frequency with which males who abandoned low burrows obtained new ones above the flooding threshold was strongly and negatively correlated with the density of larger residents defending such burrows ($r = -0.99$, $P \ll 0.001$). On most days during both mating periods the area above the position of the flooding threshold was large enough to accommodate nearly all males who sought burrows; males who courted from burrows

in the zones in which females mated averaged 34.52 mm LP with a mean coefficient of variation (CV) of 7.8%. On 6 days during the second mating period, the density of competitors relative to the area above the flooding threshold was high enough so that large males excluded small males from upbeach burrows. On these days, residents in the zones females preferred were larger and varied less in size, averaging 35.41 mm LP with a CV of 4.5%, though these differences are not significant (Mann-Whitney U-test: sizes compared, $U=43$, $P>0.10$; CVs compared, $U=34.5$, $P>0.05$). Hence, females always chose mates from an array of males who differed in size but who courted from burrows of equal quality with respect to their expected structural stabilities during the first few days of a female's breeding period.

Females who choose large males might gain in fitness in several ways over those who do not discriminate among potential mates on the basis of size. Aggressive wandering males, as well as non-breeding crabs, frequently opened and entered breeding burrows that had been plugged by residents who had attracted mates. Residents usually were successful in removing non-breeding crabs but they sometimes lost their burrows and their mates in fights with wanderers. Disturbances by intruders may adversely affect female reproductive success: copulation might be interrupted, females might be forced to look for another mate and breeding site, or, if an intrusion occurred during oviposition, females might loose eggs. Since fighting ability is correlated with size, large males would be better able to remove intruders than would be small males. By choosing a large male, a female might minimize her chance of being disturbed during breeding.

Females who choose large males might also gain ultimately by producing offspring who will tend to maximize growth times survival (Trivers 1976). Since competence in intrasexual competition and mating success are correlated with male size (Christy 1980), females who choose large males might also be assured of producing male offspring who would be more successful in competition for mates than those produced by females who choose smaller residents.

Costs of Choosing Large Males. Females who choose relatively large males among those defending preferred burrows will gain most when the variance in the sizes of males at such burrows is large. Assuming females must compare males to choose by size, the greater the variance in male size, the more males a female must sample to choose reliably one larger than the mean. The conditions most favoring choice of large males require females to sample many before choosing. There appear to be costs associated with the lengthy sampling necessary for female *U. pugilator* to choose large males. Frequent observations of predators and the behavior of receptive females suggest the longer a female samples, the greater may be her risk of predation. In addition, females who delay mate choice may find suitable burrows and large males increasingly rare due to choice by other females. Most females mated during 4 to 5 day periods which occurred twice each lunar month (Christy 1978) and most sampled soon after emerging from temporary burrows. During mating peaks, from 40 to 70% of the males at burrows above the flooding threshold mated each day. I suggest a relatively high risk of predation and low probability of finding a high quality burrow are costs that may exceed the gains to females who sample long enough to choose both a high quality burrow and a large male.

Finally, the variance in the sizes of the males defending burrows at the preferred elevations changed daily, suggesting the conditions most favoring females who sample for long periods before choosing were ephemeral. Only females who could 'predict' when the gains from sampling many males before choosing by size would exceed the costs would be more successful than those who only discriminate among burrows. It is difficult to imagine a behavioral mechanism that would permit this kind of judicious flexibility in mate choice by female *U. pugilator*.

Most theoretical discussions of the evolution of female choice have focused on comparing the relative net gains in fitness among females who breed at different times and sites, and with different males (e.g., Orians 1969; Borgia 1979; Wittenberger 1979). Fitness costs are commonly limited to those effects on reproductive success that are direct consequences of different choices. The results of this study emphasize that costs associated with the sampling behavior necessary for females to choose mates in different ways also must be considered in order to account for the evolution of mating preferences (see also Janetos 1980).

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