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## **Pillar Function in the Fiddler Crab *Uca beebei* (I): Effects on Male Spacing and Aggression**

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*With 5 figures*

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### **Abstract**

Males of 14 species of fiddler crabs (genus *Uca*) are known to build structures out of mud or sand at the entrances to burrows they court from and defend. A study of spacing, space use and aggression between courting male *Uca musica* (ZUCKER 1974, 1981) suggested that the hoods males build reduce territorial overlap and rates of aggression between neighboring males. Thus, each male may have more time to court females during limited lunar, diurnal and tidal mating periods.

I studied the courtship and aggressive behavior of male *Uca beebei* in the field to determine if the pillars males of this species build affect male behavior as do the hoods of *U. musica*. *U. beebei* occurs sympatrically with *U. musica* on the Pacific coast of Panama and is broadly similar in its ecology and mating behavior. Unlike the hoods of *U. musica*, pillars did not focus a male's activity space away from its closest neighbor nor did they reduce either overlap with neighbors' activity spaces or rates of aggressive interaction among neighbors. Pillar builders courted more but also fought their neighbors more than did males that did not build pillars. The pillars of *U. beebei* and the hoods of *U. musica* affect male behavior differently and probably have different functions.

### **Introduction**

Reproductively active males of at least 14 species of fiddler crabs (genus *Uca*, approx. 80 species) build structures out of moist sand or mud at the entrances of their burrows in the intertidal or supratidal zone on protected shores. Four species [*U. pugilator* (CHRISTY 1982; Fig. 1 a), *U. pugnax* (GREENSPAN 1984), *U. minax* (BASAN & FREY 1977), *U. tangeri* (MÜLLER 1983)] build low, massive semidomes on one edge of their burrow entrance, and two species [*U. panacea* (SALMON et al. 1978), *U. galapagensis* (von HAGEN 1968)] build rims around the burrow opening. 8 species build more delicate vertical structures which range from tall, wide hoods [*U. musica* (ZUCKER 1974; Fig. 1 b), *U. leptodactyla*

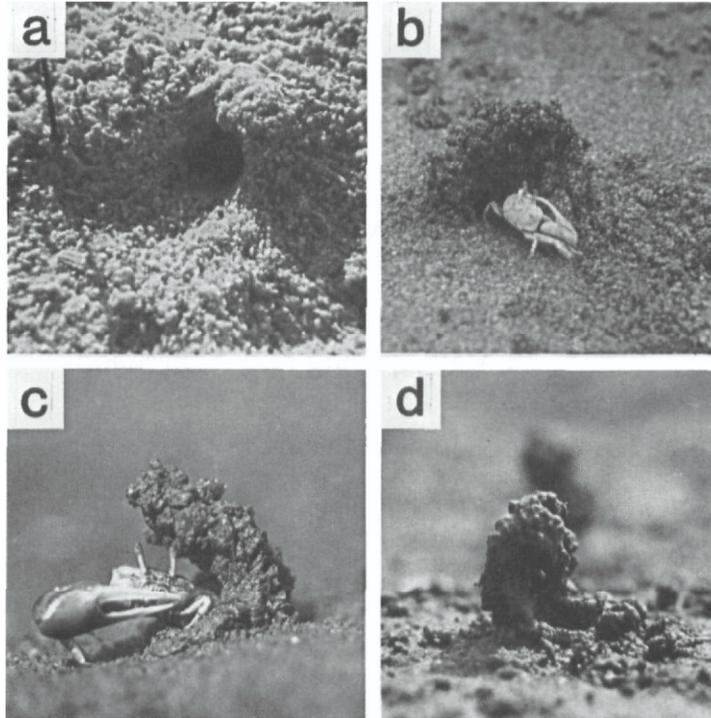


Fig. 1: Structures built by courting male fiddler crabs: a: semidome (*U. pugilator*), b: hood (*U. musica*), c, d: pillars (*U. beebei*)

(MATTHEWS 1930), *U. cumulanta* (CRANE 1975)] to tall narrow columns or pillars [*U. beebei* (Fig. 1 c, d), *U. lactea* (YAMAGUCHI 1971; LINSENMAIR 1967), *U. latimanus* (ZUCKER 1981), *U. dorotheae* (VON HAGEN 1968), *U. stenodactylus* (MÜLLER 1986)].

Burrow holding males of all structure-building species threaten and fight neighboring resident males and wandering males who fight for burrows. The burrows males defend are courtship, mating and probably oviposition and incubation (breeding) sites in most of these species (CHRISTY & SALMON 1984).

Explanations of the value of these structures to the males that build them are based on their possible function in courtship or in burrow defense and aggression among neighbors. SALMON & ATSAIDES (1968) proposed that the semidomes of *U. pugilator* might focus the sonic energy in the courtship signal males produce by rapping on the sand, thereby increasing a male's "calling range." This hypothesis was abandoned when it was discovered that females sense the substrate vibrations rapping produces but not its airborne components at natural intensities (SALMON & HORCH 1972). Observations of how males defend their burrows (HYATT & SALMON 1978; CHRISTY 1980) suggested the yet untested hypothesis (CHRISTY 1982) that semidomes might aid males in burrow defense by providing a firm brace and object to grip during the forceful stages of combat.

There are two hypotheses for the function of pillars and hoods. CRANE (1975, p. 525) thought that they may provide visual cues that females use to locate the entrance of a male's burrow after he enters it at the end of the courtship sequence. I evaluate the role of pillars in the courtship behavior of *U. beebei* in the subsequent paper (CHRISTY 1988).

ZUCKER (1974, 1981) developed the second hypothesis to explain why male *U. musica*, and perhaps *U. beebei* and *U. latimanus*, build hoods and pillars. ZUCKER'S hypothesis is based on the following observations. (1) Males court only for a few hours each diurnal low tide period and on a few days each lunar cycle. (2) Males do not always build hoods; disproportionately more are built where courting males occur at high densities. (3) Males that are visually isolated experimentally from their neighbors seldom build hoods. (4) Males vigorously defend, spend most of their time and have fewer close neighbors in the semicircular area in "front" of their hood. (5) Males fight their neighbors more when their hoods are removed than when their hoods are present. (6) Hood builders tend to be smaller than males that do not build hoods. ZUCKER proposed that hoods signal that a male will neither be active in nor defend the area behind its hood. Neighboring residents and males establishing new burrows might read the signal and adjust their activity spaces and burrow locations such that overlap of activity spaces and rates of aggressive interactions are minimized. This might give males more time to court during the limited courtship period. Hood building is especially important for small males because it allows them to avoid fights with larger males and possible displacement from their burrows (ZUCKER 1977). Finally, ZUCKER noted that the smaller, asymmetrical territories of males with hoods would permit more males to court in a given area. She suggested that females may more often choose mates where courting males are dense (ZUCKER 1974, 1981).

The purpose of this research was to test ZUCKER'S hypotheses as it might apply to the function of the pillars built by courting male *U. beebei*. *U. beebei* and *U. musica* are relatively small (about 1 cm carapace width as adults) species that often occur within a few m of each other on open tidal flats on the Pacific coast of the tropical Americas (CRANE 1975).

Preliminary observations indicated that *U. beebei* usually occurs lower in the intertidal zone (muddy sand flats) and at higher maximum densities than does *U. musica* (sand beaches and bars). ZUCKER (1978) found that wandering by female *U. beebei* (some, presumably, receptive) and courtship by males follow a lunar cycle. Hence, time spent courting may also limit mating rates of male *U. beebei*. Since courting males occur at high densities, it might be especially advantageous for males to employ mechanisms such as pillars to reduce rates of aggression with neighbors.

## Methods

### Study Sites

I studied *Uca beebei* and its pillars from May through mid-Sept. 1985 at two intertidal flats, "Diablo flat", in Diablo Heights on the east bank of the Panama Canal, about 2.5 km from its entrance to the Pacific Ocean, and "Rodman flat" near Rodman Naval Base on the west bank of the Canal, 1

km from the Bridge of the Americas. Diablo flat is a nearly level strip (2 to 4 m wide) of muddy sand bordering mangrove forest at the top of a gently sloping tidal creek bank. Rodman flat is roughly fan-shaped and lies at the intersection of two tidal creeks, about 30 m seaward of the mangrove forest. Crabs were more abundant on the creek banks than on the relatively level top of Rodman flat. *U. beebei* occurred at high densities (50 to 200 burrows/m<sup>2</sup>) at both sites and in nearly monospecific colonies covering 80 to 100 m<sup>2</sup>. Tides ranged in amplitude from approx. 2.5 to 6 m. Both flats were submerged by all high tides and exposed by all low tides for about 4.5 h. Crabs were not active on the surface before sunrise, after sunset or during heavy rain.

### Sizes of Courting Males, Burrow Spacing and Orientation

Approx. 1 h before low tide, before most males began to build pillars, small numbered wooden stakes were placed near the burrows of all males that waved their large chela (courted) in plots (1–4 m<sup>2</sup>) on the Diablo flat. Observers left the flat, returned 2–2.5 h later and recorded for each burrow: (1) the presence of a pillar, (2) pillar height, (3) burrow diameter (BD) 1 cm below the surface, (4) the distance to the nearest courting male, (5) the presence of a pillar on this burrow and (6) the direction ( $\pm 5^\circ$ ) of the neighbor relative to a line normal to the frontal plane of the pillar. Males were dug out of their burrows in two different areas on the final two days these measurements were made. The carapace length (CL) and width (CW) and the length of the propodus of the large chela (LP) of each male was measured with vernier calipers (0.02 mm precision).

### Timing of Pillar Building in the Tidal Cycle

Beginning 1 h before low tide (LT), I counted, at 5-min. intervals for the next 3 to 3.5 h, the number of courting males and the number of pillars on 10 .75 m<sup>2</sup> plots. The counts were made on 4 days at Diablo and 3 days at Rodman. Two plots were observed on 3 of the 7 days. The times of LT were taken from tide tables for Balboa (located less than 2 km from both study sites). LT on these 7 days occurred during every h-interval between 07.00 and 14.00 h.

### Effects of Courting Male Density and the Lunar Cycle

Two .75 m<sup>2</sup> plots were delimited with twine and wooden stakes at Rodman on 13 Aug., one on the bank where courting males were abundant, the other on the top of the flat where fewer males courted. I counted the number of courting males and the number of pillars on each plot daily for the next 26 days except when it rained heavily during low tide and when low tides occurred at dawn and dusk. Each day, beginning 1 h after LT, five counts at 5 min. intervals were made for each plot. I have used the maximum of the five daily counts of the number of males courting in each plot to estimate densities. The number of pillars did not vary among counts for each plot and day.

### Aggression, Space Use and Time Budgets

On 7 days (15–21 Aug.) the location and behavior of males that defended burrows were recorded on 50 by 50 cm square plots located on the banks of the Rodman flat. The plots were divided into 5 by 5 cm squares by a fine twine net which was staked to the substrate. Each square was further divided mentally into four quadrants, 2.5 cm<sup>2</sup>. The net was placed on the ground about 1.5 h before LT, all burrows (> .5 cm diameter) were marked with numbered toothpicks, their locations were recorded on scale maps and the sex of the crab at each burrow was noted. Two observers then sat 1–3 m away. Beginning at about 1 h before LT, one observer recorded the activity and location of each crab every 5-min. for 3–3.5 h, stopping about 20-min. before the flat was flooded by the rising tide. Crab behavior was recorded with respect to 11 categories (Table 1). Crab locations were recorded to the nearest quadrant. The other observer watched 1–3 males on the plot continuously and recorded the time, location and type of every agonistic interaction of each male. An agonistic interaction was scored each time a male gave or received a threat or fought another crab (Table 1). I saw only 8 combats in total of 260 interactions. The rates of aggressive interaction reported here are primarily the rates at which males gave, received or exchanged threats.

Statistical tests and procedures for data analysis follow SOKAL & ROHLF (1981), ROHLF & SOKAL (1981) and ROHLF (1984). An alpha level of 0.05 was used to reject null hypotheses.

Hereafter the acronyms P and NP will be used for males that did and those that did not build pillars, respectively.

Table 1: Categories used to score the behavior of male *Uca beebei*

Category	Description
In burrow	Crab in its burrow and can not be seen or motionless and partially visible in its burrow entrance.
Nothing	Crab motionless on the surface in a relaxed posture
Pose	Crab raised on the dactyls of its nearly straight walking legs, often with the dorsal surface of its carapace facing and inclining slightly toward the sun. Large chela usually extended laterally with its tip touching the ground. May remain in this posture for several min. Common at the beginning of the activity period.
Clean	Crab grooms parts of its body with its small chela and rubs its walking legs together.
Dig	Crab alternately enters its burrow and returns to the surface carrying material from inside its burrow and depositing it, usually > 10 cm from the burrow's entrance.
Build pillar	Male gathers material from the surface and stacks it at its burrow entrance to form a pillar.
Feed	Crab walks slowly, removes bits of substrate from the surface with its small chela, places them between its third maxillae and wipes small pellets of substrate from the bottom of its buccal region.
Wave-feed	Male rhythmically raises and extends its large chela while walking and feeding.
Wave	Same as above but not feeding. Female usually near. Male alternately moves toward its burrow and back slightly toward the female. Category includes a movement in which the male orients its major chela toward the female and raises its carpus to its highest extent but does not extend the claw. This exposes the dark ventral surface of all segments of the cheliped directly to the approaching female.
Threat	Movements and posture males direct to other crabs, usually males, that do not involve interdigitation of males' chelae. The eight subcategories include approach, chase, lateral chela, flick chela, kick, duel, dip-down and flat chela.
Combat	Movements or postures in which males' chelae usually are intertwined. Includes reach, dig-out, interdigitation, grip, attempted flip and flip.

## Results

### Pillars and Pillar Building

Male *U. beebei* build pillars by scraping muddy sand from the surface, carrying it with their walking legs (either side of the body) to their burrow and stacking it at one edge of their burrow entrance. Males usually moistened the sand with water, which was expressed from their buccal area and presumably drawn from their branchial chambers, as they tamped it into place with their walking legs and minor chela. Males entered their burrows between trips to gather and deposit sand and emerged glistening wet. They probably replaced branchial water

lost during pillar building with water drawn from moist sand at the bottom of their burrows. Males built pillars in about 9.5 min (based on the pooled time budgets of 19 P males, see Fig. 5).

Completed pillars had the general form of truncated lumpy cones with a slight hollow on the side facing the burrow entrance. Pillars often had an overhang at the top and a flared base that extended around the burrow entrance as a low raised lip (Fig. 1 b, c). Pillars averaged  $14.9 \pm 2.62$  mm wide at the base ( $N = 67$ ) and  $20.6 \pm 4.01$  mm high ( $N = 73$ ). Pillar height increased significantly, but only slightly with male size (pillar height (mm) =  $10.41 + 1.27$  BD (mm),  $F_{s(1,71)} = 4.914$ ,  $p < 0.05$ ; BD is correlated with male CL:  $r = 0.64$ ,  $N = 75$ ,  $p < 0.001$ ).

84 of 240 courting males observed on ten plots built pillars. Some (14 %) built their pillars before observations began, 1 h before LT. Pillar building continued for approximately the next 2.5 h with 50 % of the pillars built by LT and all of them built by 1.5 h after LT. Pillars often were damaged from apparently incidental contact by wandering crabs and by the males that built them. However, some males, with apparent intent, knocked over their pillars near the end of the activity period. Males usually repaired their pillars but not when they were damaged late in the activity period; pillars declined in number to about 80 % of the maximum by 2 h after LT.

#### Courtship Activity over a Lunar Cycle

The numbers of courting males on the two  $.75 \text{ m}^2$  plots on the Rodman flat did not vary significantly over the 26-day observation period but differed between the two plots (Fig. 2; 2-way ANOVA: days,  $F_{s(22,22)} = 1.159$ ,  $p > 0.25$ ; plots,  $F_{s(1,22)} = 147.987$ ,  $p < 0.001$ ). The density of courting males averaged

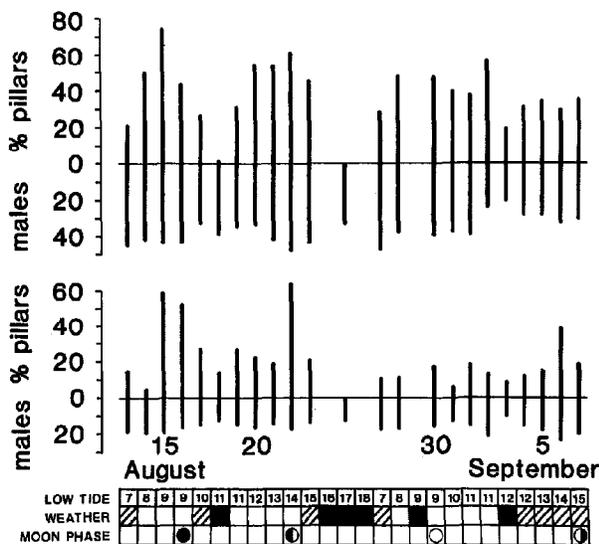


Fig. 2: Daily variation in the number of courting males and the % with pillars 1–1.5 h after LT on two  $0.75\text{-m}^2$  plots located on the bank (upper scale) and on the top (lower scale) of the Rodman flat. The time of LT (h intervals), clear (open squares), cloudy (hatched squares) and rainy (solid squares) weather and the moon phases (solid circle is the new moon) are also shown

$49.7 \pm 6.12$  males/m<sup>2</sup> on the bank and  $22.5 \pm 3.65$  males/m<sup>2</sup> on the top of the flat. Variation in courting male density among days classified according to the time of LT (h intervals) was analyzed to detect a possible semilunar periodicity. The number of courting males did not vary significantly with the time of LT, but again differed between the two plots (2-way ANOVA with replication: time of LT,  $F_{s(8,18)} = 1.450$ ,  $p > 0.10$ ; plots,  $F_{s(1,18)} = 112.758$ ,  $p \ll 0.001$ ; interaction,  $F_{s(8,18)} = 0.455$ ,  $p > 0.75$ ).

#### Effects of Weather on Pillar Building

The proportions of P males varied significantly over the 26-day period and between the plots (two-way ANOVA: days,  $F_{s(21,21)} = 2.376$ ,  $p < 0.01$ ; plots,  $F_{s(1,21)} = 20.435$ ,  $p < 0.001$ ). Heavy cloud cover and intermittent rain appeared to depress pillar building (Fig. 2). Variation in the proportion of P males on each plot was analyzed among days classified as clear, cloudy or rainy. Weather had a significant effect on pillar building on the high density plot ( $F_{s(2,20)} = 26.620$ ,  $p \ll 0.001$ ). The proportion of P males differed significantly on each of the three kinds of days (SSSTP a posteriori mean comparison). On clear days, an average of  $50.9 \pm 11.85$  % of the courting males built pillars compared to  $32.7 \pm 7.59$  % on cloudy and  $9.5 \pm 14.32$  % on rainy days. The mean percentages of P males on the low density plot on sunny, cloudy and rainy days were similarly ranked ( $27.0 \pm 20.51$  %,  $20.6 \pm 8.86$  %,  $8.5 \pm 7.81$  %) but did not differ significantly ( $F_{s(2,20)} = 2.506$ ,  $0.10 > p > 0.05$ ).

Since cloudy skies and rain tended to occur during the afternoon activity periods (Fig. 2), the decrease in pillar building on these days may have been due to an effect of the time of LT rather than the weather. To examine the possible effects of the time LT independent of correlated weather conditions, I compared (one-way ANOVAs) the proportions of P males on each plot considering only clear days on which LT occurred before 11.00 h (6 days), between 11.00 and 13.00 h (4 days), and after 13.00 h (2 days). The time of LT did not significantly affect pillar building on either plot on clear days (high density plot,  $F_{s(2,9)} = 0.699$ ,  $p > 0.50$ ; low density plot,  $F_{s(2,9)} = 0.653$ ,  $p > 0.50$ ).

#### Effects of Courting Male Density on Pillar Building

A greater proportion of pillars might be expected in high density areas if males' territories have some minimum size and if males build pillars in response to encroachment by their neighbors (ZUCKER 1974, 1981). If this or a similar density dependent mechanism controls pillar building, one would expect a disproportionate increase in the number of P males with a linear increase in density. The number of P males on clear days in the two .75-m<sup>2</sup> plots did not increase disproportionately with the number of courting males (Fig. 3). Linear regressions were run on the untransformed data and on log transformations of one or both variables. The linear model gave the best fit with the untransformed data (number of pillars / 0.75 m<sup>2</sup> =  $-7.157 + 0.6995$  number of courting males / 0.75 m<sup>2</sup>,  $F_{s(1,22)} = 93.009$ ,  $p \ll 0.001$ ), though the slopes of all regression equations were significantly different from 0. The number of P males increased in direct proportion to courting male density from 20 to 64 males/m<sup>2</sup>.

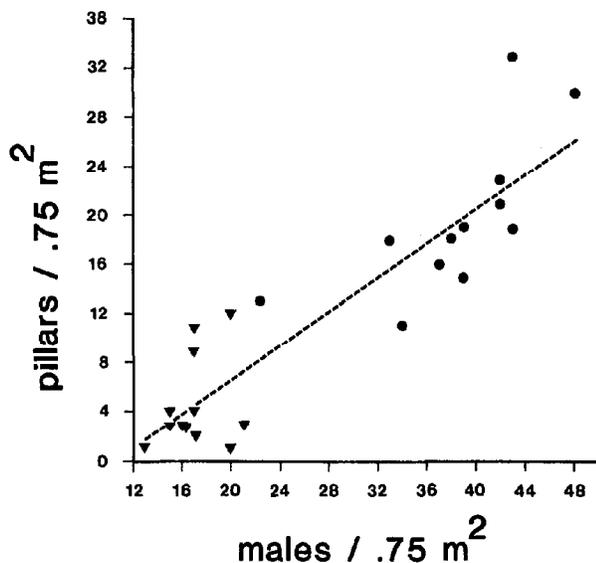


Fig. 3: Number of courting males and number of pillars on two plots on 12 clear days on Rodman flat. Circles: higher density plot on the bank of the flat; triangles: lower density plot on the top of the flat. Dashed line fitted by least squares linear regression on untransformed data

#### Male Sizes and Pillar Building

*General comparisons.* There were no significant differences in the sizes (CL, CW, LP) of P and NP males (Table 2). P males tended to be slightly larger but their BDs were significantly smaller (approx. 0.3 mm), perhaps because the raised lip on burrows with pillars narrows the burrow entrance to some degree or introduced systematic measurement errors. There were no significant differences in either CW or LP [dimensions that affect competitive ability in other fiddler crabs (HYATT & SALMON 1978; CHRISTY 1980)] relative to CL between P and NP males.

*Comparisons of neighbors.* P males that were nearest neighbors did not differ significantly in CL or LP. Neighboring NP males also did not differ significantly in size (BD). However, in pairs with only one P male, the P male was significantly larger than its neighbor (Table 2). These P males also were significantly larger in CL but not LP than both males in the pairs where both built pillars (one-way ANOVAs followed by SSSTPs: CL,  $F_{s(3,71)} = 6.129$ ,  $p < 0.001$ ; LP,  $F_{s(3,71)} = 1.647$ ,  $p > 0.10$ ).

#### Burrow Spacing and Orientation

The average interburrow distance between nearest neighbor P males was  $19.9 \pm 8.59$  cm, compared to  $16.2 \pm 6.31$  cm when only one was a P male and  $10.4 \pm 5.58$  cm when both were NP males. These distances differ significantly (one-way ANOVA:  $F_{s(2,118)} = 14.601$ ,  $p < 0.001$ ). When one or both males built pillars, their neighbors were significantly further away than when neither was a P male (a-posteriori SSSTP).

ZUCKER (1974) found that male *U. musica* tend to have fewer close (10–20 cm) courting male neighbors in the 180° sector in front of their hoods compared

Table 2: Unpaired and paired (nearest neighbor) size comparisons of male *U. beebei* that did and did not build pillars on the Diablo flat. BD, burrow diameter; CL, carapace length; CW, carapace width; LP, propodus length of the major chela. Values (mm) are means  $\pm$  1 S.D. (sample size)

Dimension	Male with a pillar, first male of a pair	Male without a pillar, second male of a pair	$t$ , $F$	$p$
<b>Unpaired comparisons of means (t tests):</b>				
BD	8.07 $\pm$ 0.794 (95)	8.37 $\pm$ 1.305 (147)	2.208	< 0.05
CL	6.99 $\pm$ 0.564 (49)	6.77 $\pm$ 0.791 (26)	1.366	> 0.10
CW	11.09 $\pm$ 1.144 (49)	10.71 $\pm$ 1.125 (26)	1.358	> 0.10
LP	17.89 $\pm$ 2.441 (49)	16.77 $\pm$ 3.319 (26)	1.660	> 0.10
<b>Comparison of means of nearest neighbors (t tests):</b>				
Both males have pillars				
CL	6.67 $\pm$ 0.455 (12)	6.59 $\pm$ 0.535 (12)	0.305	> 0.75
LP	17.67 $\pm$ 2.695 (12)	17.44 $\pm$ 3.053 (12)	0.459	> 0.50
First male has a pillar				
CL	7.31 $\pm$ 0.419 (27)	6.78 $\pm$ 0.791 (27)	3.157	< 0.005
LP	18.40 $\pm$ 1.956 (27)	16.77 $\pm$ 3.391 (27)	2.077	< 0.05
Neither male has a pillar				
BD	8.64 $\pm$ 1.319 (38)	8.29 $\pm$ 1.195 (38)	1.429	> 0.10
<b>Regressions, unpaired data (F tests):</b>				
Males with pillars (N = 49)				
CW on CL	CW = 3.377 + 1.103 (CL)		19.714	< 0.001
LP on CL	LP = -0.700 + 2.659 (CL)		28.487	< 0.001
Males without pillars (N = 26)				
CW on CL	CW = 1.982 + 1.288 (CL)		109.802	< 0.001
LP on CL	LP = -0.240 + 2.509 (CL)		12.521	< 0.01
<b>Comparison of regressions (F tests):</b>				
CW on CL	slopes		0.378	> 0.50
	elevations		0.323	> 0.55
LP on CL	slopes		0.034	> 0.85
	elevations		1.062	> 0.30

to the 180° sector behind. To determine if this was true of *U. beebei*, I measured the distances between and the orientations of the burrows of neighboring courting males, at least one of which had a pillar. The orientation of the burrow with the pillar (or one burrow when both had pillars) was ranked in order of increasing deviation away from the direction of its neighbor's burrow as determined by the position of the pillar on the burrow entrance (Fig. 4). Burrow orientations were independent of the distances to neighbors (Table 3). P males did not have fewer close courting male neighbors in the area in front of their pillars.

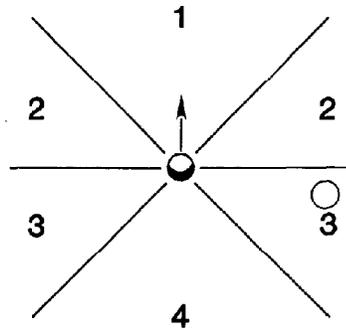


Fig. 4: Method of ranking the orientation of the burrows of pillar builders relative to the location of their nearest neighbors' burrows. The arrow shows the direction that the burrow with the pillar faces as determined by the location of the pillar (crescent) on the burrow opening. The rank of the orientation of this pillared burrow is 3 relative to its neighbor (open circle)

#### Activity Spaces of Courting Males

*Males without pillars.* The locations of 39 NP males (mean observation time per male =  $2.4 \pm 0.57$  h) were analyzed (G test of goodness of fit) to determine if they were distributed equally among 8 equal sectors arbitrarily arranged around their burrows. The activity of 10 males was evenly distributed among sectors; the other 29 were seen significantly more often in some sectors than in others. They spent, on average,  $34 \pm 9.9\%$  of their time in the relatively small  $22.5^\circ$  sector where they were seen most often.

*Males with pillars.* The locations of 15 P males in 6 sectors, oriented and ranked as described in Fig. 4, were analyzed before and after they built pillars. 7 of 15 males were active significantly more often in front of their pillars (Table 4). However, pillars significantly affected the distribution of the locations of only two males (Table 4); neither male spent significantly more time in the area in front of his pillar. Pooling the data for the "front" (1 and 2) and for the "rear" (3 and 4) sectors across males shows that P males spent significantly ( $G = 6.002, 1$  df) more time in the front sectors before they built their pillars (73 %) than after (63 %). Pillars rarely affected the shape of a male's activity space and they were neither necessary for nor effective in focusing activity to the area in front of a male's pillar.

Table 3: Frequencies of nearest-neighbor pairs of male *U. beebei* classed by the distance between and orientation of the males' burrows. Burrow orientations ranked as described in Fig. 5. At least one male in each pair built a pillar

Rank orientation	Distance (cm)					Sum
	< 10	10—15	15—20	20—25	> 25	
1	8	6	9	4	2	29
2	10	6	5	2	1	24
3	5	6	8	5	3	27
4	8	5	6	4	2	25
Sum	31	29	28	15	8	105

Burrow orientations and distances are independent.  $G$  (Williams) = 4.893,  $p > 0.90$

*Table 4:* Locations recorded at 5-min intervals of 15 courting male *U. beebei* before (B) and after (A) they built pillars and the effects of pillars on locations. Locations classed by sector as described in Fig. 4. G tests of goodness-of-fit were used to determine if males were equally active in all sectors. Locations in sectors 1 and 2 and those in sectors 3 and 4 were combined for before pillar tests. G tests of independence ( $2 \times 2$ ) were used to detect effects of pillars on locations

Male		Sectors				Locations evenly distributed?	Locations in front of burrow?	Pillar affects locations?
		1	2	3	4			
1	B	12		2		no**	yes	
	A	11	3	5	9	yes	—	yes*
2	B	17		0		no***	yes	
	A	4	6	10	1	no*	no	yes***
3	B	8		3		yes	—	
	A	11	7	6	1	no*	yes	no
4	B	10		4		yes	—	
	A	12		3		no*	yes	no
5	B	8		5		yes	—	
	A	12	5	5	3	no*	yes	no
6	B	12		4		no*	yes	
	A	15	8	4	0	no***	yes	no
7	B	10		1		no*	yes	
	A	15	3	5	5	no*	yes	no
8	B	10		1		no*	yes	
	A	22	4	3	0	no***	yes	no
9	B	12		2		no**	yes	
	A	18	6	1	0	no***	yes	no
10	B	10		4		yes	—	
	A	8	5	7	5	yes	—	no
11	B	7		7		yes	—	
	A	7	6	9	4	yes	—	no
12	B	6		2		yes	—	
	A	9	4	9	5	yes	—	no
13	B	3		6		yes	—	
	A	7	4	14	7	yes	—	no
14	B	9		10		yes	—	
	A	9		8		yes	—	no
15	B	12		4		yes	—	
	A	10	5	7	5	yes	—	no

\*  $p < 0.05$ , \*\*  $p = 0.01$ , \*\*\*  $p = 0.001$

### Effect of Pillars on Overlap of Activity Spaces

The amount of overlap in the activity spaces of 15 P males with 9 neighboring P and 18 neighboring NP males was measured before and after the 15 P males built pillars as

$$O_{12} = 1 - .5 \sum_{q=1}^n |p_{1q} - p_{2q}|$$

where  $q$  is a 2.5-cm square quadrant occupied by either or both males,  $n$  = the total number of quadrants in which the males were seen,  $p_{1q}$  = the relative frequency of the 1st male in the  $q$ th quadrant and  $p_{2q}$  = the relative frequency of the 2nd male in the  $q$ th quadrant (SCHOENER 1970).  $O_{12}$  is the average relative frequency with which the two males shared space. Males in all pairs either overlapped in their activity spaces, interacted aggressively, or both.

A plot of the number of unique quadrants in which males were seen against the amount of time they were observed showed that males continued to expand their activity spaces even after 3 h of observation. I therefore calculated overlap for equal numbers of (sequential) observations before and after males built pillars.

Overlap of the activity spaces of neighbors was small and did not differ significantly before ( $3.4 \pm 3.88\%$ ) versus after ( $3.0 \pm 4.05\%$ ) one male of the pair built a pillar (paired means comparison:  $t_s = 0.378$ ,  $p > 0.50$ ). Overlap increased after pillars were built for 10 (4 P—P) pairs, decreased for 8 (3 P—P) pairs and remained the same for 9 (2 P—P) pairs. These results are not a consequence of observing only distant neighbors, whose activity spaces might overlap less than those of near neighbors (correlation, number of observations and distance,  $r$  (Pearson) = 0.12,  $n = 27$ ,  $p > 0.05$ ). The average interburrow distance for these pairs of males was  $10.6 \pm 4.89$  cm.

### Effects of Pillars on Rates of Aggressive Interactions

I obtained continuous records of the agonistic behavior of 13 P males that interacted or overlapped with the activity spaces of 10 P and 24 NP neighboring courting males. I observed these 34 pairs for an average of  $42.9 \pm 21.75$  min. before and  $114.6 \pm 35.81$  min after the 13 P males built pillars. Rates of aggressive interactions were not correlated with the amount of time I observed these pairs before ( $r = 0.04$ ) or after ( $r = -0.04$ ) pillars were built. Thus I assume that my estimates of interaction rates are not biased by the unequal observation periods before and after pillars were built.

Pillars did not significantly affect rates of aggressive interaction either between neighboring P-P male pairs (before pillar:  $1.9 \pm 2.79$ /h; after pillar:  $2.8 \pm 5.29$ /h;  $t_s = 0.375$ , 9 df,  $p > 0.50$ ) or between neighboring P—NP male pairs (before pillar:  $3.9 \pm 7.65$ /h; after pillar:  $1.4 \pm 2.15$ /h;  $t_s = 1.426$ , 23 df,  $p > 0.10$ ). Interaction rates for P—P versus P—NP male pairs did not differ significantly either before ( $t_s = 0.697$ , 32 df,  $p > 0.40$ ) or after ( $t_s = 1.144$ , 32 df,  $p > 0.20$ ) the 13 P males built pillars. Overall, males exchanged threats with a given neighbor about 2.5 times per h (approx. once every 24 -min).

Interaction rates declined, but not significantly, with distance between males (before and after pillars pooled:  $r = -0.11$ ,  $N = 68$ ,  $p > 0.25$ ). I observed near and distant neighbors for about the same amount of time (correlations, time

observed vs. distance; before pillars:  $r = -0.028$ ; after pillars:  $r = -0.011$ ). Clearly, neighbors interacted infrequently regardless of the distance between their burrows and the presence of a pillar on one male's burrow. I did not time interactions precisely. However, nearly all were threats or threat exchanges that lasted no more than a few s.

### Time Budgets

P and NP males apportioned their time differently among nine categories of behavior (Fig. 5; G test of independence:  $G = 461.398$ ,  $p \ll 0.001$ ). P males spent more time courting (wave and wave and feed,  $G = 269.368$ ,  $p \ll 0.001$ ), less time feeding ( $G = 232.332$ ,  $p \ll 0.001$ ) and more time in aggressive interactions with neighbors and wandering males ( $G = 11.448$ ,  $p < 0.01$ ). P males courted more than NP males but not because they spent less time threatening and fighting their neighbors.

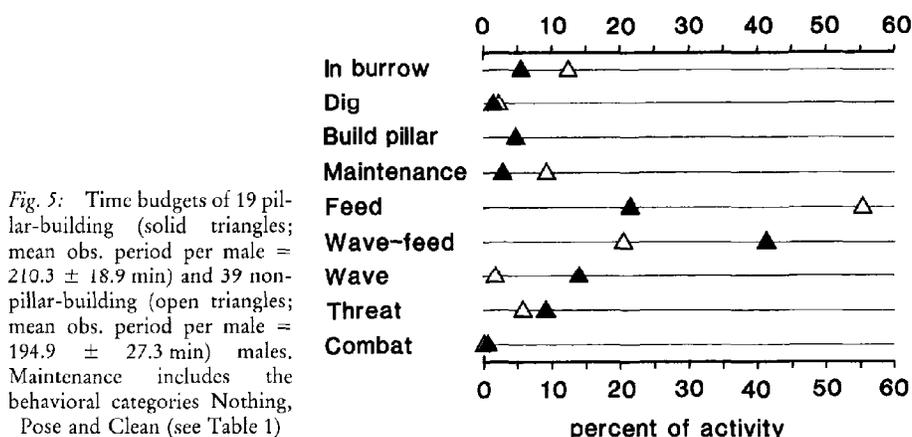


Fig. 5: Time budgets of 19 pillar-building (solid triangles; mean obs. period per male =  $210.3 \pm 18.9$  min) and 39 non-pillar-building (open triangles; mean obs. period per male =  $194.9 \pm 27.3$  min) males. Maintenance includes the behavioral categories Nothing, Pose and Clean (see Table 1)

### Discussion

*Uca beebei* and *U. musica* are similar in size, distribution, general ecology and many features of their mating behavior. However, pillars and hoods, the contexts in which they are built and their effects on male behavior differ so substantially in nearly all respects (Table 5) that it is unlikely that they function similarly in the two species. Here I review some of these differences and their possible causes, and I point out some unanswered questions raised by ZUCKER's hypothesis.

Hoods and pillars differ most distinctly in their width. Both structures are about 2 cm high (ZUCKER 1981; this study) but hoods are as wide or wider than their height (ZUCKER 1974; Fig. 1 b) while pillars (above their base) are about 1 cm wide. This difference in width may account for some of the differences in how hoods and pillars affect male space use, spacing and aggression between neighbors.

Table 5: Comparison of the hoods built by male *Uca musica* with the pillars built by male *U. beebei*, the males that build them, the contexts in which they are built and their effects on male behavior

Feature compared	Hoods — <i>Uca musica</i>	Pillars — <i>Uca beebei</i>
Structure	Tall, broad, delicate cupped hood.	Tall, tapering cupped cone or pillar.
When built	Within about 1 h of LT on the four to five days each semilunar cycle that LT occurs in mid-day. Building more frequent during one semilunar period each lunar month. Weather effects unknown.	Construction begins before LT and continues for the next 2.5 h. Lunar or semi-lunar cycle probable (ZUCKER 1978) but not observed in this study. Building reduced on overcast and rainy days.
Effect of courting male density	The number of hoods increases disproportionately with density.	The number of pillars increases linearly with density.
Male sizes — unpaired comparisons	Hood builders tend to be smaller than those that do not build hoods.	Pillar builders same size as males that do not build pillars.
Male sizes — nearest neighbors	No data.	Sizes equal when both or neither male are pillar builders. Pillar builders larger than non-pillar building neighbors.
Burrow spacing and orientation	Hood builders may have close neighbors behind but not in front of their hoods. Distances to nearest neighbors of hood builders and non-hood builders not reported.	Nearest neighbors of pillar builders are more distant than are the nearest neighbors of males that do not build pillars. Pillar builders may have close neighbors both in front of and behind their pillars.
Activity spaces	Hood builders spend most of their time in front of their hoods.	Pillars do not affect the locations of males around their burrows.
Overlap in activity spaces	Not measured directly but probably less with males located behind hoods.	Overlap slight and declines with distance between neighbors. Does not change after males build pillars.
Aggression	Hood builders that have had their hoods removed fight their neighbors more than when their hoods are present.	Pillars do not affect rates of aggression between neighbors.
Time budgets	Hood builders fight less often but not known if they therefore court more.	Pillar builders fight and court more than do males that do not build pillars.
Mating rates	Not known.	Higher for pillar builders (CHRISTY 1988)

Courting male *U. musica* that do not build hoods (NH males) defend roughly circular areas around their burrows whereas hood builders (H males) are more active in and more vigorously defend the semicircular area in front of their hood (ZUCKER 1974, 1981). In contrast, about 75 % of NP male *U. beebei* were active primarily in a relatively small sector around their burrow. While P males also commonly restricted their activity to a particular area, it was not consistently located in front of their pillar. Moreover, P males spent significantly more time in

the area in "front" of their pillars before than after they built them. Broad hoods but not narrow pillars may effectively limit a male's movements away from its burrow entrance to the area in front of the hood. Male *U. musica* probably adjust the orientation of their hoods so that they face away from any close neighbor they have not displaced from its burrow early in the activity cycle before they build hoods and court (ZUCKER 1974, 1977). This behavior may reduce the frequency with which neighbors encounter each other on the surface and interact aggressively. The pillars of male *U. beebei* were not oriented consistently relative to the location of their closest neighbor regardless of the distance between the males. Pillars affected neither the amount of spatial overlap nor the rate of aggression between neighbors.

These contrasts follow from a mechanistic explanation of how hoods but not pillars direct males' movements around their burrows. Yet the explanation seems inadequate. Why must male *U. musica* build hoods simply to limit their own movements away from their closest neighbor when they could (logically) do so simply by avoiding their neighbors? Do hoods function to reduce rates of aggression through some other mechanism?

Hoods, due to their width, may visually screen residents from their closest neighbors. HB males may seldom fight with their close neighbors not only because they encounter them infrequently but also because their neighbors see them and thus initiate aggressive interactions less often. This suggestion accords with the observation that males that are visually isolated from their neighbors seldom build hoods (ZUCKER 1981). However, H males do see and threaten (at low intensity) crabs that approach them from behind their hoods (ZUCKER 1974). Hoods may also conceal sexually receptive females as they enter a male's burrow and reduce rates of courtship disruption by close neighbors. Narrow pillars would be less effective than wide hoods as visual screens perhaps explaining, in part, why pillars did not affect interaction rates.

ZUCKER (1981) suggested that hoods may reduce interaction rates through a different mechanism. She argued that hoods may signal other males that the H male will limit its activity and defense to the area in front of its hood. Neighbors and males seeking burrows might adjust their activity spaces and settlement patterns respectively such that overlap in defended areas and rates of aggressive interaction are minimized. There is, however, no direct evidence that hoods function as signals in this way. Elsewhere (CHRISTY 1988) I show that the narrow pillars of *U. beebei* function effectively as visual guideposts females use to find the burrows of courting males. If both hoods and pillars have signal function, then it is not clear why they differ so substantially in width. Perhaps it is not possible for male *U. musica* to build a structurally sound column or pillar from the nearly pure sand in which they usually burrow. The behavioral mechanism by which hoods but not pillars reduce rates of aggressive interaction among neighboring courting males remains poorly known.

ZUCKER's (1981) hypothesis rests on three important assumptions: (1) there is an inverse relationship between the amount of time males spend fighting their neighbors and courting, (2) the mating rates of H males are greater than they might have been had they not built hoods because with hoods they spend less

time fighting and more time courting and because (3) females so prefer to choose mates where courting males are dense that the higher mating rate per male more than offsets any increase in local competition among males to attract females.

The first assumption probably is true for *U. musica*. ZUCKER (1981, Table V) showed that H males interacted with their neighbors at a rate of about 1.5 interactions per h (one per 41 min) when their hoods were intact. Interaction rates increased to 3.5 per h (one per 17 min) when males' hoods were removed. These rates are relatively low and comparable to the interaction rates of male *U. beebei* after (one per 33.8 min) and before (one per 18.7 min) they built pillars. However, aggressive interactions among neighboring male *U. musica* often may last many min (ZUCKER, pers. comm.) rather than the few s typical of a threat exchange between male *U. beebei*. This contrast might be expected if hoods normally reduce interaction rates in *U. musica* and behavioral conventions do so in *U. beebei*. It is not known whether the time male *U. musica* spend fighting their neighbors reduces the time they spend courting. ZUCKER (1977, 1978) found that most aggression occurs early in the activity cycle, before males build hoods and begin to court, and stated (ZUCKER 1978) that males fight more on the days that they will later court. Hence, levels of aggression and courtship appear to be directly related on a daily basis but disassociated in time. P male *U. beebei* spent about 2.5 times as much time courting (54.2 %) as did NP males (22.1 %) even though they interacted aggressively about 1.5 times more often (9.1 % compared to 5.9 %). Since aggressive interactions usually were brief during courtship periods, it seems unlikely that the time they took caused males to miss courtship opportunities. Male *U. beebei* stopped threatening or fighting their neighbors (but not wandering males seeking burrows) when females were near and courted instead; neither the time spent fighting nor the fights themselves appeared to interfere with courtship. Males did aggressively disrupt courtship sequences but they usually directed threats to the females that responded to their neighbors not to their neighbors themselves.

Mating rates of male *U. musica* have not been measured so it is not possible to verify or reject the second assumption for this species. Elsewhere (CHRISTY 1988) I show that P male *U. beebei* attract females to their burrows about 1.5 times more often per courtship encounter than do NP males. This difference is due primarily to the effects of pillars on female behavior. Once a female enters a male's burrow the chance that she will stay and mate is the same whether or not the burrow has a pillar. Since P males court about 2.5 times as much as NP males, their mating rates should be 3—4 times higher (assuming both kinds of males encounter receptive females at the same rate when courting), even though they interact aggressively more often with their neighbors.

ZUCKER (1981) presented the results of an experiment that she suggested were consistent with the third assumption. She manipulated the density of "courting" male *U. musica* on 3 adjacent m<sup>2</sup> plots by removing males and filling their burrows or adding dead, white (courtship coloration) males and artificial burrows. The third plot was left at natural densities. She periodically frightened crabs into burrows and then counted the number of wandering females that emerged from burrows on each plot. 38 females emerged from burrows on the

high density (25 males, most dead; 1.5 females/male) plots compared to 18 from the low (3 males; 6 females/male) and 21 from the natural (mean = 4.5 males; 4.7 females/male) density plots. She concluded that females preferred to wander on the high density plots and that by building a hood a male (especially a small male) might be able to remain in a high density area and thereby encounter more females (ZUCKER 1981). However, these counts were not corrected for the number of burrows on each plot in which females could take refuge when frightened (about 7 times as many on the high density plots compared to the others?) and it was not known which females, if any, were seeking mates. Even discounting these criticisms, the ratio of wandering females to courting males was 3 and 4 times greater on the natural and low density plots, respectively, than on the high density plot. There is currently no evidence that male *U. musica* benefit by courting in areas with high densities of courting males.

The basis of female choice in *U. musica* is not known. Logically, females might gain by seeking mates in areas with high densities of courting males because they would have many from which to choose. They could, therefore, select a mate quickly, perhaps avoiding prolonged exposure to avian predators, which feed primarily on crabs moving on the surface (CHRISTY 1980, 1983, and unpubl.). However, both *U. musica* and *U. beebei* (CHRISTY 1987) probably have resource-defense mating systems in which the highest densities of courting males occur where males can dig, defend and provide to females the best mating (*U. musica*) and mating and breeding sites (*U. beebei*). If true, female choice probably is based both on male display and burrow quality. Male mating rates would be determined by how well they compete at attracting females into their burrows and the quality of their burrows as mating or breeding sites rather than by an effect of density alone on female mating preferences. Females might more often choose mates where males are dense simply because that is where good mating or breeding sites are found.

More data are needed to critically test the three major assumptions that underlie ZUCKER's hypothesis for the function of hoods. Pillars clearly do not function in *U. beebei* as ZUCKER (1981) suggested they might. If ZUCKER's hypothesis is correct for *U. musica*, then why does it not apply to *U. beebei* since these two species are otherwise so similar?

The observation that male *U. musica* court for only a short time each tidal and lunar cycle lies at the core of ZUCKER's hypothesis. ZUCKER (1976, 1978) found that *U. musica* courts primarily during the 2 h following LT and that most courtship occurs on only 4–5 days during the lunar cycle at a site not covered by neap high tides. Even a small loss of courtship time may substantially reduce mating rates of male *U. musica* (ZUCKER 1981). Male *U. beebei* that build pillars also court primarily after LT, but courtship activity remains high (> 55 % of a male's time budget) up to 3 h after LT (CHRISTY 1988). Male *U. beebei* did not exhibit semilunar or lunar cycles of courtship (or pillar building) during this study. This is unusual for a fiddler crab (CRANE 1958; FEEST 1969; VON HAGEN 1970; CHRISTY 1978; ZUCKER 1976, 1978; SALMON & HYATT 1983; GREENSPAN 1984; SALMON 1984, 1987) and contrasts with the lunar cycles of courtship ZUCKER (1978) found in this species in other years. A recent study (CHRISTY &

MORGAN, unpubl.) of egg production and hatching in *U. beebei* suggests that females at the Rodman flat reproduce on a semilunar schedule. However adult females are able to receive sperm at any time (their genital opercula are always mobile) and they are behaviorally receptive for long periods (CHRISTY 1987). It appears that courtship and mating in *U. beebei* are not closely tied to underlying cycles of oviposition and egg hatching. Selection favoring behavioral mechanisms such as hoods that may increase the time available for courtship may be weaker in this species than in *U. musica*. Differences in temporal constraints on courtship could explain why ZUCKER's hypothesis does not apply to pillar function in *U. beebei*.

Pillar building by male *U. beebei* appears to be part of a behavioral syndrome, phase (CRANE 1958) or tendency (ZUCKER 1976) characterizing males that are fully devoted to courtship and competition for mates. P male *U. beebei* were more aggressive, courted more, fed less and tended to have fewer close neighbors than did NP males regardless of the neighbor's location relative to the direction the P male's burrow faced. Especially large [probably competitively dominant (HYATT & SALMON 1978; CHRISTY 1980)] P males tended to have smaller NP males as their nearest neighbors, perhaps because they ousted smaller P males nearby or tolerated only NP males as neighbors. The advantages of increased spacing among courting males are not known but may include maintenance of a neighbor-free area for courtship signaling (ZUCKER 1977), reduction of aggressive disruptions of courtships by neighbors, or an increase in the isolation of burrow shafts and chambers females use for breeding (CHRISTY & SALMON 1984).

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