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Behavior and activity pattern of *Minuca osa* (Brachyura: Ocypodidae) from Ponuga, Veraguas, Panama

Comportamiento y patrón de actividad de *Minuca osa* (Brachyura: Ocypodidae) en Ponuga, Veraguas, Panamá

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ABSTRACT

From November 2022 to February 2023, observations to describe the behavior and the activity pattern of *Minuca osa* were conducted in Ponuga, Veraguas, Panamanian Pacific. Quadrants (5 m²) over four substrate types were also laid and the number and burrow diameter were recorded for density and relative fiddler crab associations to the substrate. Nine discrete behaviors were observed, with feeding and locomotion being the most frequent. There was a significant difference in elapsed time and frequency proportions among behaviors. Combat and waving were male-exclusive behaviors, and more time was spent waving than in combat. Behaviors were displayed non-randomly throughout the observation period with highest frequency between 10:30 a.m. and 12:30 p.m. The sex ratio was skewed towards males (2.4:1), while the carapace width of males and females averaged 23.40 mm and 18.42 mm, respectively. Quadrants covered with *Hymenocallis littoralis* had the most burrows (20.45 burrows/m²) with the smallest diameter, while the largest diameter burrows were found in mixed-cover quadrants. Maximum temperature and monthly accumulated rain significantly influenced the number of active crabs on the surface.

Keywords: burrow; carapace; fiddler crabs; major claw; quadrant; waving.

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RESUMEN

Entre noviembre de 2022 y febrero de 2023, se realizaron observaciones para describir el comportamiento y patrón de actividad de *Minuca osa* en Ponuga, Veraguas, Pacífico panameño. También se colocaron cuadrantes (5 m²) sobre cuatro tipos de sustratos y se registraron el número y diámetro de las madrigueras para estimar la densidad y las asociaciones relativas de los cangrejos violinistas al sustrato. Se observaron nueve comportamientos discretos, siendo la alimentación y la locomoción los más frecuentes. Se encontró una diferencia significativa en el tiempo transcurrido y las proporciones de frecuencia entre los comportamientos. La lucha y el gesto de “saludo” fueron comportamientos exclusivos de los machos, los cuales invirtieron más tiempo en el gesto de “saludo” que en combate. Los comportamientos se exhibieron de manera no aleatoria a lo largo del período de observación, con mayor actividad entre las 10:30 a.m. y las 12:30 p.m. La proporción de sexos estuvo sesgada hacia los machos (2.4:1), mientras que el ancho del caparazón de machos y hembras promedió 23.40 mm y 18.42 mm, respectivamente. Los cuadrantes cubiertos con *Hymenocallis littoralis* contaron con la mayor cantidad de madrigueras (20.45 madrigueras/m²) y con el diámetro más pequeño, mientras que las madrigueras con el diámetro más grande se encontraron en cuadrantes con cobertura mixta. La temperatura máxima y la precipitación mensual acumulada influyeron significativamente en el número de cangrejos activos en superficie.

Palabras clave: cangrejos violinista; carapacho; cuadrante; gesto de saludo; madriguera; quela mayor.

INTRODUCTION

Fiddler crabs are highly social crustaceans (Crane, 1975; Zeil et al., 2006) that have been the subject of numerous studies on behavior and ecology (Crane, 1975; Christy and Salmon, 1984; Christy, 1987; Rosenberg, 2014, 2020; Shih et al., 2016). One area of research that has received particular attention is their time budgets, which refer to the allocation of time between different activities such as feeding, mating, combat, etc (Altmann, 1974). Time budgets are shaped by a variety of factors, including environmental pressures, social interactions, and predation risk (Lima and Dill, 1990; Koga et al., 2001; Christy, 2007; Neylan et al., 2019; Tina et al., 2019).

For example, during reproductive bouts, males allocate a significant amount of time to courtship and mate guarding, while females spend more time foraging and mate sampling (Crane, 1975; Christy and Salmon, 1984; Caravello and Cameron, 1987; Backwell and Passmore, 1996; Mokhlesi et al., 2011; Tina et al., 2019). Other studies have demonstrated that there are costs associated to social behavior and that fiddler crabs adjust their time budgets in response to predation risk, increasing their burrowing and flight behaviors under predation risk (Lima and Dill, 1990; Backwell et al., 1998; Koga et al., 1998, 2001; Christy, 2007; Takeshita and Nishiumi, 2022). Overall, these studies highlight the importance of time budgets and underlying factors that shape the behavior and ecology of fiddler crabs.

There are 35 recognized species of fiddler crab in Panama. Seven species, divided into three subgenera, may be found in the Caribbean: four species of *Minuca*, two species of *Uca*, and *Leptuca thayeri*. There are 28 species in the Panamanian Pacific, which are divided into four subgenera. Sixteen of these species are in the genus *Leptuca*, six in the genus *Uca*, five in *Minuca*, and *Petruca panamensis* (Rosenberg, 2014, 2020).

Minuca osa was recently reported in the Ponuga River, Eastern Montijo Gulf, Panamanian Pacific (Lombardo, 2022). The species had previously been described from Golfo Dulce, on the Pacific coast of Costa Rica (Landstorfer and Schubart, 2010). Aside from the former reports, there are no known studies on *M. osa* or its behavioral ecology; thus, understanding the time budget can provide valuable insights into its ecology. This is important, since the role of fiddler crabs as ecosystem engineers (Kristensen, 2008) is critical for the flow of energy, while connecting basal and upper trophic levels in mangrove ecosystems (Smith et al., 1991; Macintosh et al., 2002; Lindquist et al., 2009).

Males and females, have been preliminarily observed while performing various activities (e.g., feeding, waving), which creates a context where inter- and intra-specific interaction, especially between males and females, may allow the observation of contrasting adaptive strategies (Christy, 1983, 1987; Tina et al., 2019; Pardo et al., 2020). This makes fiddler crabs excellent models for studying the selective forces behind their adaptive responses. It is for this reason and the above-mentioned, that the objective of this investigation was to describe the behavioral repertoire of *M. osa* from the mangroves of the Ponuga river, Veraguas, Panama.

MATERIALS AND METHODS

Study site

Our study site was situated on the banks of the Ponuga River (7.864271°N/-81.014618°W), Veraguas, and is distinguished by a dense forest with a sandy-muddy substrate and woody vines flanking its borders. The substrate composition is an alluvium of fluvial-marine origin, characterized by permanent hydromorphism, clay texture, and saline saturation (Cámara et al., 2004). The typical vegetation of the area is dominated by canopy-forming mangrove species, which includes *Prioria copaiifera*, *Rhizophora racemosa*, *Pelliciera rhizophorae*, and *Avicennia germinans*. The understory is shaded and primarily composed of shrub-forming ferns (*Acrostichum aureum*) and lilies (*Hymenocallis littoralis*) (Lombardo and Rojas, 2022). The rainy season generally lasts from mid-April to late-December (ETESA, 2023).

Biometry, burrow abundance and density

A sample of 35 crabs was collected randomly for biometry reporting and analysis. Variables were carapace width (CW), carapace length (CL), chelae length (QL) and total weight (TW); a caliper (0.01 mm) and scale (0.01g) were used to measure individuals. The student t-test was used to compare the sexes and the relationships between biometric variables were explored with regression.

The relationship between substrate cover and burrow diameter and abundance was explored within ten randomly selected plots (5 m²). Substrate cover types consisted of: *H. littoralis*, *A. germinans* pneumatophores, a mix of *H. littoralis* and pneumatophores, and exposed mud. Burrow diameter past the entrance was measured using a compass and a caliper. Density and abundance of burrows were calculated, and the diameter by substrate cover was tabulated to identify possible size classes within groups. Normality and equality of variances were analyzed with the Anderson-Darling and Levene's test, correspondingly. Burrow diameters were compared with Welch's one-way ANOVA and Games-Howell post hoc test for pairwise contrasts. Burrow abundance through the transition from wet to dry season (November 2022 to February 2023) were evaluated with the Chi-squared test.

Behavioral repertoire

From November to December 2022, 94 focal *Minuca osa* individuals were randomly selected and observed within an open area under the shade of trees. Two observers recorded the behavior of focal individuals at a minimum distance of three meters, from different vantage points to avoid double sampling. Observations began from 06:30 a.m. to 4:30 p.m., or until rain forced the crabs to retreat to their burrows earlier. Focal individuals were selected randomly and observed through binoculars (10x42 mm) for 30 minutes. Observations were distributed over five sampling campaigns, each consisting of four consecutive days. Each day, new sampling patches were selected for unobstructed observation of crabs; thus, avoiding resampling of previous focal individuals.

Discrete behavior elements were recorded during field trips based on descriptions in the specialized literature (Crane, 1966, 1975; Christy and Salmon, 1984; Caravello and Cameron, 1987; Tina et al., 2019; van Himbeek et al., 2019). To further capture behavior without observer effects, two ground level cameras (Casio, 26mm, 1:2.8-6.5) were placed near active burrow entrances to record video of *M. osa* individuals. Video capture was set to 90 minutes, time after which the cameras were placed in a different area. Footage was reviewed using opensource VLC media player at varying speed (0.33x-8x) to describe

behavior. To identify potential predators of *M. osa*, another set of five trail cameras were installed from December 2022 to February 2023.

Total elapsed time for each behavior was converted to minutes with two decimal places and analyzed with the Chi-squared goodness of fit test to explore potential differences in frequency proportions between behaviors. Elapsed time among behaviors was treated with the Box-Cox transformation and then tested for normality; prior to the one-way ANOVA test. Pairwise comparisons were run with the Games-Howell test to identify the direction and significance of potential differences between behaviors. To compare the sexes elapsed time by behavior, the data was treated with the same transformation and then tested for normality (Anderson-Darling); male and female variance for each behavior were tested for equality (Bonett's test) prior to the student t-test ($\alpha = 0.05$).

To determine if behavior frequency was asymmetric in relation to specific day time segments, time bins were created from 6:30 a.m. to 4:30 p.m., where frequencies for each behavior were allotted. A plot was generated for each behavior where the "x" and "y" axes corresponded to time bins and frequencies, respectively. A center line representing the median of all data was drawn to quantify the number of runs (up or down) about the median. P-values for clustering of said frequencies (cumulative probability to Z) were calculated with the following equation:

$$Z = \frac{R - 1 \frac{2mn}{N}}{\sqrt{\frac{2mn(2mn - N)}{N^2(N - 1)}}}$$

where R is the total number of runs, m is the number of runs above the center line, n is the runs below the center line and N is the total number of frequency records for behaviors at specific time bins (Bujang and Sapri, 2018). To statistically determine which time bin accumulated the highest frequency, a Chi-squared test was conducted; contribution to the Chi-square statistic of each bin were used as criteria for diagnosis.

Activity patterns

In order to quantify the number of active crabs on the surface based on the prevailing weather conditions, censuses were carried out three times a day during seven sampling campaigns. Fiddler crabs were counted with binoculars in a permanent 78 m² quadrant marked by stakes. The quadrant was under a patch of *P. copaiifera* trees, where counts took place in the morning (6:30 a.m.), noon (12:30 p.m.), and afternoon (4:30 p.m.); the census was performed by the same observer to avoid potential bias. The sex ratio was evaluated using the Chi-squared goodness of fit test for each census.

A general linear model was fitted (stepwise) with the total number of crabs on the surface as response variable, while the predictors were the time of day, tide (high, ebb, low and flood), lunar phase, air temperature (min. max. and avg.), and monthly accumulated rain from each sampling campaign. Temperature and weather data were gathered from ETESA (2023) records. The aim was to explore the relationship between these factors and fiddler crab activity on the plot surface, by using their numbers as proxy.

RESULTS

Biometry, burrow abundance and density

A total of 35 individuals, twenty-six males and nine females, were captured for general biometric measurements (Fig. 1). The sex ratio (2.9:1) of this sample was significantly skewed towards the males ($\chi^2 = 8.26$, $P = 0.004$). The CW of males and females averaged 23.40 ± 2.15 mm and 18.42 ± 1.73 mm, respectively (Table 1). All comparisons yielded significant difference between the sexes, where males

were larger and heavier than females (Table 1). The best predictors of male CW were CL ($r^2 = 0.733$, $F_{(1,21)} = 57.54$, $P < 0.001$) and TW ($r^2 = 0.819$, $F_{(1,21)} = 94.99$, $P < 0.001$), while the relationship between female CW and CL ($r^2 = 0.951$, $F_{(1,7)} = 135.46$, $P < 0.001$) was the strongest.

Quadrants covered with *H. littoralis* had the most burrows (N = 454), with a density of 20.45 burrows/m². Two distinct groups were detected within this cover type; the first, averaged 21.36 ± 1.43 mm, while the second had 14.79 ± 1.60 mm mean diameter ($t = -26.37$, d.f. = 52, $P < 0.001$) (Table 2). There was no difference in diameter among quadrants within single cover types; however, the diameter difference was significant between cover types. Largest burrows in diameter were found in the mixed cover quadrants, while the smallest were located in *H. littoralis* quadrants (Fig. 2A). Difference in burrow abundance across date was only detected in quadrants covered by *H. littoralis* ($\chi^2 = 12.90$, $P = 0.012$) and *A. germinans* pneumatophores ($\chi^2 = 27.53$, $P < 0.001$). The cover types exhibited a significant contrast in the number of burrows counted during the transition from wet to dry season (Fig. 2B).

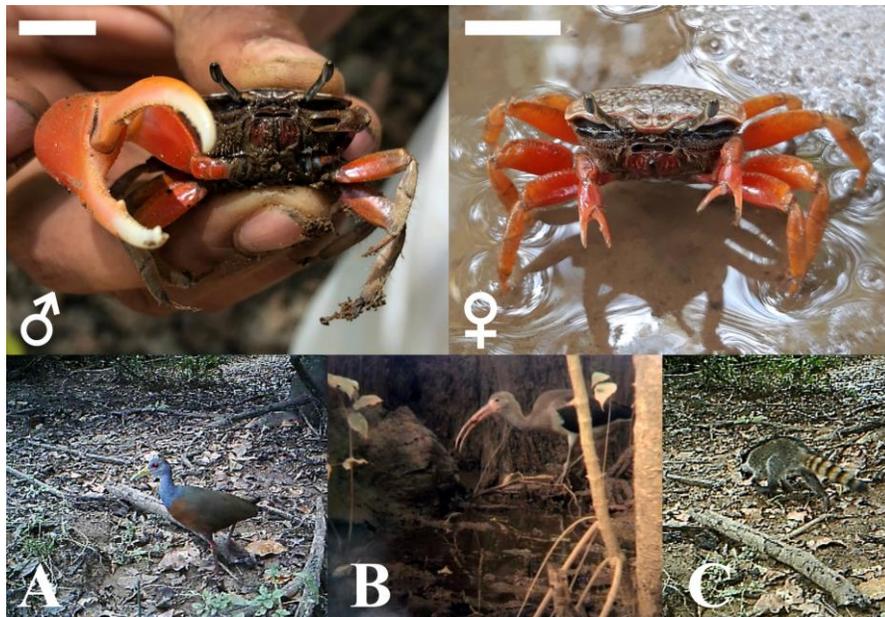


Fig. 1. *M. osa* and predators detected by camera traps in Ponuga, Veraguas, Panama. Top panels: male and female *M. osa*; scale: ♂ and ♀ = 10 mm. Panel A: gray-necked rail (*A. cajaneus*), B: white ibis (*E. albus*) and C: Raccoon (*P. lotor*)/Fig. 1. *M. osa* y depredadores detectados mediante cámaras trampa en Ponuga, Veraguas, Panamá. Paneles superiores: macho y hembra *M. osa*; escala: ♂ y ♀ = 10 mm. Panel A: rascón de cuello gris (*A. cajaneus*), B: Ibis blanco (*E. albus*) y C: Mapache (*P. lotor*).

Table 1. Biometrical statistics and comparison between the sexes in *M. osa* from the Ponuga River, Veraguas, Panamanian Pacific. CW is the carapace width, CL is the carapace length, QL is the chela length, and TW is the total weight (g). Standard deviation is SD, while the difference between means is DM/Tabla 1. Estadística biométrica y comparación entre sexos en *M. osa* del río Ponuga, Veraguas, Pacífico panameño. CW es el ancho del caparazón, CL es la longitud del caparazón, QL es la longitud del chela, y TW es el peso total (g). La desviación estándar es SD, mientras que la diferencia entre medias es DM.

Variable	Mean ± SD	Mín. - Max.	N	DM	t-test
♂ CW	23.40 ± 2.15	18.64 - 27.97	26	4.98	t = 6.27, d.f. = 33, P < 0.001
♀ CW	18.42 ± 1.73	14.97 - 20.95	9		
♂ CL	15.54 ± 1.18	13.09 - 18.08	23	2.31	t = 5.16, d.f. = 30, P < 0.001
♀ CL	13.23 ± 1.02	11.11 - 14.84	9		
♂ QL	35.74 ± 6.50	19.51 - 44.70	25	23.4	t = 10.65, d.f. = 32, P < 0.001
♀ QL	12.32 ± 1.00	10.71 - 13.82	9		
♂ TW	5.89 ± 1.30	2.91 - 8.14	23	3.25	t = 7.33, d.f. = 30, P < 0.001
♀ TW	2.64 ± 0.39	2.10 - 3.33	9		

Table 2. Burrow features of *M. osa* in quadrants (5 m²) with different substrate cover types from the Ponuga river, Veraguas, Panama. Cover types include HL-1 and HL-2 (*H. littoralis*), EX (exposed mud substrate), PNEU (*A. germinans* pneumatophore cover), and MIX (combination of the aforementioned types)/**Tabla 2.** Características de las madrigueras de *M. osa* en cuadrantes (5 m²) con diferentes tipos de cobertura de sustrato en el río Ponuga, Veraguas, Panamá. Los tipos de cobertura incluyen HL-1 y HL-2 (*H. littoralis*), EX (sustrato de lodo expuesto), PNEU (neumatóforos de *A.a germinans*) y MIX (combinación de coberturas).

Cover type	N	Av. burrow/quad.	Burrow/m ²	Diameter
HL-1	409	102.25	20.45	21.36 ± 1.43
HL-2	45	11.25	2.25	14.79 ± 1.60
EX	32	32	6.40	22.63 ± 5.65
PNEU	137	34.25	6.85	23.57 ± 3.82
MIX	42	42	8.40	27.39 ± 4.90

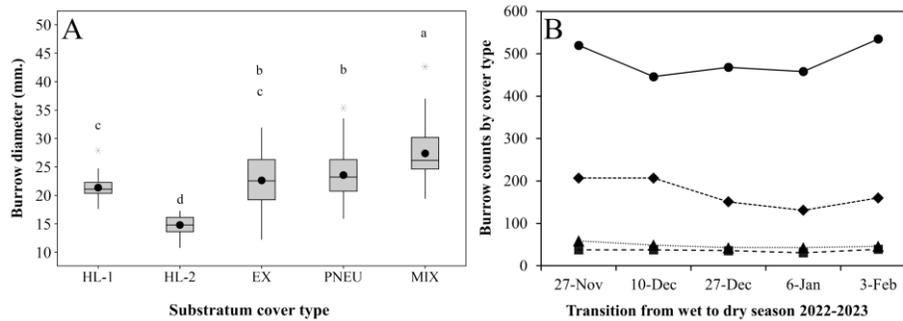


Fig. 2. Diameter of burrows by cover type (A) and burrow abundance during the transitional period from the rainy to the dry season of 2022-2023 (B). Cover types include HL-1 and HL-2 (*H. littoralis*), EX (exposed mud substrate), PNEU (*A. germinans* pneumatophore cover), and MIX (combination of the aforementioned types). Quadrat markers: circles = *H. littoralis*, diamonds = *A. germinans* pneumatophores, triangles = mix of cover types, and squares = exposed substrate. Boxes that share letters indicate no significant differences between the means of the respective categories/**Fig. 2.** Diámetro de madrigueras por tipo de cobertura (A) y abundancia de madrigueras a través de meses de transición de época lluviosa a seca 2022-2023 (B). Los tipos de cobertura incluyen HL-1 y HL-2 (*H. littoralis*), EX (sustrato de lodo expuesto), PNEU (neumatóforos de *A. germinans*) y MIX (combinación de coberturas). Marcadores para tipo de cobertura por cuadrante: círculos = *H. littoralis*; diamante = neumatóforos de *A. germinans*; triángulos = combinación de coberturas y cuadrados = sustrato expuesto. Cajas que comparten letras no presentan diferencias entre medias.

Behavioral repertoire

Out of 94 focal individuals, 66 were males while 28 were females (2.4:1); the ratio was significantly skewed towards the males ($\chi^2 = 15.36$, $P < 0.001$). *M. osa* individuals were observed displaying nine discrete behaviors; among them, feeding was the most frequently observed, closely followed by locomotion (Fig. 3A). There was difference among total elapsed time ($\chi^2 = 4066.90$, $P < 0.001$) and in the frequency proportions ($\chi^2 = 1519.91$, $P < 0.001$) of the nine behaviors. Elapsed time and behavior frequency were significantly related ($r^2 = 0.9836$, $F_{(1,7)} = 419.94$, $P < 0.001$) (Fig. 3B).

There was difference in the mean elapsed time between behaviors (ANOVA $F_{(1,8)} = 6.43$, $P < 0.001$) (Fig. 4A). Eight significant contrasts were found in pairwise comparisons, where grooming accumulated less elapsed time compared to five other behaviors (Table 3). Combat and waving were exclusively male expressed behaviors, with average durations of 1.20 ± 1.11 min. and 3.24 ± 2.81 min., respectively. Males spent on average more time waving than in combat ($W = 2042.00$, $P = 0.025$) (Fig. 4B). Comparisons between the sexes in elapsed time by common behavior showed no significant difference, except for burrow excavation, where male average elapsed time was higher (Table 4 and Fig. 4C).

Table 3. Differences between behaviors in *M. osa* from Ponuga, Veraguas, Panama. Stationary (STA), waving (WA), mobile (LOC), excavating (CTN), feeding (FD), grooming (CLN) and foaming (BU), all with mean display duration and standard deviation. The difference between means is DM, while P-values correspond to Games-Howell pairwise comparisons on transformed data/**Tabla 3.** Diferencias entre comportamientos en *M. osa* de Ponuga, Veraguas, Panamá. Estático (STA), “gesto de saludo” (WA), locomoción (LOC), excavar madriguera (CTN), alimentación (FD), acicalado (CLN) y espumando (BU), todos con duración media de visualización y desviación estándar. La diferencia entre las medias es DM, mientras que los valores P corresponden a las comparaciones por pares de la prueba Games-Howell en los datos transformados.

Behaviors		DM	95% C.I.	t	P
STA (1.09 ± 0.19)		0.569	(0.098, 1.040)	4.00	0.009
WA (1.18 ± 0.23)		0.666	(0.190, 1.142)	4.61	0.001
LOC (1.14 ± 0.22)	CLN (0.52 ± 0.84)	0.622	(0.151, 1.092)	4.37	0.003
CTN (1.14 ± 0.18)		0.620	(0.140, 1.101)	4.25	0.004
FD (1.12 ± 0.29)		0.603	(0.132, 1.074)	4.23	0.005
STA (1.09 ± 0.19)	LOC (1.14 ± 0.22)	-0.053	(-0.1054, -0.0002)	-3.11	0.048
WA (1.18 ± 0.23)	STA (1.09 ± 0.19)	0.098	(0.001, 0.194)	3.21	0.045
	BU (0.26 ± 0.96)	0.929	(-0.010, 1.868)	3.62	0.054

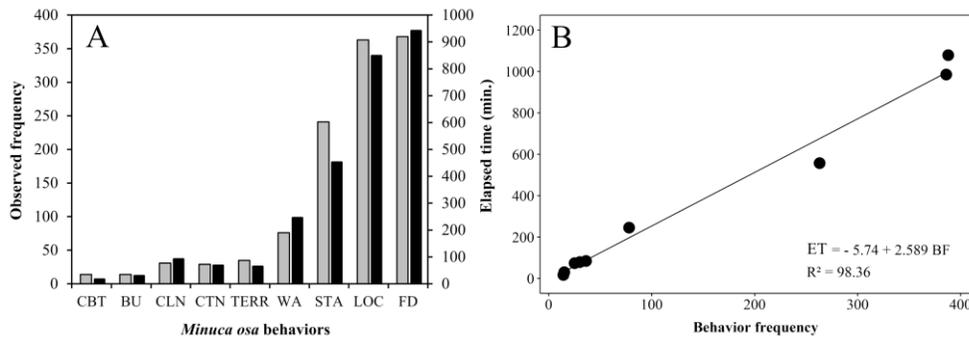


Fig. 3. Relationship of frequency and elapsed time in the expression of behaviors of *M. osa* from the Ponuga river, Veraguas, Panama. Panel A bars in gray are frequencies of observed behavior and black bars are elapsed time. Foaming (BU), combat (CBT), grooming (CLN), burrow excavation (CTN), feeding (FD), locomotion (LOC), stationary (STA), territorial display (TER) and waving (WA) in minutes/**Fig. 3.** Relación de frecuencia y tiempo transcurrido en la expresión de conductas de *M. osa* del río Ponuga, Veraguas, Panamá. Las barras grises del Panel A son frecuencias del comportamiento observado y las barras negras son el tiempo transcurrido. Espumar (BU), combate (CBT), acicalado (CLN), excavar madriguera (CTN), alimentación (FD), locomoción (LOC), estático (STA), exhibición territorial (TER) y “gesto de saludo” (WA) en minutos.

Table 4. Elapsed time by behavior between the sexes in *M. osa* from Ponuga, Veraguas, Panama. Common behaviors (Bx) in males and females: foaming (BU), grooming (CLN), burrow excavation (CTN), feeding (FD), locomotion (LOC), stationary (STA) and territorial display (TER) in minutes. Standard deviation is SD and asterisk indicates comparison significance on transformed data/Tabla 4. Tiempo transcurrido por comportamiento entre sexos en *M. osa* de Ponuga, Veraguas, Panamá. Comportamientos comunes (Bx) en machos y hembras: espumar (BU), acicalado (CLN), excavar madriguera (CTN), alimentación (FD), locomoción (LOC), estático (STA) y exhibición territorial (TER) en minutos. La desviación estándar es SD y el asterisco indica la significancia de la comparación en los datos transformados.

Bx	N	Mean ± SD	t-test
BU	♂ 12	2.24 ± 2.79	t = -0.42, d.f. = 10, P = 0.685
	♀ 2	1.16 ± 0.22	
CLN	♂ 29	1.79 ± 1.00	t = 0.90, d.f. = 4, P = 0.419
	♀ 5	3.58 ± 3.48	
CTN	♂ 23	2.63 ± 1.80	t = -2.86, d.f. = 21, P = 0.009*
	♀ 6	1.28 ± 0.52	
FD	♂ 256	2.51 ± 2.52	t = 0.46, d.f. = 206, P = 0.650
	♀ 112	2.66 ± 2.55	
LOC	♂ 260	2.34 ± 1.78	t = -0.20, d.f. = 183, P = 0.841
	♀ 103	2.32 ± 1.81	
STA	♂ 177	1.86 ± 1.60	t = 0.73, d.f. = 127, P = 0.465
	♀ 64	1.91 ± 1.60	
TER	♂ 18	2.67 ± 3.17	t = 1.18, d.f. = 29, P = 0.246
	♀ 13	3.34 ± 2.89	

Table 5. Test for randomness of behavior displays in *Minuca osa* from the Ponuga river, Veraguas, Panama. Behaviors (Bx), median (K), expected runs (ER), observed (longest) run about the median (OB), total runs ($\leq K$), runs above the median ($> K$), p-value for clustering (CLU), contribution to Chi-square (CO), time bin (TB) with highest frequency. Foaming (BU), combat (CBT), grooming (CLN), burrow excavation (CTN), feeding (FD), locomotion (LOC), stationary (STA), territorial display (TER) and waving (WA) in minutes. Asterisk indicates significance for clustering around a time bin/Tabla 5. Prueba de aleatoriedad de las manifestaciones de comportamiento en *Minuca osa* del río Ponuga, Veraguas, Panamá. Comportamientos (Bx), mediana (K), carreras esperadas (ER), carrera observada (más larga) sobre la mediana (OB), carreras totales ($\leq K$), carreras por encima de la mediana ($> K$), valor-P para agrupamiento (CLU), contribución a Chi-cuadrado (CO), intervalo de tiempo (TB) con mayor frecuencia. Espumar (BU), combate (CBT), acicalado (CLN), excavar madriguera (CTN), alimentación (FD), locomoción (LOC), estático (STA), exhibición territorial (TER) y “gesto de saludo” (WA) en minutos. El asterisco indica significancia.

Bx	K	ER - OB	$\leq K$	$> K$	CLU	Test	CO	TB
BU	1	6.09 - 3	7	4	0.016*	$\chi^2 = 19.47, P = 0.035$	5.10	11:30 - 12:30
CBT	1	5.36 - 5	8	3	0.382	$\chi^2 = 21.00, P = 0.021$	-	-
CLN	3	6.45 - 3	6	5	0.013*	$\chi^2 = 27.56, P = 0.002$	10.02	10:30
CTN	3	5.36 - 5	8	3	0.382	$\chi^2 = 33.80, P < 0.001$	-	-
FD	18	6.45 - 3	6	5	0.013*	$\chi^2 = 347.98, P < 0.001$	154.1	10:30
							1	
LOC	19	6.45 - 5	6	5	0.175	$\chi^2 = 361.94, P < 0.001$	-	-
STA	13	6.45 - 3	6	5	0.013*	$\chi^2 = 248.31, P < 0.001$	109.1	10:30
							8	
TER	3	6.09 - 5	7	4	0.225	$\chi^2 = 90.42, P < 0.001$	-	-
WA	3	6.45 - 3	6	5	0.013*	$\chi^2 = 67.47, P < 0.001$	26.95	10:30

Table 6. General linear model for the effect of significant predictor variables on the number of active *M. osa* crabs on the surface from a census plot in Ponuga, Veraguas, Panama/Tabla 6. Modelo lineal general para el efecto de variables predictoras significativas sobre el número de cangrejos *M. osa* activos en la superficie de una parcela censal en Ponuga, Veraguas, Panamá.

Factors	DF	Coef.	t	F	P
Constant		341.8	3.50		0.002
Max. temp.	1	-10.01	-3.36	11.32	0.003
Accum. rain	1	4.55	2.43	5.91	0.024
Max. temp.*Accum. rain	1	-0.1400	-2.38	5.68	0.027
Error	21				
Total	24				

Video observations

Individuals foraged near their burrow entrance and picked up substrate bits with the small chela. Crabs also cut dry leaf fragments before consuming them; on occasion, leaves were carried back to the burrow. Digging for burrow maintenance was common; however, we could not observe burrows being built *de novo*. Individuals carried a mass of mud between the small chela and the second ambulatory appendix and manipulated it by turning and rolling the mass in the immediate vicinity of the burrow entrance. *M. osa* individuals scooped fresh rolled mud to the third maxillipeds and sorted particles with intermittent bubble formation in the buccal region.

There was no construction of hoods or chimneys; rolled mud accumulated outside the burrow, forming a funnel-like entrance with a distinct path formed by the continuous transit of the resident. The third maxilliped is involved in grooming, specifically of the eye stalk, which is lowered into the ocular orbit for cleaning. As a result of digging, crabs were often covered in mud, which is often cleaned with the small chela and ingested as well.

Movement on the surface was slow, always near the burrow entrance, except for wandering females and during territorial displays, when crabs were observed charging at "trespassers". Burrow defense seemed to vary according to tenant sex; when approached by another individual, tenant females displayed three behaviors: they remained motionless until the distance was critical, lifted the body while raising both chela to the front and pointing down. Occasionally, the territorial display included extension of both second and fourth ambulatory appendixes to raise the body higher, leaving the first pair of ambulatories above ground. Alternatively, females fled inside the burrow or engaged in chasing away intruders by tackling them.

Males were recorded waving in the proximity of other males and also females. There seemed to be invisible boundaries to the space of both males and females; however, the criteria used by crabs regarding risk assessment and burrow defense remain unknown. When male tenants were approached, their large claw was raised and slightly opened. Threat displays included rising the body while exposing the merus and raising the major claw. Tenants faced approaching or nearby invaders by laterally moving the major claw in two almost seamless steps of upward and downward motion that could be repeated multiple times. The intensity of the display varied as the major claw was delayed while at the top of motion, the small chela was also raised while open, and the third ambulatory appendix was outwardly extended. Males seldom engaged in combat, but when threat displays failed to deter invaders, both males engaged in ritualized major claw waving, leading up to the crossing of the claws. Male major claws met at the base of the dactylus-pollex and seemed not to clasp their opponent. At this stage, the males pushed each other back and forth until one member of the pair withdrew.

We were not able to observe females being attracted to particular males during or after waving, but we did observe females entering burrows held by males. Females were observed wandering away from their burrow by several body lengths to enter other burrows, then moving on to different areas. Not all female visits were welcomed, as males were observed rejecting approaching females by pushing them away with the major claw.

Trail cameras captured three potential predators during daytime hours: raccoons (*Procyon lotor*), gray-cowled wood-rails (*Aramides cajaneus*), and white ibis juveniles (*Eudocimus albus*); the latter was the only confirmed case of predation observed directly in the field (Figs. 1A-C).

Activity Patterns

As elapsed time between the sexes was not significantly divergent, the pooled data was used to test for randomness in the frequency of behavioral displays in relation to the time of day. Five behaviors were displayed non-randomly with significant difference in their frequency throughout the observation period (Table 5). The majority of behaviors in the focal individual group were displayed between 10:30 a.m. and 12:30 p.m. (Fig. 5).

Similarly, fiddler crabs from the activity pattern plot also remained on the surface in a significantly higher proportion during the morning hours ($\chi^2 = 58.11$, $P < 0.001$). There was a disproportioned number of males on the surface throughout the day in all the census ($\chi^2 = 593.92$, $P < 0.001$), on occasion with a skewed sex ratio as high as 23:1. For this reason, no further analysis involving sex as a factor were conducted. The mean number of crabs on the surface also varied according to moon phase (ANOVA $F_{(1,3)} = 8.26$, $P = 0.004$), where crabs were significantly more abundant during crescent and last quarter moons (Fig. 6A). There was no difference in the mean number of crabs on the surface between tides (ANOVA $F_{(1,3)} = 0.87$, $P = 0.490$) (Fig. 6B). Other predictor variables with significant effect on the number of active crabs on the surface were maximum temperature, accumulated rain, and their interaction term max. temp.*accum. rain ($r^2 = 0.8445$) (Table 6 and Figs. 6C-D).

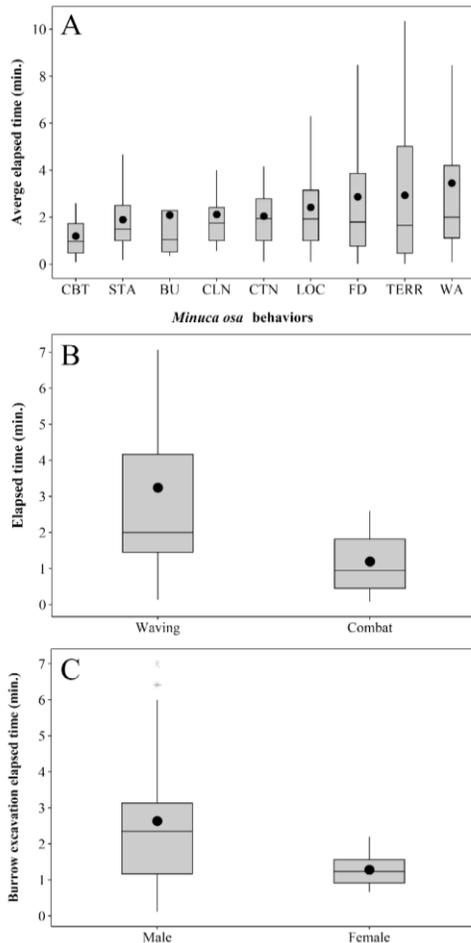


Fig. 4. Distribution of time spent in different behaviors of *M.osa* in Ponuga, Veraguas, Panama. Foaming (BU), combat (CBT), grooming (CLN), burrow excavation (CTN), feeding (FD), locomotion (LOC), static (STA), territorial display (TER), and waving (WA) in minutes/ Fig. 4. Distribución del tiempo transcurrido en diferentes conductas de *M. osa* en Ponuga, Veraguas, Panamá. Espumar (BU), combate (CBT), acicalado (CLN), excavar madriguera (CTN), alimentación (FD), locomoción (LOC), estático (STA), exhibición territorial (TER) y “saludo” (WA) en minutos.

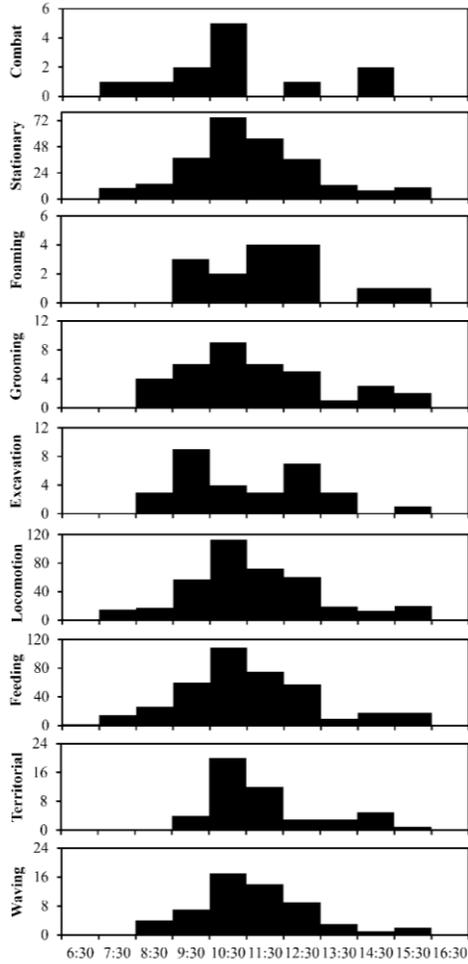


Fig. 5. *M. osa* discrete behaviors and their frequencies along daytime activity from Ponuga, Veraguas, Panama/ Fig. 5. Elementos discretos de conducta y sus frecuencias en *M. osa* durante actividad diurna en Ponuga Veraguas, Panamá.

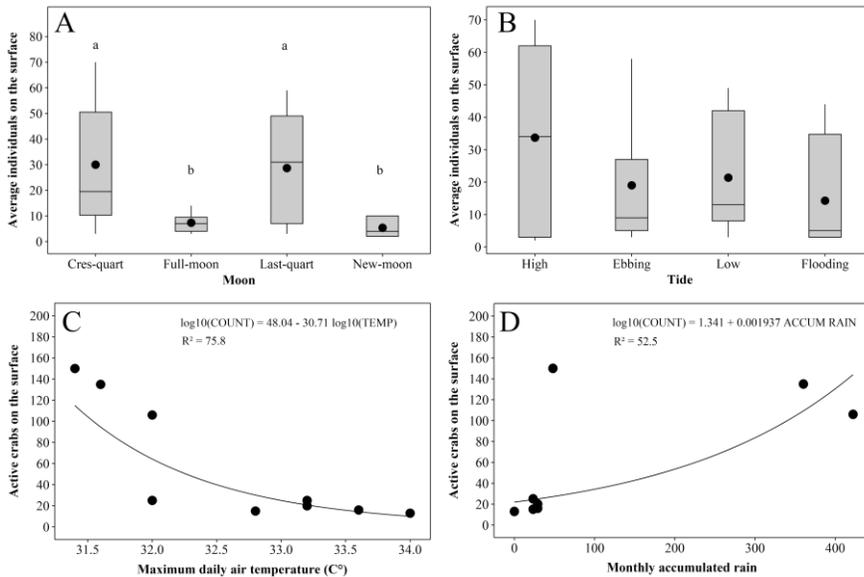


Fig. 6. Relationship between thermal tensors by prevailing meteorological variables, tides and phases of the moon and *M. osa* number of active crabs on the surface from Ponuga, Veraguas, Panama/ Fig. 6. Relación entre tensores térmicos por variables meteorológicas predominantes, mareas, fases de la luna y número de cangrejos *M. osa* activos en superficie de Ponuga, Veraguas, Panamá.

DISCUSSION

Comparatively, specimens captured in this study were larger than those from Golfo Dulce (Landstorfer and Schubart, 2010) as well as those from a previous sample from Ponuga and Mata Oscura (Lombardo, 2022). Our results confirm prior research showing that in most fiddler crab species, males are larger than conspecific females (Crane, 1975; Negreiros-Fransozo et al., 2003; Cardoso and Negreiros-Fransozo, 2004). This is the case since fiddler crabs are sexually dimorphic, with males' major claw accounting for up to 40% of their total body mass, a structure contributing to such size differences between the sexes (Crane, 1975). Allometric growth in relation to maturation can also explain such size differences; as demonstrated in *L. leptodactyla*, where males mature at larger sizes than females, most likely because for males, mating success typically depends on size; thus, they invest energy in growth, whereas females invest in egg production (Cardoso and Negreiros-Fransozo, 2004).

In marine crustaceans, deviations from a 1:1 sex ratio are common (Wenner, 1972; Johnson, 2003). Many fiddler crab species show male-biased sex ratios, such as *M. pugnax* (Wolf et al., 1975; Christy and Salmon, 1984), *Austruca lactea* (Frith y Brunenmeister, 1983), *A. annulipes*, *A. bengali*, *A. perplexa*, *Gelasimus hesperiae*, *Tubuca forcipate*, *T. urvillei* (Jaroensutasinee y Jaroensutasinee, 2004). In general, skewed sex ratios in fiddler crabs could be caused by size class differences and sex specific mortality (Johnson, 2003); although, the relative contribution of predation to the male-biased sex ratio in *M. osa* may not be trivial. Fiddler crabs are regular constituents of *E. albus* diet (Kushlan, 1979; Christy, 1982), and it was observed preying on *M. osa*. Other known crustacean predators such as *P. lotor* (Lotze and Anderson, 1979) and *A. cajaneus* (Silva e Silva and Olmos, 2015) are present; however, it remains to be demonstrated if these predators favor females over males as prey (Bildstein et al., 1989); if so, this could shift the sex ratio towards males.

This is the first time the distribution of *M. osa* has been described in relation to specific substrates. The most burrows and highest density were found in *H. littoralis* quadrants. The intensity of physiological stressors in this microhabitat might be comparatively lower due to the combined effect of shade from its foliage, considering that canopy cover influences temperature and water availability (Nobbs and Blamires, 2015, 2017). This might be the case, as fiddler crab spatial distribution across the mangrove ecosystem is influenced by physiological stressors independently of sympatric interactions (Nobbs, 2003; Nobbs and Blamires, 2017; Peer et al., 2018).

In *M. osa*, the burrow diameter was different between cover types; thus, physiological stressors, especially during the transition from the rainy to the dry season, may condition burrow distribution. This is likely the case, as the smallest diameter burrows were located in the *H. littoralis* quadrants, while the larger diameter burrows were in the mixed-cover quadrants. Perhaps larger individuals can tolerate desiccation rates in exposed habitats more efficiently (da Silva et al., 2020; Levinton, 2020). Provided crab size is correlated with burrow features (Maheta and Vachhrajani, 2023), the observed distribution pattern according to substrate cover type might be primarily determined by such physiological stressors.

Minuca osa individuals spent more time feeding and moving than in seven other behaviors. This might be indicative of nutrient-poor diet through sediment and dry leaves (Wolcott and O'Connor, 1992). Fiddler crabs might adjust their time budgets by adopting two possible strategies, for example, *Paraleptuca chlorophthalmus* expends minimal energy by remaining almost motionless and feeding despite nutrient-poor sediment near the burrow. Alternatively, *G. vocans* is highly mobile, exploiting nutrient-poor sediment over a large area (Weis and Weis, 2004; Nallos and Macusi, 2023). In contrast, *G. tetragonon* feeds on nutrient-rich algae and its time budget for feeding is significantly smaller compared to the former species (Weis and Weis, 2004).

Similar to *M. osa*, variation in allocated time and frequency of antagonistic behaviors, foraging, locomotion, and grooming has been reported in various species, including *A. annulipes* (Tina et al., 2016; Nallos and Macusi, 2023), *L. panacea* (Caravello and Cameron, 1987), *T. capricornis*, *T. urvillei*, *T. alcocki*, and *P. crassipes* (Nallos and Macusi, 2023). However, in this study, there was no difference in time budget between males and females, except for burrow construction. Because both sexes rely on stored energy during their reproductive periods, both male and female crabs devote a significant proportion of their time to foraging, promoting the observed similar time budget (Caravello and Cameron, 1987; Tina et al., 2016). Interestingly, aside from combat and waving being exclusive to males (Crane, 1966, 1975), the allocated time for burrow construction was higher in males.

A possible explanation for this difference, is *M. osa* males could be under sexual selection to construct additional chambers for females, implying this might be an underground copulating species (Christy and Salmon, 1984); mating on the surface was not observed. Apparently, wandering females as well as instances of such females entering male burrows in the absence of other stimuli might suggest this is the case (Zucker, 1984; Peso et al., 2016). This result should be interpreted with care, as our study period can be considered short, and the existence of such additional chambers in male burrows is yet to be confirmed in *M. osa*.

Burrows are critical for the reproduction and survival of fiddler crabs; for example, males defend a territory containing a burrow within an invisible border, where they signal at females that also defend a burrow (Crane, 1966, 1975; Christy, 1983; Peso et al., 2016; Pardo et al., 2020). Usually, territorial defenses concentrate on a single burrow (Mautz et al., 2011), thus considering nutritional resources are scarce and burrow construction is costly (Mokhtari et al., 2016; Carvalho et al., 2018; Pardo et al., 2020), territorial displays in males and females are expected, as observed in this study.

In this study, waving and territorial displays were observed in the same context; thus, it is difficult to determine if waving was directed at females, males "too close", or both; high burrow density further complicates the issue. These displays could serve the dual purpose of attracting a mate and repelling rivals (Crane, 1966, 1975; Christy and Salmon, 1984; Pope, 2005). Although it is not within the scope of our research, distance between burrow-holding individuals and the threat of other crabs' proximity seemed to play a role in the defense-escape response of *M. osa*; as demonstrated in *G. vomeris*, crabs modify their assessment of a threat depending on their distance away from the burrow and that of the threat (Hemmi and Zeil, 2003).

The investigation of fiddler crab activity is crucial for comprehending the impact of these invertebrates on the functioning of ecosystems (Kristensen, 2008; Kim and Christy, 2015; De Grande et al., 2018). Several studies have indicated that fiddler crabs feed, burrow, mate, and carry out other surface activities during diurnal low tide only and remain inside their burrows during high tide (Crane, 1975; Zeil et al., 2006; Kim and Christy, 2015); this is not the case for *M. osa*, as individuals were active on the surface independently. *M. osa* inhabits higher mangrove areas; thus, flooding tides are episodic and mainly concentrated during the rainy season (Lombardo, 2022; Lombardo and Rojas, 2022), allowing such extended activity.

The present study examined the relationship between temperature, precipitation, moon phase and crab counts on the surface. Our findings indicate that as the air temperature decreased, more crabs emerged from their burrows. This trend is consistent with previous research that suggests the number of crabs on the surface is influenced by their tolerance to thermal stress (da Silva et al., 2020; Levinton, 2020). Although we did not observe mating or spawning in the field, higher *M. osa* crab counts on the surface during crescent and last quarter moons might be related to reproductive timing (Christy, 2003). This might be the case, provided that female fiddler crabs remain inside burrows to incubate eggs and most release larvae close to the time of high tide on large amplitude tides near sunrise and sunset on two days of each semi-lunar tidal amplitude cycle, normally near full and new moons (Christy, 1983, 2003; Kerr, 2015). In contrast, an increased number of crabs is expected to be active in crescent and last quarter

moons, as females may be on the surface and receptive to male courtship displays (Backwell and Passmore, 1996; Murai y Backwell, 2005); more research is required to confirm this pattern in *M. osa*.

The spatiotemporal distribution, activity, and abundance of fiddler crabs have been shown to be related to physiological stressors (Christy, 2003; Kerr, 2015; Nobbs and Blamires, 2015, 2017), and timing with tides and moon phase (Christy, 1983, 2003; Kerr, 2015), which may explain the trend observed in this study. However, more accurate measurements and consideration of other factors, such as habitat quality, predation risk, and resource availability, may improve future studies to better understand crab behavior and population dynamics in *M. osa*.

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