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Lunar phase effects on spatial distribution, male size and claw waving in the Fiddler Crab U*ca Heteropleura* at El Agallito beach, Panama

Efecto de fase lunar en la distribución espacial, talla de los machos y movimiento de pinza en el cangrejo violinista U*ca Heteropleura* en playa El Agallito, Panamá

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Abstract

A population of *Uca heteropleura* was studied to examine the effects of lunar phases, male size, and reproductive behavior on courtship activity at El Agallito beach, Panama. Distribution patterns were analyzed with the Morisita and nearest neighbor indices, while surface activity was recorded by counting crabs three times during diurnal low tides. Courtship was measured by recording waves per minute from 386 focal males. In September 2024, the fiddler crab density was 5.71 crabs · m^2, with a male-biased sex ratio. In October, *U. heteropleura* density was 14.30 crabs · m^2, exhibiting a clumped distribution. Activity was higher during new moon compared to the quarter moon; although, crabs during the new moon were smaller. Waving frequency was higher during new moon, driven by the higher proportion of smaller males. Male size was not correlated with waving frequency. These results suggest that two male size classes are active at different times in the semilunar cycle. Influenced by female choice, larger males are favored earlier, while smaller males increase waving later, closer to the spring tide. Larger males may secure mates early through agonistic interactions and mate multiple times before females retreat for incubation. In contrast, smaller males may compensate for lower competitiveness in territory defense and mate guarding by increasing waving frequency to attract the last receptive females before egg incubation.

Keywords: Carapace, synchrony, tides, moon phase, mudflat.

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Resumen

Se estudió una población de *Uca heteropleura* para examinar el efecto de las fases lunares, tamaño de los machos y comportamiento reproductivo en la actividad de cortejo en playa El Agallito, Panamá. Se analizaron patrones de distribución con los índices de Morisita y vecino más cercano, mientras que la actividad superficial se midió contando cangrejos tres veces al día durante mareas bajas diurnas. El cortejo se evaluó registrando la cantidad de “saludos” por minuto en 386 machos focales. En septiembre 2024, la densidad general fue 5.71 cangrejos · m^2, con proporción de sexos sesgada hacia los machos. En octubre, la densidad de *U. heteropleura* fue 14.30 cangrejos · m^2 con una distribución agregada. La actividad fue mayor durante luna nueva que en cuarto creciente; aunque los cangrejos fueron más pequeños en cuarto creciente. La frecuencia de movimientos de pinza también fue mayor en luna nueva, impulsada por una proporción mayor de machos pequeños; aunque, el tamaño no estuvo correlacionado con la frecuencia de “saludos”. Los resultados sugieren que dos clases de talla de machos están activas en distintos momentos del ciclo semilunar, influenciadas por la preferencia de las hembras: los machos grandes son favorecidos al inicio, mientras que los pequeños incrementan su cortejo cerca de la marea de sicigia. Los machos grandes obtienen cópulas múltiples antes de la incubación, mientras que los pequeños compensan su menor competitividad aumentando la frecuencia de movimientos de pinza para atraer a las últimas hembras receptivas del ciclo.

Palabras claves: Caparazón, sincronía, mareas, fase lunar, planicie lodosa.

Introduction

Fiddler crabs are key components of wetland, mudflat, and mangrove ecosystems worldwide (Crane, 1975). Although they are not part of economically significant fisheries, they play essential ecological roles as ecosystem engineers, contributing to bioturbation and nutrient cycling (Aschenbroich et al., 2016; Kristensen, 2008). Their burrowing activity enhances sediment oxygenation and influences soil composition, impacting plant recruitment and organic carbon distribution (Agusto et al., 2021; Booth et al., 2019). Additionally, they serve as primary consumers and are an important food source for migratory birds and other predators, making them integral to energy flow within coastal ecosystems (Backwell et al., 1998; Lombardo, 2023b).

Members of the family Ocypodidae, fiddler crabs exhibit pronounced sexual dimorphism, with males developing a single hypertrophied major claw used for signaling and reproductive competition, while females retain two similarly sized claws (Crane, 1975). Their behavior and ecology have been extensively studied, particularly in the context of communication, mating strategies, and spatial organization (Christy, 1978, 2007; Christy & Salmon, 1984; Crane, 1966; Kim &

Christy, 2015; Ribeiro et al., 2010). In Panama, the most recent inventory reports 39 species, with 32 occurring along the Pacific coast (Lombardo, 2025). Among them, the American Red Fiddler Crab, *Uca heteropleura* Smith (1870), is one of the most abundant species in intertidal mudflats. Despite its prevalence, studies on this species have primarily focused on visual mechanisms and signal evolution (How et al., 2014; Perez et al., 2012), leaving key aspects of its behavioral ecology unexplored.

Fiddler crabs employ two primary mating strategies: active mate searching and territory-based courtship displays. In the first mode, both males and females move across the mudflat in search of mates, with males often engaging in direct competition (Ribeiro et al., 2010). In the second, males remain near their burrows and attract females through claw waving and other visual signals (Backwell, 2019). The choice between these strategies is influenced by factors such as population density, habitat conditions, and the presence of competitors (Ribeiro et al., 2010). In El Agallito, *U. heteropleura* seems to exhibit the second mode where males wave their major claw above, raising the carapace while extending the first and/or fourth ambulatories (Crane, 1975); see Lombardo (2025) annex, figure 14.

However, mate searching involves trade-offs, requiring individuals to assess potential mates while balancing the costs of time, energy, and predation risk (Gruber et al., 2019; Heatwole et al., 2018; Koga et al., 1998; Koga et al., 2001; Lima & Dill, 1990; Takeshita & Nishiumi, 2022). Female reproductive timing, in particular, is constrained by environmental factors that optimize larval survival (Christy, 2011). Many fiddler crab species exhibit reproductive synchrony with lunar cycles, as females time incubation and larval release to coincide with favorable tidal and temperature conditions (Christy, 1978, 2011a; Kerr et al., 2014; Reaney & Backwell, 2007b).

Reproductive synchrony is a widespread and adaptive phenomenon among fiddler crabs, where males also time their courtship and mating behaviors to occur a few days before spring or neap tides (Christy, 1978; Kim et al., 2004). Given the selective advantages of this timing, it is plausible that *Uca heteropleura* exhibits similar reproductive synchronization as well. This implies *U. heteropleura* males should adjust their courtship activity accordingly, increasing display effort as female receptivity aligns with the lunar cycle (Christy, 1978, 2003, 2011). Furthermore, given that spatial distribution influences courtship displays in other species, *U. heteropleura* males may similarly modify their signaling based on conspecific density and environmental cues (Araujo et al., 2013). However, the specific timing and extent of these reproductive behaviors in *U. heteropleura* remain unknown. We hypothesize the signature of male *U. heteropleura* adjustment would manifest in potential shifts in spatial distribution, the number of individuals in the surface and their waving frequency. Therefore, the objective was to determine the spatial distribution pattern of *U. heteropleura* and evaluate the influence of lunar phases, male size, and reproductive behaviors.

Materials and methods

El Agallito Beach (8° 0' 8.12" N, 80° 24' 10.37" W) is a large, unvegetated, intertidal mudflat located in Chitré, Republic of Panama (Fig. 1A). Situated within the Parita Gulf, the mudflat experiences a tropical savanna climate (Aw) (Beck et al., 2018; Köppen, 1936) and distinct seasonal precipitation patterns. Annual rainfall ranges from 1,000 to 2,000 mm, with a pronounced dry season from December to April and a rainy season from May to November, characterized by heavy rainfall (1,500 to 2,500 mm), particularly in October (IMHPA, 2024a). Year-round, the mudflat is influenced by warm temperatures ranging from 24–30°C, with minimal seasonal variation (Lombardo, 2025). Salinity levels in the mudflat range between 18–35‰, while sediment contributions from the Parita River at El Agallito result in a mixture of mud and sand deposits, creating varying degrees of stability across substrates (Backwell et al., 1998).

Abundance, density and distribution pattern

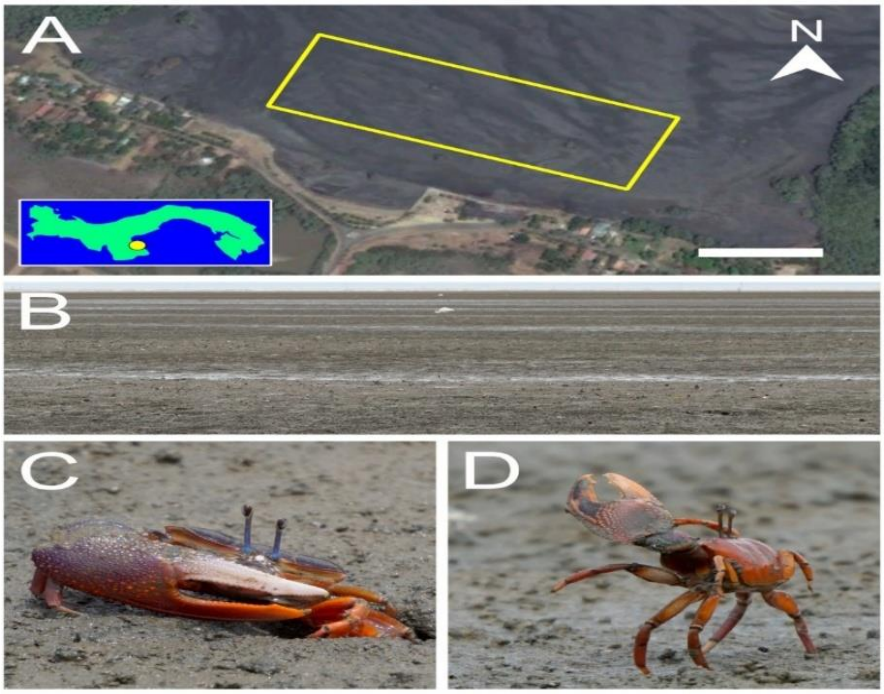
Our study was carried out over three sampling trips during September–October 2024 to the intertidal mudflat during diurnal low tides (Fig. 1B). In September, the overall abundance and density of fiddler crabs were assessed across 11 transects and six 1 m^2 quadrats, each. To analyze the data, the total abundance was calculated as the sum of all individuals and burrows recorded across quadrats. The density was determined by averaging the number of crabs/burrows · m^2. The spatial distribution pattern was evaluated using the Morisita index (I_M), a measure that quantifies whether the distribution is uniform, random, or clumped, using the formula:

$$I_M = \frac{n \sum x_i(x_i - 1)}{X\,(X - 1)}$$

where n is the total number of quadrats, x_i is the number of crabs/burrows in the i-th quadrat, and X is the total number of crabs/burrows across all quadrats (Morisita, 1962). To assess the uncertainty of the index, a bootstrap method was employed, generating 1,000 iterations with replacement from the original data to compute a 95% confidence interval (CI) in RStudio (Core Development Team, 2020). Species identification of observed specimens (Fig. 1C-D) was carried out using specialized identification keys (Crane, 1975; Lombardo, 2025).

Figure 1

Study site and representative Uca heteropleura at El Agallito Beach, Panama.



Note: **A**. Site location. Scale = 100 m. **B**. Panoramic view of the mudflat with active fiddler crabs. C. Male Uca heteropleura (large, 3.51 cm carapace width). D. Waving Uca heteropleura male during courtship, may 18th, 2024 (five days before full moon).

Uca heteropleura spatial distribution & census

Density and abundance of burrows were calculated using 1 m^2 PVC quadrats in October. Quadrats were laid over 11 transects, one meter wide and 30 meters in length. In each transect, two quadrats were placed at random positions within the 30 meters. The spatial distribution of *U. heteropleura* burrows was analyzed using the nearest neighbor index (NNI) to determine whether the observed burrow patterns deviated significantly from a random (NNI = 1), clustered (NNI < 1), or uniform distribution (NNI > 1). To complete our estimation first, the observed mean distance (d_o) and expected mean distance (d_e) to burrows were calculated as follows:

$$NNI = \frac{d_o}{d_e}$$

$$d_o = \frac{\sum_{i=1}^{N} d_i}{N}$$

$$d_e = 0.5 \times \sqrt{\frac{Area}{Number\ of\ burrows}}$$

where d_i represents the distance to the nearest neighbor for the *i*-th burrow, and *N* is the total number of burrows sampled in that quadrat (Clark & Evans, 1954). Burrows in the 22 quadrats were counted, and the distance to their nearest neighbor was recorded (mm) for 30 randomly selected burrows from the total counts.

To evaluate whether the NNIs deviated significantly from randomness (NNI = 1), the Wilcoxon signed-rank test was applied to the entire set of 22 NNI values. This non-parametric test assessed whether the median NNI differed significantly from 1, a value indicative of a random spatial distribution. The test was implemented though an RStudio (Core Development Team, 2020) routine, evaluating whether the NNIs deviated significantly from randomness. To assess the uncertainty of the NNI estimates, a bootstrapping procedure was performed, resampling the distances to nearest neighbors within each quadrat 1,000 times. For each bootstrap iteration, we recalculated the NNI, and derived 95% confidence intervals (CIs) based on the 2.5th and 97.5th percentiles of the bootstrap distribution. This approach was applied to each quadrat individually to obtain NNI estimates and their corresponding CIs in order to generate a plot for diagnosis.

In order to quantify the number of active crabs on the surface (Fig. 1C-D) based on the prevailing weather conditions, censuses were carried out three times a day (10:00:00, 12:00:00 and 14:00:00) during new moon (NE) and quarter moon (QM). These time points were selected to span the midday period, when fiddler crabs are typically most active under daylight low tide conditions (Crane, 1975). Sampling during this interval ensured standardized observation under consistent environmental light and temperature conditions, while avoiding early morning or late afternoon variability. Fiddler crabs were counted with binoculars (Bushnell 10 × 42 mm) in eleven 25 m^2 quadrats marked by stakes and string. To examine differences in crab activity between moon phases and census times, a two-way analysis of variance (ANOVA) was performed with interaction terms for moon phase and census time. Additionally, to investigate potential quadrant-specific effects, a repeated measures ANOVA was performed by including the quadrat as a random effect in the model, where applicable. Post hoc Tukey's (HSD) tests were conducted when significant differences were identified to further explore pairwise comparisons. This routine was run in RStudio, where additionally, a boxplot was created using the "ggplot2" package to visualize crab activity patterns across census times and moon phases.

Biometry

After burrow counts, their diameter (BD) past the entrance was measured using a compass and a caliper; the diameter was recorded as the distance between the compass tips. Specimens were then hand-caught for morphological measurements in the field. Besides clear claw asymmetry, the sex of crabs was alternatively determined by the shape of the abdomen (Hendrickx, 1995), and the reproductive state of the females (ovigerous or not) was recorded. Crab size was analyzed in general terms by recording the carapace width (CW), carapace length (CL), chelae length (ChL) and chelae height (ChH) with a digital Vernier caliper (0.01 mm). Descriptive statistics were calculated in RStudio for each variable and the relationships between them were explored with regression. Normality and equality of variances were analyzed with the Anderson-Darling and Levene's test, correspondingly (Core Development Team, 2020; Sokal & Rohlf, 1987).

Waving frequency

The intensity of courtship was measured by counting the number of times male crabs waved their large claw within a minute (waves · min^{-1}). A total of 386 focal males were selected at random from outside census quadrats. Once waving

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frequency (WF) was recorded, the males were captured by hand or digging the burrow with a small garden shovel. The width (CW) and length (CL) of the carapace and major claw (ChH and ChL) were measured using a Vernier digital caliper (0.1 mm). Normality of waving frequency data was analyzed with the Anderson-Darling test (Anderson & Darling, 1952). To compare waving frequency between new moon (NE) and quarter moon (QM), a Welch's t-test was conducted. This test was selected because it does not assume equal variances, addressing potential heteroscedasticity in the data (N = 386, AD = 2.63, $P < 0.05$; skewness = 0.73, kurtosis = 0.98). Despite slight deviations from normality, the Welch's t-test was deemed appropriate due to its robustness to moderate non-normality, particularly given the large sample size (Welch, 1947).

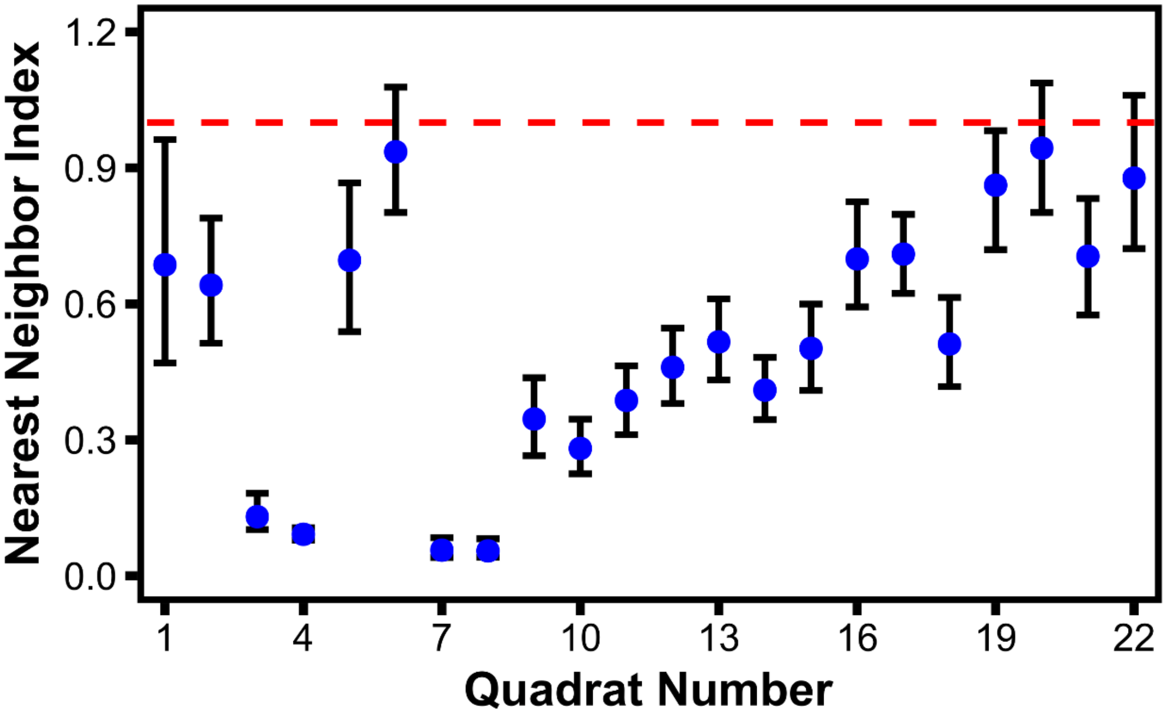
Results

Besides *U. heteropleura*, the most common species identified were: *U. princeps*, *U. stylifera*, *U. ornata*, *Leptuca beebei* and *Leptuca stenodactylus* (see Lombardo, 2025). In September 2024, a total of 417 fiddler crabs were recorded at a density of 5.71 crabs · m^2. Of these, 251 were males and 162 were females, resulting in a significantly skewed sex ratio favoring males at 1.5:1 (Chi-square; X2 = 19.18, d.f. = 1, $P < 0.001$). The Morisita index was 1.49 (95% CI = 1.32–1.67), indicating an overall clumped distribution of crabs. A total of 2,734 burrows were counted, yielding an overall density of 42.06 burrows · m^2. The burrow distribution pattern was also clumped with a Morisita index of 1.20 (95% CI = 1.11–1.31).

In October, the average NNI for *U. heteropleura* was 0.52 ± 0.28 (mean ± SD). All 22 quadrat NNI values were below 1, a statistically significant difference (Wilcoxon signed-rank test; $P < 0.001$), consistent with a clumped distribution pattern (Fig. 2). A total of 472 *U. heteropleura* individuals were recorded in October at a density of 14.30 crabs · m^2. The mean number of individuals active on the surface was 368.67 ± 128.69 during NE and 288.61 ± 170.82 during the QM (Table 1).

Figure 2

Nearest Neighbor Index (NNI) analysis of Uca heteropleura spatial distribution at El Agallito Beach, Panama.



Note: *Each point represents a quadrat (±95% CI); the red dashed line marks thresholds for clumped (NNI < 1), random (=1), and uniform (>1) distributions*

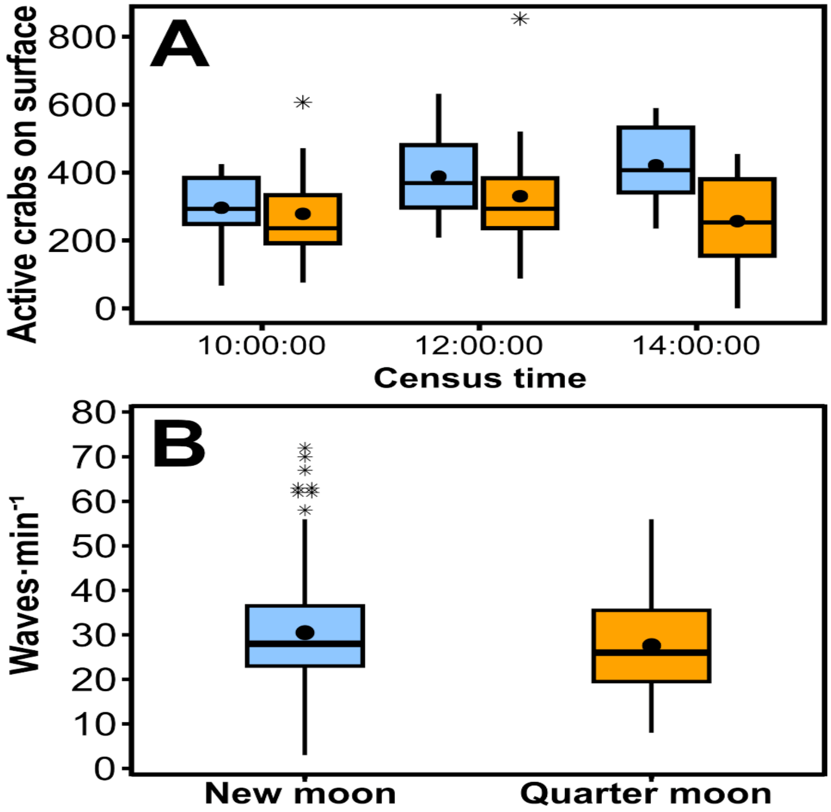
Table 1

Uca heteropleura surface activity (counts per 5 m² quadrat) at El Agallito Beach, Panama, during new moon (NE) and quarter moon (QM) phases. Data are from 11 quadrats and include SD, minimum, and maximum values across three time points.

Moon phase	Time	Mean	SD	Min	Max
NE	10:00:00	296	107	67	425
	12:00:00	388	132	208	632
	14:00:00	422	122	235	590
QM	10:00:00	279	153	76	607
	12:00:00	330	212	88	853
	14:00:00	257	149	0	455

Figure 3

Uca heteropleura activity and waving frequency at El Agallito Beach, Panama, across times of day and lunar phases



Note: ***A***. *Surface activity by time and moon phase (light blue = new moon, orange = quarter moon).* ***B***. *Waving frequency (per minute) during each phase.*

No significant differences were found among quadrat or census times in the number of *U. heteropleura* observed on the surface. The interaction between moon phase and census times was also not significant; however, the number of active crabs on the surface differed significantly between moon phases (Fig. 3A), where the NE had higher individual counts (Table 2).

Table 2

Two-way ANOVA testing moon phase, census time, and their interaction on Uca heteropleura activity at El Agallito Beach, Panama.

Terms	**d.f.**	**Sum of squares**	**Mean squares**	**F**	**P**	**Tukey HSD**	**Diff.**	**Adj. P**
Moon phase	1	105760	105760	4.74	0.034	QM - NE	-80.06	0.033
Census time	2	60510	30255	1.36	0.266			
Moon:Census	2	63433	31716	1.42	0.250			
Residuals	60	1339749	22329					

Note: Table shows degrees of freedom (d.f.), pairwise differences (Diff.), and adjusted p-values (Adj. P) for new moon (NE) and quarter moon (QM) phases.

The waving frequency of 237 focal males was recorded during the NE phase, with an average of 30.43 ± 11.44 waves · min^{-1}. During the QM phase, the waving frequency of 149 crabs averaged 27.58 ± 10.81 waves · min^{-1}. Waving behavior differed significantly between the two lunar phases (Welch's t-test; t = 2.46, d.f. = 327, P = 0.014), with higher frequencies during NE (Fig. 3B). Male size also varied by lunar phase: larger crabs were more active during QM, while crab ChH was slightly greater during NE (Table 3). No significant associations were found between CL, CW or ChL and waving frequency. However, ChH was negatively associated with waving frequency ($F_{(1\text{-}379)} = 15.46$, $P < 0.001$; Fig. 4A).

Table 3

Welch's t-test comparing male Uca heteropleura size and waving frequency (waves/min) between new moon (NE) and quarter moon (QM) at El Agallito Beach, Panama.

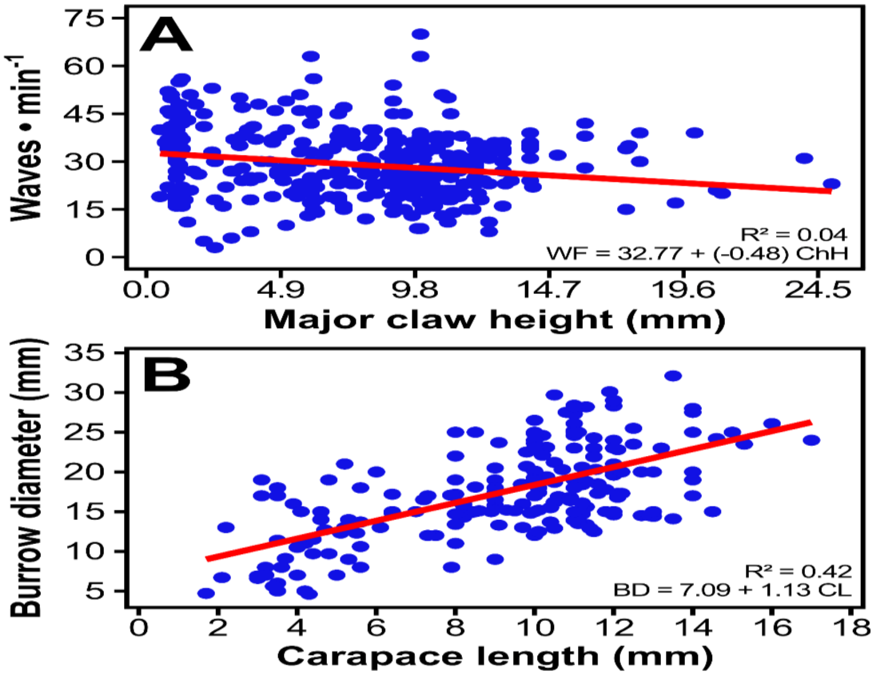
Biometry	Moon phase	Mean	SD	Diff. mean	t	d.f.	P
CL	NE	9.60	3.58	- 3.01	- 8.37	330	< 0.001
	QM	12.60	3.34				
CW	NE	14.09	4.92	- 3.24	- 7.85	383	< 0.001
	QM	17.33	3.17				
ChL	NE	17.48	8.08	- 2.80	- 3.16	297	0.002
	QM	20.28	8.69				
ChH	NE	8.41	3.67	1.01	2.08	241	0.039
	QM	7.40	5.16				

Note: Includes standard deviation (SD) and degrees of freedom (d.f.).

Burrow diameter was significantly associated only with carapace length ($F_{(1-202)} = 137.56$, $P < 0.001$; Fig. 4B).

Figure 4

*The relationship between Uca heteropleura major claw height and waving frequency (**A**), and the association between burrow diameter and carapace length (**B**) at El Agallito Beach, Panama.*



Discussion

In general, the density of fiddler crabs observed at the beginning of our study (5.71 crabs · m^2) can be considered low, consistent with densities of *Minuca pugnax* (6–15 burrows · m^2) in expanded ranges (Martínez-Soto et al., 2024). Similarly, the densities reported for species such as *M. rapax* (19.4 ± 5.7 crabs · m^2) and *M. vocator* (18.3 ± 8.7 crabs · m^2), as reported by Koch et al. (2005), can also be considered low relative to other species, such as *L. beebei* (50–200 crabs · m^2) in Panama (DeRivera et al., 2003) or *L. cumulanta* (56.3 ± 22.1 crabs · m^2) and *U. maracoani* (79.1 ± 9.6 crabs · m^2) in the Caeté mangrove estuary, Brazil (Koch et al., 2005). In contrast, the burrow density in our study (42.06 burrows · m^2) falls within the medium-density range, comparable to *M. osa* (20.45 burrows · m^2) in Ponuga, Panama (Lombardo, 2023a).

This discrepancy may also indicate a population with high turnover of surface activity, where a portion of individuals remain underground at any given time, possibly as a predator-avoidance or thermoregulation strategy. Alternatively, it could reflect age or sex differences in surface emergence (Backwell et al., 1998; Gruber et al., 2019; Koga et al., 2001; Reaney & Backwell, 2007). Fiddler crabs are known to retreat into and plug their burrows during overcast or rainy conditions, which reduces their visibility during counts (DeRivera et al., 2003).

Interestingly the density of *U. heteropleura* was higher (14.30 crabs · m^2) in October during favorable morning weather conditions. This aligns with the exceptionally heavy rainfall observed in Panama during the 2024 rainy season (IMHPA, 2024b; SINAPROC, 2024), which may have amplified this effect. Moreover, habitat variability plays a key role in burrow density, as seen in *M. pugnax* (Luk & Zajac, 2013), where densities varied from 17.92 burrows · m^2 in vegetated marshes to 127.52 burrows · m^2 in open marsh areas (Bertness & Miller, 1984). These factors highlight the need to interpret burrow counts cautiously, considering both behavioral and environmental influences.

The distribution patterns of the general population and *U. heteropleura* were consistently clumped, as confirmed by two different calculation methods. DeRivera et al. (2003) suggested that this pattern may be linked to drainage systems. A major factor influencing sediment heterogeneity and thus crab distribution is sediment grain size, which determines the availability of sediment-rich food patches for fiddler crabs (Mokhtari et al., 2015, 2016).

This heterogeneity likely contributes to the clumped spatial distribution of *U. heteropleura*, which aligns with optimal foraging theory (Pyke, 2019). A similar clumped pattern has been reported in *L. beebei*, which shares the same habitat, suggesting that comparable mechanisms may shape the behavioral and reproductive dynamics of *U. heteropleura*. For example, at high male densities, *Leptuca beebei* and *Austruca mjoebergi* females tend to seek mates, likely because nearby burrow abundance provides shelter from predator attacks, thereby lowering the risks and costs of mate-searching (DeRivera et al., 2003; Reaney & Backwell, 2007a; Gruber et al., 2019; Peso et al., 2016). In response, males shift their strategy, reducing mate-searching, increasing burrow defense and waving displays, possibly due to increased female activity and heightened competition among signaling males (DeRivera et al., 2003; Milner et al., 2011; Heatwole et al., 2018).

This study also examined the relationship between lunar phases, male size, and reproductive behaviors in *U. heteropleura*. In fiddler crabs, such as *L. pugilator*, adults regulate the timing of larval release in alignment with biweekly or monthly tidal cycles by adjusting the timing of courtship, mating, ovulation, and the onset of female incubation (Christy, 1978, 2011b). After mating and incubation, females release their broods during higher amplitude tides (new and full moons) to maximize larvae survival by reducing predation risk, improving dispersal, and ensuring larvae reach suitable habitats (Christy, 2003, 2011; Reaney & Backwell, 2007b). Errors in synchrony could result in larvae mortality due to inefficient transport or exposure to suboptimal temperatures (Christy, 2011; Kerr, 2015; Kerr et al., 2014). Similarly, our results show significant differences in both the activity of males and their morphological traits in line with lunar phase, particularly between the quarter moon and new moon. Larger *U. heteropleura* males were more active during the quarter moon, a pattern also observed in *L. pugilator* (Christy, 1978), suggesting their reproductive cycle is linked to neap tides. This pattern is also common in *A. mjoebergi*, where the mating period lasts 6–8 days during neap tides in each semilunar cycle. Correspondingly, sexually receptive females move through the population in search of a mate. To attract these females, males perform a conspicuous waving display near their burrows (Reaney & Backwell, 2007b), a behavior that was also evident in *U. heteropleura* during our study. Synchrony with neap tides may also provide a stable window for courtship and mating without the disturbance of stronger spring tides, giving larger males more opportunity to defend burrows and attract females (Christy, 1978, 2003).

Larger males are typically more successful in agonistic interactions and territoriality (Jennions & Backwell, 1996), allowing them to secure mates before the peak reproductive window closes (Reaney & Backwell, 2007b). Consistent with previous studies, these larger males mate with multiple females, who then retreat to incubate eggs in preparation for larval release during the full or new moon (Christy, 1978, 1987, 2003; Reaney & Backwell, 2007b).

Conversely, our study found that smaller *U. heteropleura* males, characterized by relatively shorter but taller major claws, were more active during the new moon. This increased activity was associated with a higher waving frequency. The increased waving frequency of these smaller males likely serves as a compensatory strategy to attract females that are still receptive before they retreat to begin egg incubation (Christy, 1978). This pattern is consistent with findings in *A. mjoebergi*, where females that mated later in the cycle selectively chose smaller males (Reaney & Backwell, 2007b). Thus, the increase in small *U. heteropleura* male activity during new moon may reflect a strategy to maximize mating opportunities before females become unavailable. This pattern suggests a conditional mating tactic in which smaller males strategically intensify their signaling investment later in the cycle. By doing so, they avoid the risk of engaging in competition (e.g., mate guarding or combat) with larger, more competitive males (Backwell & Passmore, 1996; Callander et al., 2012; Jennions & Backwell, 1996; Lima & Dill, 1990).

In most fiddler crab species, females time larval release to coincide with the following nocturnal spring tide and must therefore leave sufficient time for embryonic development after mating (Christy, 2011; Kerr, 2015). As a result, they face time constraints when selecting mates. Backwell & Passmore (1996) demonstrated that these temporal constraints influence female choosiness by limiting search time. They report that, at the beginning of the sampling period (when time constraints are minimal), females selectively sample the larger males in the population. Near the end of the sampling period (when the temporal constraints increase the costs of sampling), females are less choosy. Both larger and smaller *U. heteropleura* males seem to adopt different reproductive strategies in response to the lunar cycle and female choice. While larger males were more active on the surface during the quarter moon, smaller males took advantage of the new moon by ramping up surface activity, particularly through increased waving frequency.

This may allow both size classes of males to maximize their chances of mating in relation to context-dependent female choice. This dual strategy highlights the plasticity of reproductive behaviors and suggests that mating success in this species is highly context-dependent, influenced by both environmental cycles and intraspecific competition (Christy & Salmon, 1984; Callander et al., 2012).

Given that fiddler crabs experience multiple reproductive cycles, they are expected to show behavioral plasticity in their mating strategy whenever the payoffs of using different mating modes differ between reproductive events (Ribeiro et al., 2010). The observed patterns in activity and morphology support the hypothesis that lunar synchrony plays a crucial role in fiddler crab reproductive strategies (Christy, 1978, 2003, 2011b), including *U. heteropleura*. Our findings suggest that alternative reproductive strategies might be employed by different male size classes to secure matings. Larger *U. heteropleura* males dominate early in the reproductive cycle, probably due to superior waving quality or female choice, while smaller males appear to compensate by increasing waving intensity during the peak reproductive window around the new moon.

These findings highlight the importance of lunar timing in regulating fiddler crab reproductive behavior. The synchronization of courtship and egg incubation with lunar phases underscores its evolutionary significance for fitness and offspring survival (Christy, 2003). While our study provides valuable insights into the relationship between lunar phases and *U. heteropleura* behavior, further research is needed to better understand how individual crabs adjust their reproductive strategies over time, particularly as they grow and potentially transition between mating tactics.

Conclusion

This study supports the hypothesis that *U. heteropleura* adjusts courtship activity in synchrony with the lunar cycle, as observed in other fiddler crab species (Christy, 1978; Kim et al., 2004). Our results demonstrate that smaller males increased surface activity and waving during the new moon, when females are presumably more receptive, while larger males were more active during the quarter moon, indicating a size-based partitioning of reproductive effort (Christy & Salmon, 1984; Callander et al., 2012; Christy, 2003, 2011).

These findings fulfill the objective of identifying spatial distribution patterns and the influence of lunar phase and male size on reproductive behavior. The evidence that courtship activity shifts with both lunar phase and male size contributes to the growing understanding of how reproductive synchrony and alternative mating tactics evolve in relation to ecological cues and intraspecific competition (Backwell & Passmore, 1996; Araujo et al., 2013).

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