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Sand disposal of the painted ghost crab *Ocypode gaudichaudii* (Decapoda: Ocypodidae): a possible role in courtship

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Abstract. In 1991/1992, we studied the sand disposal behavior of the painted ghost crabs *Ocypode gaudichaudii* on the Pacific coast of Panamá. *O. gaudichaudii* either kick, dump or tamp sand they excavate from their burrows. Here we relate these three kinds of sand disposal to burrow structure and distribution, as well as to crab size and sex. Our objective was to determine whether tamping may be a male courtship signal. Burrows whose owners tamped sand were on average longer, deeper, and higher on the beach than were burrows whose owners kicked or dumped sand. Five burrow shapes were distinguished, with half-spiral and spiral shapes being most common among tamped burrows. All crabs excavated from tamped burrows were males. Tamped burrows peaked in abundance around full and new moons. These observations, together with what is known about mating and breeding behavior of other ghost crabs, suggest that tamping may be involved in *O. gaudichaudii* courtship.

Introduction

Acoustic and visual signals predominate in the reproductive behavior of ocypodid crabs, perhaps as adaptations to semi-terrestrial life (Hartnoll 1969). Some species of ghost crabs (genus *Ocypode*) produce air-borne sounds and substrate vibrations by either rapping or stridulating (Horch 1975). Vibrations emitted from males' burrows are an important part of courtship, especially in night-active, supratidal species (Salmon 1983). Visual behavioral courtship signals have been reported for two species: a male waving display in *O. ryderi* (Vannini 1976, Vannini 1980a), and a chela-forward display in *O. gaudichaudii* (Wright 1968). The pyramid-shaped sand piles that males of some species make from excavated material beside their burrows also may be visual courtship signals (Linsenmair 1965, 1967, Jones 1972).

Besides building sand pyramids, male ghost crabs often manipulate excavated material in other ways. Male *Ocypode saratan* and *O. ryderi* tamp sand with the outer surfaces of both chelae and ambulatory dactyls as part of pyramid building (Linsenmair 1967, Jones 1972). Crane (1941) and Rajabai (1972) suggested that tamping is a male courtship behavior in *O. gaudichaudii* and *O. macrocera*, respectively, neither of which build pyramids. *O. quadrata* and *O. ceratophthalmus* also tamp (Vannini 1980b).

Although surface matings have been observed in some ghost crabs (*Ocypode occidentalis* and *O. quadrata*: Hughes 1973, Horch 1975), male-defended burrows are courtship and mating sites in *O. saratan* (Linsenmair 1965, 1967), *O. macrocera* (Rajabai 1972), *O. quadrata* (Hughes 1973), *O. ceratophthalmus* (Hughes 1973, Brooke 1981), and perhaps in *O. cursor* (Linsenmair 1967) and *O. ryderi* (Jones 1972, Vannini 1980a, b). Male mating burrows of *O. saratan* and *O. ceratophthalmus* are readily distinguishable by their spiral shape (Vannini 1980b).

Ocypode gaudichaudii is mostly day-active on intertidal sand beaches from the Gulf of Fonseca, El Salvador to Chile and the Galápagos Islands (Crane 1941). Adults are deposit-feeders and opportunistic scavengers and predators (Trott 1988). Both sexes dig burrows that are their primary retreat from predators, environmental extremes, and conspecifics, and in which they stay when covered by the tide. During maintenance of burrows, the crabs dispose of and manipulate excavated sand in three ways: kicking or scattering, dumping and tamping. In this study, we determined how burrow and crab characteristics are related to sand disposal behavior in general and to tamping in particular, and we described the spatial and temporal patterns of tamping behavior. Our aim was to evaluate Crane's (1941) suggestion that tamping by *O. gaudichaudii* may be related to male courtship.

Materials and methods

Study site and period

The study site was a sheltered intertidal sand beach on Culebra Island (8°54′N; 79°31′W), located on the east side of the Pacific

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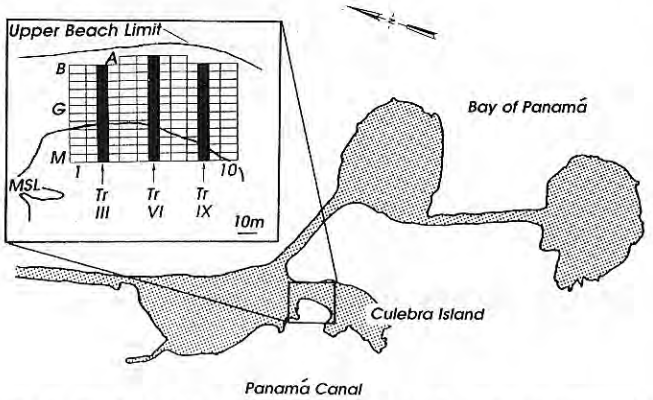

Fig. 1. Study beach on Culebra Island. Study plots are referenced by A–M for rows and 1–10 for columns. Transects III, VI and IX are colored black. MSL: mean sea-level isopleth

entrance to the Panamá Canal (Fig. 1). Tides are semidiurnal, with a mean and spring range of 3.8 and 5.0 m, respectively (Balboa Tide Tables, U.S. Coast & Geodetic Survey). The slope of the beach face was about 5%.

We marked a 6200 m^2 area with 148 steel stakes, arranged in 11 columns and 14 rows. These divided the area into 124 5 m × 10 m plots, referenced by letters for rows and numbers for columns (Fig. 1). The stakes also formed coordinates that allowed us to identify specific burrow locations. We conducted this study between February and September 1991, and in March of 1992.

Sand-disposal behavior

We observed individual *Ocypode gaudichaudii* while they dug or maintained burrows during all daylight hours during which burrows were emersed. Crabs deposited sand they dug from their burrows by "kicking", or by "dumping", and they manipulated deposited sand by "tamping" (see Fig. 2). We defined kicking as a sideways flinging of sand from under the crab by a sudden flexion of the walking legs carrying the sand. Kicking scattered and widely distributed the sand. Dumping crabs dropped entire loads of sand, which remained either as irregular or partially broken-up balls. Crabs tamped sand by pounding it with the outer area of both chelae and the inward pointing dactyls of the ambulatory legs.

Although excavating crabs may alternately kick and dump sand, we analyzed only patterns of disposal derived from a single kind of deposition. Analyses of the spatial patterns of sand disposals were based on scale sketches of the outlines of disposed sand from 155 burrows. We measured the inclusive angle of the disposal, minimum and maximum distances between disposed sand and burrow opening, and the surface area covered by disposed sand.

Burrow and crab characteristics in relation to sand disposal

Most crabs completed burrow maintenance by 2 h before low tide. Beginning at this time, we selected burrows so that we sampled each disposal category across the entire area with burrows. We excavated those burrows, measured their lengths and depths, and assigned them to one of five shapes: straight, bow-shaped, S, half-spiral or spiral. We captured resident crabs, recorded their gender, and measured with vernier calipers their carapace width, carapace length and propodus length of the larger chela. We recorded the location of each burrow by measuring the distances to the nearest upper left and right stakes for subsequent determination of burrow elevations (see "Elevation of the beach slope" below).

On 10 d, we observed crabs while they were excavating their burrows, and we categorized their sand-disposal behavior. We collected samples of freshly excavated sand and stored them in air-tight bags. These samples were weighed, dried at 60 °C for 48 h, then reweighed to determine their percentage of moisture by weight loss. We used 83 of these substrate samples for grain-size analysis, following Buchanan (1984).

We measured the burrow-opening diameters of 60 burrows, excavated the residents, sexed them, and measured them as described above. We used these data to determine the relationship between opening diameter and resident crab size and sex.

Spatial and temporal patterns of sand disposal

We established three permanent, 5 m-wide transects centered on Stake Columns III, VI, and IX. Transects extended from Rows A to M (VI) or B to M (III and IX); however, no burrows occurred lower than Row G (Fig. 1). Every second day, beginning at 1 h after low tide, we marked all burrows within the transects. We recorded the plot in which each burrow was located, the category of disposal (including "no disposal"), and the opening diameter. We then placed a tooth-pick across the burrow opening and checked it for displacement at least 20 min later. If the tooth-pick had been moved, we rated the burrow active. On 12 d, we took surface-sand samples from the center of each plot and determined the moisture content as described in foregoing subsection.

Elevation of the beach slope

Twice monthly from March to September 1991 we used a transit-level and leveling rod to measure the beach elevation at each grid stake. Elevations were referenced to a local datum. We determined the elevation of the datum relative to mean sea level (MSL) by making several timed measurements of water level on the beach on one day. These measurements were referenced to MSL by consulting digital tide records provided by the Panamá Canal Commission.

Data analyses

Statistical procedures followed Sokal and Rohlf (1981) and the computer program SYSTAT (Wilkinson 1990). We ran autocorrelations (Wilkinson 1990) to detect periodicities in the temporal series of measurements of the percentage of tamped burrows (number of tamped burrows × 100 ÷ by total number of burrows) and the total number of burrows. We calculated crosscorrelations to detect temporal relationships between the percentage of tamped burrows and the total number of burrows, as well as between each of these variables and the height of the high tide immediately prior to the sampling period. Since we sampled the data every second day, missing values were interpolated by using distance-weighted mean squares (see Wilkinson 1990 and Fig. 5 of present study).

Results

Sand-disposal behavior

Sand deposition and manipulation behavior of *Ocypode gaudichaudii* was similar to that described by Crane (1941). Crabs transported sand from their burrows to the surface using the walking legs of the side with the smaller chela. The sand was either deposited next to the burrow entrance or was carried up to 150 cm away. Some crabs tamped sand they excavated and (usually) dumped.

Table 1. *Ocypode gaudichaudii*. Sand-disposal characteristics. Underlining connects means that do not differ significantly at $P=0.05$ (Tukey means-comparisons test). ***: $P<0.001$; *: $P<0.05$. Data from scale sketches

Parameter		Kicked	Dumped	Tamped	ANOVA	
					F	P
Area (cm^2)	N	33	71	50		
	mean ± SE	382.9 ± 68.01	390.9 ± 34.91	1009.4 ± 99.27	28.03	***
Maximum distance (cm)	N	33	71	51		
	mean ± SE	78.9 ± 5.69	45.3 ± 3.69	62.3 ± 3.98	14.37	***
Minimum distance (cm)	N	33	71	51		
	mean ± SE	29.4 ± 5.28	9.6 ± 2.08	11.4 ± 2.22	11.49	***
Inclusive angle (degree)	N	33	71	51		
	mean ± SE	74.2 ± 13.23	112.1 ± 8.79	85.0 ± 6.91	4.40	*

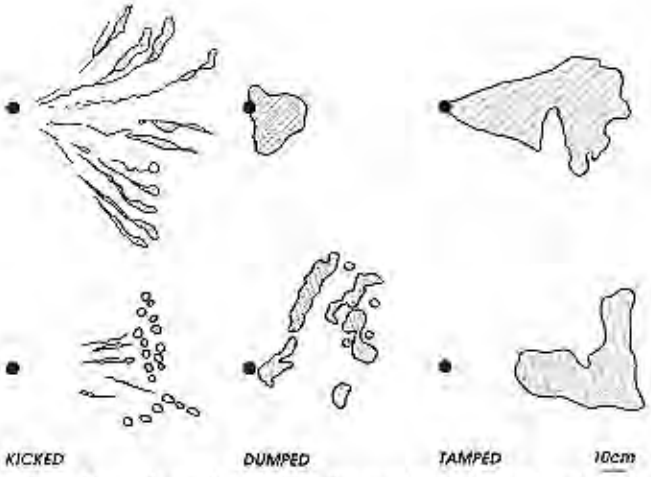

Fig. 2. *Ocypode gaudichaudii*. Patterns of sand disposal and manipulation. Within each category, crabs deposited sand either next to (upper row) or away from (lower row) their burrow entrances (•)

Tamping also occurred on the beach surface itself and not as a part of sand disposal.

The three types of sand disposal behavior resulted in different patterns of deposited sand (Fig. 2, Table 1). On average, tamped sand covered a significantly larger area than both kicked and dumped sand. Generally, kicked sand was found farther away from the burrow entrance than dumped and tamped sand. There were no significant sex-specific differences ($P \geq 0.05$) in any of the dimensions of kicked-sand disposals. However, males and females differed in the minimum and maximum distances from the burrow entrance at which they dumped sand ($n=71$, $F=4.10$, $P<0.05$ and $F=7.87$, $P<0.01$, respectively): males dumped sand farther from their burrows. There was a significant positive correlation between the length of a burrow and the area covered by excavated sand for males ($n=120$, $r=0.51$, $P<0.001$), but not for females ($n=30$, $r=0.33$, $P>0.05$). Within males, only dumped and tamped sand showed this correlation (dumped: $n=44$, $r=0.35$, $P<0.05$; tamped: $n=50$, $r=0.52$, $P<0.001$; kicked: $n=26$, $r=0.30$, $P>0.05$).

Burrow and crab characteristics in relation to sand disposal

We excavated 32 kicked, 70 dumped, and 52 tamped burrows. Out of 153 crabs captured, 123 (80%) were males. This male-biased (G-test for goodness of fit; $G=104.33$, $P<0.001$) sex ratio of about 4:1 was consistently observed in *Ocypode gaudichaudii* sampled on different occasions and by different techniques throughout the study period (Schober unpublished data).

Relationships between types of disposal and burrow and crab characteristics are shown in Table 2. On average, residents of tamped burrows were larger than those of both kicked and dumped burrows. Tamped burrows had wider openings, and their shafts were deeper and longer compared to dumped burrows. Such burrows also were generally at higher elevations, and tamped sand was drier than kicked and dumped sand. Mean grain size did not differ significantly among disposal types.

Burrow characteristics varied with crab size and sex. Mean carapace width and propodus length were significantly ($P<0.001$) smaller in females (28.8 ± 0.69 mm and 18.4 ± 0.44 mm; $n=68$) than in males (35.1 ± 0.45 mm and 25.4 ± 0.35 mm; $n=261$). Female burrows were significantly ($P<0.001$) shallower and shorter (23.3 ± 1.52 cm and 33.5 ± 2.26 cm; $n=30$) than male burrows (33.6 ± 1.11 cm and 50.7 ± 1.58 cm; $n=121$). Females also dug their burrows lower on the beach than did males (90.5 ± 9.94 cm above MSL, $n=36$ vs 120.4 ± 4.69 cm above MSL, $n=139$; $P<0.01$).

Burrow depth and length were positively correlated (♂♂: $n=121$, $r=0.86$, $P<0.001$; ♀♀: $n=30$, $r=0.85$, $P<0.001$). Carapace width and burrow length were positively correlated in males ($n=121$, $r=0.46$, $P<0.001$), but negatively in females ($n=30$, $r=-0.45$, $P<0.05$). Burrow depth and elevation were positively correlated in both sexes (♂♂: $n=118$, $r=0.47$, $P<0.001$; ♀♀: $n=30$, $r=0.45$, $P<0.05$); carapace width and elevation, however, were correlated only slightly in males ($n=120$, $r=0.19$, $P<0.05$) and not in females ($n=30$, $r=0.26$, $P>0.05$).

Table 2. *Ocypode gaudichaudii*. Burrow and crab characteristics in relation to types of disposal. Underlining connects means that do not differ significantly at $P=0.05$ (Tukey means-comparisons test). ***: $P<0.001$; NS: not significant. Data are from burrow excavations, unless indicated differently. MSL: mean sea level

Characteristic		Kicked	Dumped	Tamped	ANOVA	
					F	P
Carapace width (mm)	N	31	71	51		
	mean ± SE	31.7 ± 1.48	29.4 ± 0.93	37.3 ± 0.78	17.82	***
Propodus length (mm)	N	31	71	51		
	mean ± SE	22.3 ± 1.13	20.1 ± 0.71	26.8 ± 0.56	22.61	***
Burrow depth (cm)	N	32	70	52		
	mean ± SE	34.5 ± 2.21	25.5 ± 0.99	39.1 ± 1.79	23.83	***
Burrow length (cm)	N	32	70	52		
	mean ± SE	53.6 ± 3.72	36.1 ± 1.63	59.7 ± 2.68	29.73	***
Burrow opening (diam, cm)[a]	N	1381	1798	1621		
	mean ± SE	2.9 ± 0.02	3.0 ± 0.02	3.5 ± 0.02	260.35	***
Elevation[b] (cm above MSL)	N	1140	1273	947		
	mean ± SE	111.3 ± 0.99	113.6 ± 1.07	129.6 ± 1.24	70.56	***
Percent moisture[c]	N	43	17	50		
	mean ± SE	17.1 ± 0.67	18.9 ± 1.07	13.2 ± 0.62	14.54	***
Grain size[c] % at 125 µm	N	38	7	39		
	mean ± SE	67.6 ± 1.65	66.9 ± 2.55	70.2 ± 1.24	0.98	NS

[a] Data from transects including all burrows
[b] Data from transects including all burrows rated active
[c] Data from sand samples collected separately

Table 3. *Ocypode gaudichaudii*. Comparative statistics of male burrow and crab characteristics related to types of disposal. Underlining connects means that do not differ significantly at $P=0.05$ (Tukey means-comparisons test). ***: $P<0.001$. Data from burrow excavations

Characteristic		Kicked	Dumped	Tamped	ANOVA	
					F	P
Carapace with (mm)	N	27	45	51		
	mean ± SE	32.8 ± 1.58	30.5 ± 1.33	37.3 ± 0.78	10.09	***
Propodus length (mm)	N	27	45	51		
	mean ± SE	23.3 ± 1.19	21.6 ± 0.99	26.8 ± 0.56	10.77	***
Burrow depth (cm)	N	26	44	51		
	mean ± SE	33.6 ± 2.17	27.3 ± 1.99	38.9 ± 1.83	12.88	***
Burrow length (cm)	N	26	44	51		
	mean ± SE	54.3 ± 3.98	37.9 ± 2.11	59.8 ± 2.73	18.49	***
Elevation (cm above MSL)	N	27	45	48		
	mean ± SE	114.6 ± 7.41	94.1 ± 8.33	142.0 ± 7.54	10.33	***

All residents of tamped burrows were males. Four out of 31 (13%) kicked and 26 out of 71 (36%) dumped burrows were occupied by females. These sex frequencies were significantly different from those expected with a 4:1 sex ratio: male-biased in kicked (G-test for goodness of fit; $G=8.97$, $P<0.005$) and female-biased in dumped ($G=17.96$, $P<0.001$) burrows. Most females were found in dumped burrows. On average, males that tamped were larger than those that kicked or dumped sand, and their burrows were significantly deeper, longer and higher on the beach compared to dumped but not kicked burrows (Table 3).

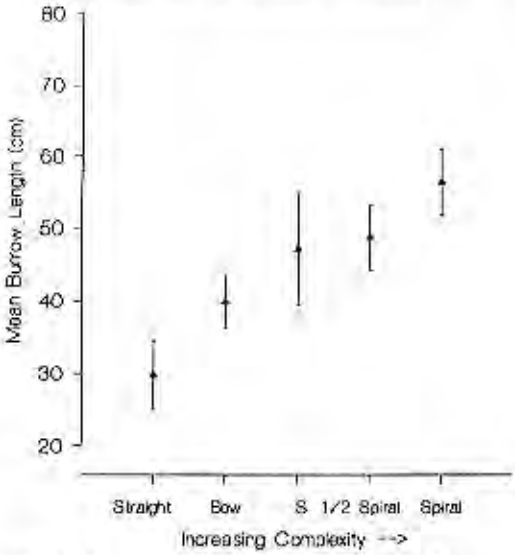

Fig. 3. *Ocypode gaudichaudii*. Relationship between burrow length and shape. ▲: mean values; vertical bars show two standard errors

Male and female burrows tended to have different shapes. Half-spiral and spiral shapes were found in 27.8 and 18% of male burrows compared to only 10 and 3.3% of female burrows ($G=12.8$, $df=4$, $P<0.05$). Bow-shaped burrows were most common in both sexes (♂♂: 38%, ♀♀: 56.7%). For male burrows, half-spiral and spiral shapes were found more than twice as often in tamped than in other burrows (66.7 vs 30.9%). In general, there was a strong positive association between complexity of shape and length of burrows (Fig. 3). Half-spiral and spiral burrows were significantly longer than straight and bow-shaped burrows (Fig. 3; Tukey's means-comparison test, $P<0.001$).

Density and distribution of burrows

Transect samples include data on kicked, dumped and tamped burrows as well as open burrows without associated sand disposal. Mean burrow density ranged from 0.001 to 0.78 per m^2, with the highest densities in Rows A through C. Mean percentage of moisture of surface sand (28.9 to 9.4%) and mean elevation of plots (−21.8 to 190.2 cm relative to MSL) showed a significant inverse correlation ($n=240$, $r=-0.85$, $P<0.001$), as did burrow density and percentage of moisture of surface sand ($n=240$, $r=-0.65$, $p<0.001$).

The diameters of nearly all (99.8%) burrows ($n=5427$) were between 1.5 and 5.5 cm. The size-frequency distributions of burrow diameters differed significantly among all types of disposal (Kolmogorov-Smirnov two-sample tests, all $P<0.001$), but not between kicked and no-disposal burrows (Fig. 4). Overall, burrow diameter and resident carapace length were positively correlated ($n=60$, $r=0.86$, $P<0.001$). Although there was also a statistically significant positive correlation between burrow-opening diameter by size class and elevation, this result is probably due to a high n value ($n=4915$, $r=0.04$, $P<0.05$), and has no biological significance.

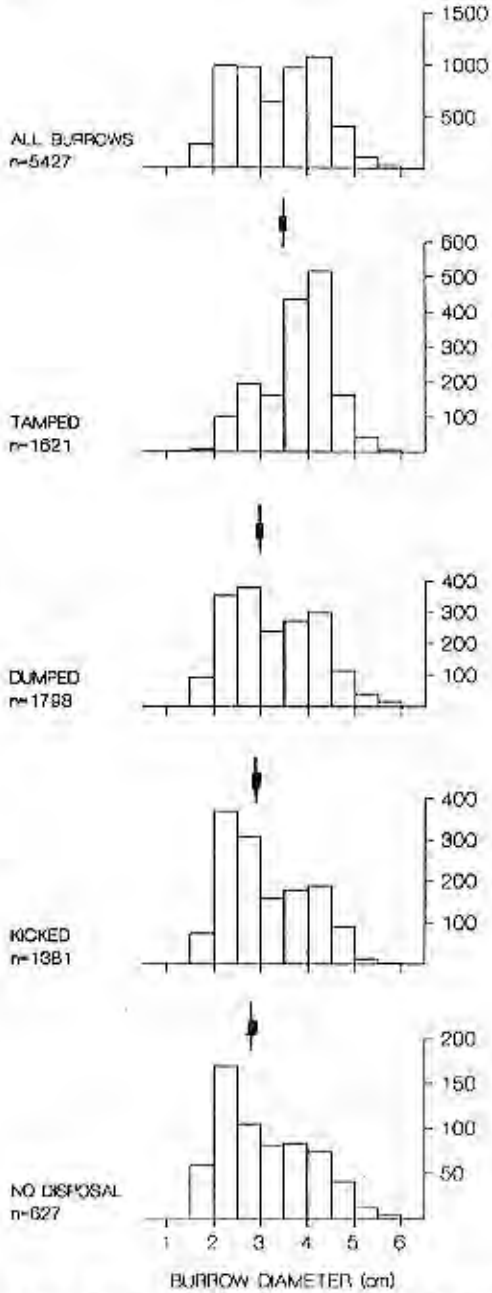

Fig. 4. *Ocypode gaudichaudii*. Frequency distributions of burrow-opening diameters for burrows categorized by type of disposal. Vertical lines show mean diameter; ■: standard errors

Patterns of burrowing activity and tamping behavior

Burrow abundance and tamping activity varied in relation to tidal regime and lunar cycle (Fig. 5). Autocorrelation of the percentage of tamped burrows ($n=70$ including interpolated values) revealed no statistically significant rhythmicity. The amount of tamping on a given day was correlated with the amount of tamping 1 ($r=0.82$) to 2 ($r=0.59$) days later. Similar results were obtained by the autocorrelation of the total number of burrows (Lag 1: $r=0.80$; Lag 2: $r=0.54$).

Tamping activity was significantly correlated with tidal amplitudes 0 to 4 d later. Hence, tamping peaks

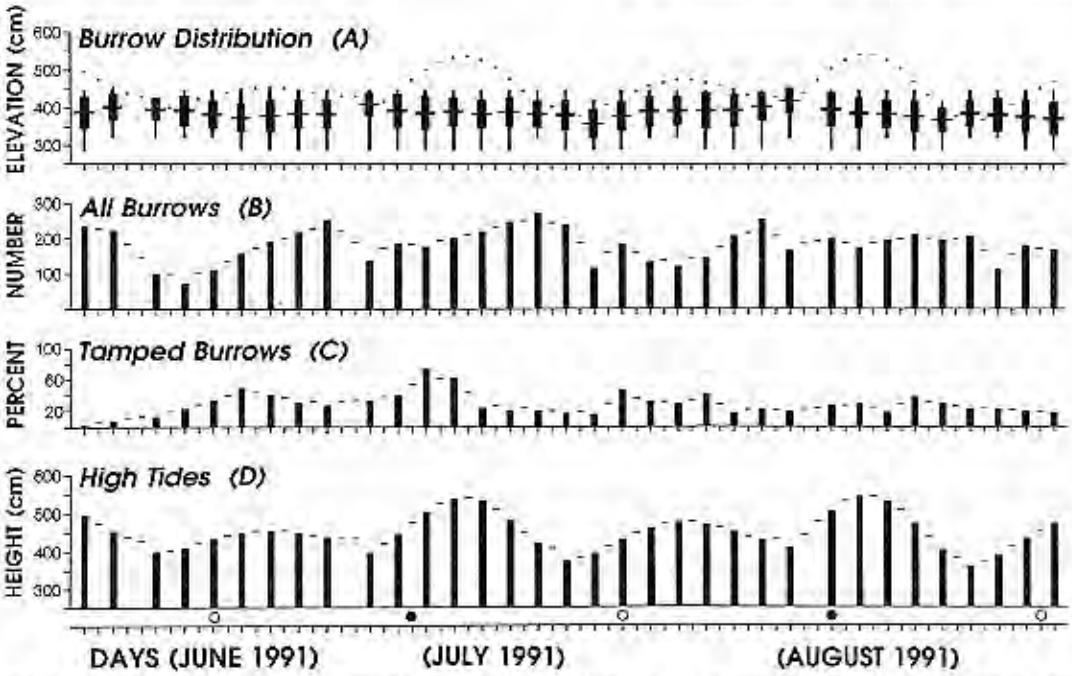

Fig. 5. *Ocypode gaudichaudii*. Burrowing and tamping activity in relation to heights of high tides and to lunar cycle. (A) Burrow elevation means (horizontal lines), standard deviations (vertical bars) and ranges (vertical lines); dots show relative heights of high tides derived from (D). (B), (C) Number of burrows and percentage of tamped burrows, respectively, from counts (bars) or estimates (horizontal lines) interpolated by distance-weighted mean squares (Wilkinson 1990). (D) Tide heights from tables; elevation and tide heights are in relation to mean low-water springs (256.03 cm below MSL). o, •: new and full moons, respectively

occurred 0 to 4 d before the semilunar spring tides. The height of the high tide immediately prior to the sampling period was significantly positively correlated with the total number of burrows 1 to 5 d later. Finally, the percentage of tamped burrows and total number of burrows were not significantly correlated on the same day. However, there was a marginal negative correlation at lags of 2 to 4 d, i.e., a high total number of burrows was followed by a low value of percentage of tamped burrows 2 to 4 d later.

Discussion and conclusions

Sand-disposal behavior

This and previous studies (Crane 1941, Koepcke and Koepcke 1953) have shown that *Ocypode gaudichaudii* either dump or kick sand they excavate from their burrows. These two kinds of sand disposal correspond to the "narrow fan" and "wide fan" categories Linsenmair (1967) distinguished in his study of *O. saratan*, and they occur in other ghost crabs as well (Vannini 1980 b). We found that *O. gaudichaudii* more often dumped (37.5%) than kicked (28.8%), and that both sexes used both kinds of disposal. Sand-moisture content, grain size and burrow elevation did not differ between the two kinds of disposal. Crane (1941) noted a positive correlation between crab size, the size of sand loads, and the frequency of dumping. We found no significant difference between the sizes of male dumpers and kickers; too few ($n=4$) female kickers were observed and measured to test for size differences between dumpers and kickers of this sex. Dumped-burrow diameters were significantly larger than kicked-burrow diameters (Table 2, Fig. 4), but the difference between the means was very small (0.1 cm). Hence, it is yet unclear what determines whether crabs dump or kick.

Tamping and its possible role in courtship

Several species of ghost crabs tamp sand they excavate from their burrows (Vannini 1980 b). Interpretations of the function of tamping vary. Tamping may make less apparent the burrows of *Ocypode quadrata* (Cowles 1908) and female *O. cursor* (Linsenmair 1967). In other species, tamping is associated with male courtship. Male *O. ryderi* (Jones 1972) and *O. ceratophthalmus* (Barrass 1963) tamp the surface of their sand pyramids, perhaps to prevent wind-blown sand from sliding into their burrows (Vannini 1980 b). Male *O. saratan* tamp a runway between their burrow and sand pyramid (Linsenmair 1967), and mature male *O. macrocera* tamp courtship-display grounds around their burrows (Rajabai 1972). The present and previous studies (Crane 1941, Koepcke and Koepcke 1953) have shown that *O. gaudichaudii* tamp deposited sand around their burrows, a behavior that Crane suggested might prove to be a part of male courtship. Our results are consistent with this idea because only male *O. gaudichaudii* tamped sand. Here we speculate on the possible role of tamping in *O. gaudichaudii* courtship. Our argument is based entirely on indirect evidence; we never saw interactions that could

unequivocally be interpreted as courtship and we never found a female carrying eggs.

Tamping by male *Ocypode gaudichaudii* could serve as a courtship signal in two ways. First, since tamped sand is found only in the vicinity of males' burrows, it could provide females a tactile or visual guide to a potential mate. We saw wandering crabs of undetermined sex probe with their dactyls patches of tamped sand while the resident crab was underground. Sometimes the wanderers then entered the associated burrow. However, all the intruders left the burrow again, sometimes after repeated descents. Second, tamping could provide an acoustical or vibratory signal to wandering females. Male *O. gaudichaudii* often tamped the beach surface around their burrow entrance, even after having finished the excavation process. This behavior was observed only in males that had previously tamped excavated sand.

Additional indirect evidence supports a possible link between tamping and courtship in *Ocypode gaudichaudii*. Peaks of tamping were recorded 0 to 4 d prior to spring tides (Fig. 5). Little is known about hatching rhythms and the length of incubation periods in ghost crabs. Female *O. ceratophthalmus* may have a lunar reproductive cycle, with an incubation period of about 16 d and a peak of larval release around new moons (Brooke 1981). Other genera of the family Ocypodidae have similar incubation periods. Incubation averages 18.5, 17.6, and 18.5 d, respectively, at 25°C in *Scopimera globosa, Ilyoplax pusillus*, and *Macrophthalmus japonicus* (Henmi 1989), but can be as short as 13.6, 13.4, and 14.1 d, respectively, at 30°C (Henmi and Kaneto 1989). Incubation periods for several species of *Uca* are 12 to 15 d (Christy and Salmon 1984). If the length of egg incubation is similar in *O. gaudichaudii*, and if larvae are released at times of largest-amplitude nocturnal tides, as in several species of *Uca* and many other intertidal brachyuran crabs (Forward 1987), then a peak in male courtship signaling around the full and new moons would correspond to expected peaks in mating and ovulation that would lead to larval release during an optimum period.

Tamped burrows as mating and incubation sites

The shapes and dimensions of tamped *Ocypode gaudichaudii* burrows compare favorably with the shapes and dimensions of burrows known to be used for breeding by other ghost crabs. We found half-spiral and spiral shapes more than twice as often in tamped than in other burrows. Copulation occurs in spiral-shaped male burrows of *O. saratan* (Linsenmair 1965, 1967) and *O. ceratophthalmus* (Hughes 1973, Lighter 1974, Brooke 1981). In *O. gaudichaudii*, tamped burrows tended to be longer and deeper than all other burrows. Their mean opening diameter was significantly larger than that of other burrows and showed no significant correlation with the size of the resident male. Male *O. quadrata* (Hughes 1973) and *O. cursor* (Linsenmair 1967) dig burrows that are larger than female burrows, and the diameters of the spiral mating-burrows of *O. saratan* and *O. ceratophthalmus* are generally much larger than the carapace width of the resident crab (Vannini 1980 b). In ocypodid crabs, small males can copulate with large females (e.g. Yamaguchi et al. 1979, Christy 1983, Nakasone et al. 1983, Salmon 1984). Hence it may be important that the entrances to the copulation burrows are sufficiently wide to allow even large females to descend. These results and the fact that surface copulation has never been observed in *O. gaudichaudii*, suggest that tamped male burrows serve as copulation sites in this species.

In conclusion, our study produced several lines of indirect evidence supporting a role for tamping in *Ocypode gaudichaudii* courtship. It is remarkable that we found no direct evidence of mating and breeding during our study. Male and female pairs have been found together in burrows of *O. saratan* (Linsenmair 1967), *O. macrocera* (Rajabai 1972), and *O. quadrata* (Hughes 1973). Although we excavated over 150 burrows, we never found such pairs. Ghost crabs can have very distinct reproductive seasons (Jackson et al. 1991). In Peru, ovigerous female *O. gaudichaudii* were encountered during December and January (Koepcke and Koepcke 1953). Although our study spanned 8 mo, it is possible that we missed the reproductive season. However, the 4:1 male biased sex ratio we found on Culebra beach is unusual for an ocypodid crab (e.g. Vannini 1976, Brooke 1981, Simons and Jones 1981) suggesting that our methods inadequately sampled females. Specifically, we may have missed ovigerous females that were in plugged burrows incubating their eggs (Fellows 1973). A study that focused on the natural history of breeding and on the responses of crabs to tamping might provide direct evidence for a role of tamping in *O. gaudichaudii* courtship.

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