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Variation in antipredator responses of the fiddler crab *Uca heteropleura* (Brachyura: Ocypodidae) at El Agallito beach, Panama

Variación en las respuestas antipredatorias del cangrejo violinista *Uca heteropleura* (Brachyura: Ocypodidae) en playa El Agallito, Panamá

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Abstract

A population of *Uca heteropleura* was studied to examine variation in male antipredator and reproductive behaviors across contrasting lunar phases at El Agallito Beach, Panama (April–July 2025). Crab responses to simulated avian predator fly-bys were quantified using a bird model passed over 5 m² quadrats. Habituation was assessed with repeated exposures (three passes), while single-pass trials evaluated baseline escape responses. Focal individuals were measured (carapace width-length and major chela height-length), and waving frequency and reemergence time were recorded as proxies of reproductive effort and risk-taking, respectively. A total of 616 individuals were recorded with a mean carapace width of 15.9 ± 4.1 mm. Repeated predator exposure significantly reduced escape responses, indicating rapid habituation. In single-pass trials, surface activity and waving frequency were significantly higher during full and new moons compared to quarter moons. Waving

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frequency showed a weak but significant negative relationship with body size. Escape probability declined with increasing carapace width, with larger individuals less likely to flee and more likely to remain on the surface. Similarly, non-responsive individuals were significantly larger than those that escaped. Reemergence time was shorter during full and new moons, suggesting higher risk tolerance under peak reproductive conditions. These results indicate that antipredator behavior, signaling effort, and risk-taking are modulated by both body size and lunar phase. This coupling of individual state and environmental context highlights the dynamic nature of risk-taking behavior, where crabs continuously adjust their responses to balance predation risk against reproductive and foraging benefits.

Keywords: Spring tide, predator, escape, burrow, semilunar cycle

Resumen

La variación en los comportamientos antipredatorios y reproductivos de machos de *Uca heteropleura* fue estudiada durante fases lunares contrastantes en playa El Agallito, Panamá (abril–julio, 2025). Las respuestas ante depredadores aviares simulados se cuantificaron mediante el paso de un modelo de ave sobre cuadrantes de 5 m². La habituación se evaluó con exposiciones repetidas, mientras que ensayos de un solo pase del modelo midieron las respuestas de escape basales. En individuos focales se midió el caparazón y la que la mayor, registrando la frecuencia de movimientos de esta y el tiempo de reemergencia como indicadores de esfuerzo reproductivo y tolerancia al riesgo de depredación. Se registraron 616 individuos con ancho medio del caparazón de 15.9 ± 4.1 mm. La exposición repetida al modelo redujo los escapes, evidenciando habituación. En ensayos de un solo pase, la actividad en superficie y la frecuencia de movimiento de quela fueron significativamente mayores durante luna llena y nueva en comparación con fases de cuarto. Dicha frecuencia mostró una relación negativa con la talla, y la probabilidad de escape disminuyó con el aumento del ancho del caparazón. El tiempo de reemergencia fue más corto durante luna llena y nueva, sugiriendo mayor tolerancia al riesgo de depredación en picos de actividad reproductiva. Los resultados indican que el comportamiento y el esfuerzo reproductivo están modulados por la talla y la fase lunar, permitiendo a los cangrejos equilibrar estratégicamente la toma de riesgos y la reproducción.

Palabras clave: Marea viva, depredador, escape, madriguera, ciclo semilunar

Introduction

Animal boldness is generally defined as the tendency of an individual to take risks when facing novel or potentially dangerous situations (Sih et al., 2004; Ward et al., 2004). Under predation pressure, risk-taking behavior can directly affect escape success and survival, with important consequences for population structure and dynamics. At the same time, excessive risk avoidance may limit access to critical resources such as food, mates, or breeding territories (Lima & Dill, 1990). These opposing selective pressures create a trade-off between survival and future reproductive success, providing a framework for the evolution of risk-taking strategies that maximize fitness under variable ecological conditions (Réale et al., 2010; Gruber et al., 2019). Risk-taking behavior is closely linked to reproductive state, with individuals increasing exposure to predation when reproductive

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opportunities are high (Magnhagen & Löf, 2006).

Uca heteropleura (Smith, 1870) is a common fiddler crab inhabiting open intertidal mudflats in the Pacific coast of Panama, where males display a conspicuous repertoire of courtship behaviors including claw waving, body lifting and leg movements (Crane, 1975; Lombardo, 2025b; Fig. 1D). At El Agallito Beach (Herrera Province, Panama), *U. heteropleura* occurs alongside a diverse assemblage of avian predators that forage visually on surface-active crabs (Backwell et al., 1998; Hugie, 2004; Lombardo, 2025a). Predators primarily detect fiddler crabs visually, from above or at low angles, making overhead movement and rapid fly-bys salient cues of predation risk for crabs (Backwell et al., 1998; Hugie, 2004). This ecological context is therefore well suited for examining trade-offs between male survival and reproductive investment, as conspicuous courtship displays may enhance mating success while simultaneously increasing visibility to predators (Backwell & Passmore, 1996; Reaney & Backwell, 2007).

Previous studies have shown that boldness and antipredator responses in fiddler crabs are highly context dependent, influenced by factors such as body size, local density, and social environment, and are closely tied to trade-offs between reproductive and survival behaviors (Backwell & Passmore, 1996; Reaney & Backwell, 2007; Lombardo, 2025a). For example, *Gelasimus vomeris* as well as *Uca princeps* have been shown to make graded escape decisions based on perceived predation risk, including whether to retreat and how long to remain inside burrows, indicating that antipredator responses reflect active risk assessment rather than fixed reaction patterns (Hemmi, 2005a; Hugie, 2004). Body size and claw morphology may further mediate these decisions, as costs and benefits of risk-taking under predation pressure might be experienced differently between large and small crabs (Backwell & Passmore, 1996; Reaney & Backwell, 2007).

The reproductive activity of various fiddler crab species is synchronized with

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lunar cycles (Table 1) driven by tidal amplitude, with peaks in courtship and surface activity occurring near new and full moons, when spring tides prevail (Christy, 1978; Morgan, 1996; Kerr, 2015). Accordingly, antipredator behavior may vary with lunar phase, consistent with theoretical expectations of trade-offs between predator avoidance and reproductive activity (Lima & Dill, 1990; Gruber et al., 2019). Such variation could be evaluated using escape decisions and time to reemerge from burrows following predator exposure, two commonly used indicators of perceived predation risk in fiddler crabs (Hemmi, 2005a; Hugie, 2004).

In contrast, during lunar phases associated with lower tidal amplitudes, such as quarter moons (neap tides), reproductive activity may be reduced or less synchronized (Christy, 1978; but see Kim et al., 2004). During these periods, the potential benefits of risk-taking could be lower, and individuals may adopt conservative strategies, characterized by a greater likelihood of retreat and longer reemergence times following perceived predation risk (Lima & Dill, 1990; Gruber et al., 2019).

The general objective of this study was to examine how male *U. heteropleura* balance reproductive activity and antipredator behavior across contrasting lunar phases by quantifying their responses to simulated avian predator fly-bys. To address this objective, we pursued two specific objectives: to assess changes in surface activity before and after predator exposure as an indicator of reproductive and above-ground activity, and to evaluate individual retreat decisions and reemergence time as indicators of antipredator and risk-taking behavior. Based on the trade-off between predation risk and reproductive investment, we predicted that (1) surface activity prior to predator exposure would differ across lunar phases, and that the proportional reduction in surface activity following predator fly-bys would vary with lunar phase; and (2) individual males would differ in their likelihood of retreat and in their time to reemerge following predator exposure across lunar phases. Together, these predictions allow evaluation of how antipredator behavior,

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recovery dynamics, and reproductive activity are integrated in an ecological context.

Table 1

Summary of reproductive timing and cycle type in fiddler crab species across latitudinal gradients.

Species	Region	Reproductive timing relative to spring tides	Reproductive cycle	Source
Leptuca pugilator	Atlantic, USA	Mating ~ 4–5 days before; larval release ~7 days after.	Semilunar	Christy (1978)
Minuca pugnax	Atlantic, USA	Mating ~4–5 days after.	Semimonthly	Greenspan (1982)
Austruca annulipes	Mideast, Kuwait	Activity and emergence vary with lunar phase and tidal amplitude.	Semilunar	Al-Musawi & Wagner (2012)
Leptuca terpsichores *Leptuca deichmanni*	Panama, Pacific	Larval release synchronized with spring tides; timing shifts with temperature.	Semilunar	Kerr et al. (2014)

Note: *Reproductive timing is expressed relative to spring tides (periods of maximum tidal amplitude during new and full moons). Semimonthly cycles indicate activity occurring twice per lunar month, whereas semilunar cycles reflect synchronization with the spring–neap tidal cycle.*

Materials and methods

Study site & sampling

Fieldwork was conducted at El Agallito Beach (8°00′13.2″ N; 80°24′11.2″ W), Llano Bonito, Chitré District, Herrera Province, on the Gulf of Parita (Fig. 1A). The site was selected for its accessibility and the high detectability of *U. heteropleura* during low tide, allowing direct behavioral observations.

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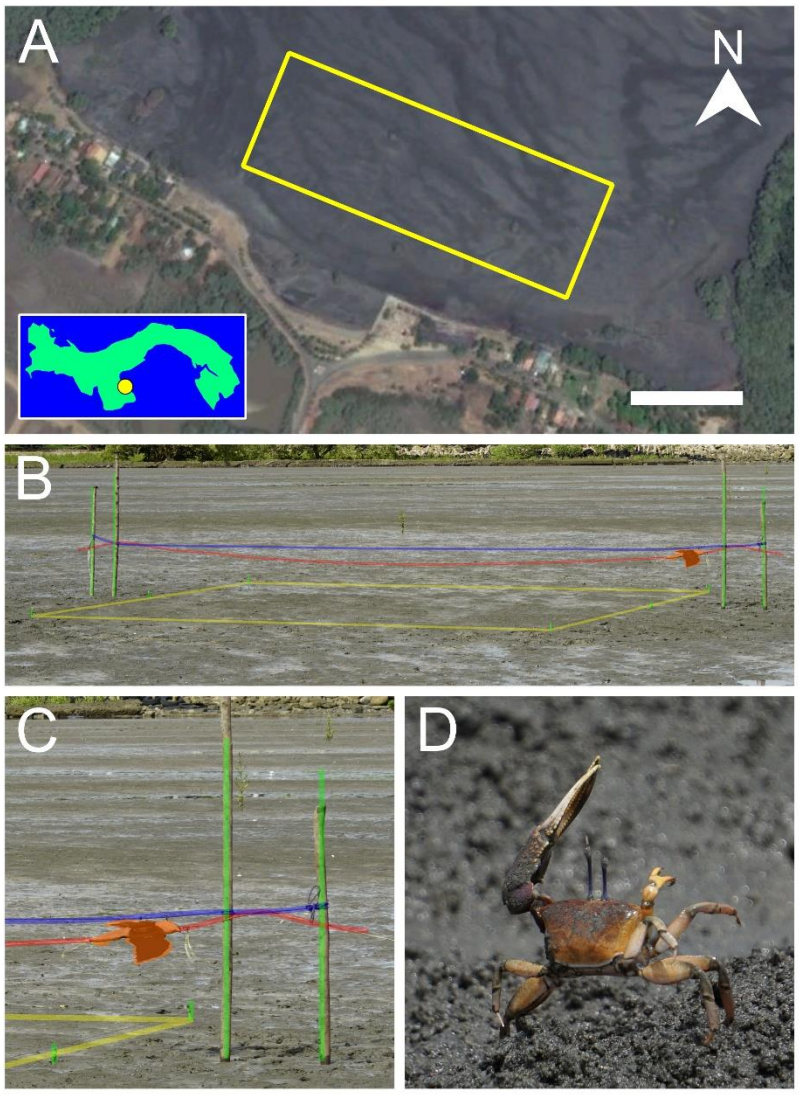
Figure 1

Sampling setup for trials evaluating the response of Uca heteropleura males to a simulated avian predator at El Agallito Beach, Pacific coast of Panama.



Note: *(A) Study site with general area of quadrat location in yellow (scale = 100 m). (B) Panoramic view of the 5 m² sampling quadrat (2.25 × 2.25 m), outlined in yellow; supporting stakes and poles are shown in green. (C) Bird model (orange) suspended*

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from the main line (blue), controlled by red guide lines for movement across the quadrat. (D) Waving male U. heteropleura during courtship.

The site is an intertidal flat (sandy-muddy), with tidal recession reaching up to 1.6 km (Delgado, 1998). Vegetation on the edges includes mangrove species such as *Avicennia germinans*, *Rhizophora mangle*, *Laguncularia racemosa* and *Conocarpus erectus* (Tejada et al., 2022). The climate is tropical savanna (Köppen, 1936), with temperatures ranging 24–30°C and annual precipitation ~1,250 mm (IMHPA, 2024; Beck et al., 2018). Rainfall peaks in September, while the dry season extends from January to March (Delgado, 1998).

Sampling was conducted during five field trips between May and July 2025, strategically distributed across lunar phases: two during full or new moons and three during quarter phases. Sampling dates were treated as independent replicates within each lunar phase category. This design enabled the evaluation of antipredatory behavior under contrasting lunar conditions (Table 2).

Table 2

Sampling schedule during 2025 at El Agallito Beach, Pacific coast of Panama. Observations of Uca heteropleura activity were conducted during diurnal low tides. Tidal amplitude is presented in centimeters.

Sampling	Date	Lunar phase	Tidal amplitude
1	April 13	Full moon	15–448
2	May 17	1st quarter - Waxing half moon	61–451
3	June 7	3rd quarter - Waning half moon	110–405
4	June 17	3rd quarter - Waning half moon	421–439
5	July 22	New moon	64–442

Predation stimulus

Multiple quadrats were established per sampling date to test for habituation

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and single-pass behavioral trials, as repeated exposure to stimulus or disturbance can lead to habituation and reduced antipredator responses in prey species (Jennions et al., 2003). Separating habituation from single-pass trials ensured that behavioral responses measured in the latter were not confounded by prior exposure to the stimulus.

At each sampling date, 5 m^2 quadrats were randomly established within the activity area of crabs during low tide (Fig. 1B). To stimulate crabs on the surface, an approaching predatory bird was simulated using a silhouette model consisting of a wooden body (20 cm) and plastic wings (70 cm) (Fig. 1C). The bird model was mounted on a 6 m nylon line stretched between two 1.8 m posts positioned 2.5 m outside the quadrat. Two auxiliary lines allowed controlled movement of the model back and forth across the quadrat, simulating low flight ~30 cm above the substrate. Observers remained 5 m from the quadrat to minimize disturbance, and observations were conducted using binoculars (7 × 50 mm).

Habituation test

After establishing the experimental setup, initial counts of surface-active crabs were conducted within each quadrat (n = 32). To evaluate whether male *U. heteropleura* habituated to repeated predator exposure, we fitted a general linear model with three consecutive bird model passes as a fixed factor and quadrat as a random blocking factor to account for non-independence among repeated observations within quadrats. The response variable was the number of non-responsive crabs on the surface after each bird model pass. Model assumptions were evaluated by inspecting residual plots for normality and homoscedasticity. When the effect of simulated predator exposure was significant, pairwise comparisons were performed using the HSD Tukey test.

Single-pass trials

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A set of 37 quadrats was set in a similar fashion as above, and one pass of the predator bird model was then applied to evaluate antipredator responses. For each pass, the number of *U. heteropleura* individuals was recorded pre- and post-stimulus, classifying individuals as escape (retreated into burrow) or non-responsive (remained on the surface after bird model exposure). Variation in the number of individuals among sampling trips was assessed using a chi-square goodness-of-fit test, whereas comparisons between lunar phase categories were performed using independent two-sample *t*-tests. Analyses of crab abundance were conducted at the quadrat level, pooling observations within lunar phase categories (full and new moon *vs.* quarter phases). Differences in abundance between lunar phases, both prior to and after predator model passes, were assessed using independent two-sample *t*-tests. Differences in carapace width between behavioral categories (escape vs. non-responsive), as well as variation in the size of non-responsive individuals across lunar phases, were also evaluated using the same approach. Additionally, a binary logistic regression was used to examine the relationship between antipredator response (escape = 1, non-responsive = 0) and body size, with carapace width as predictor. The combined use of these approaches allowed assessment of both the predictive effect of body size on response probability (logistic regression) and direct comparisons of size between groups (*t*-tests).

Latency to reemergence was used as a proxy for risk-taking behavior, and it was defined as the time elapsed from burrow entry to reemergence at the surface following exposure to the bird predator model. Focal individuals were randomly selected during trials, including both behavioral categories. These crabs were captured manually and measured for carapace width and length (CW, CL) and major chela length and height (ChL, ChH) to examine size-dependent variation in risk-taking behavior. The effect of lunar phase (full and new moon *vs*. quarter phases) on latency was tested using an independent two-sample *t*-test. Focal individuals that did not reemerge within the observation period (90 seconds) following the stimulus

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were classified as non-reemerged.

In addition, chela-waving rates (movements min^{-1}) were recorded for randomly selected individuals, during each sampling date, outside quadrats to avoid disturbance effects associated with the experimental setup. These focal individuals were subsequently measured to evaluate relationships among signaling effort, body size, and lunar phase. Waving was also compared between lunar phases using independent two-sample *t*-tests.

Prior to analysis, data from single bird model passes were evaluated for normality and homogeneity of variances. Chi-square tests were performed on raw counts, while density values are presented for descriptive purposes. All analyses were conducted using a significance level of $\alpha = 0.05$. Model assumptions were assessed by evaluating normality and homogeneity of variances, and by inspection of residual plots for regression models. Data were curated in Microsoft Excel and subsequently analyzed in Minitab 19.

Results

Between April and July 2025, a total of 616 individuals were quantified on the surface of quadrats at El Agallito Beach. Mean carapace width was 15.9 ± 4.1 mm, whereas descriptive biometric measurements across sampling dates are summarized in Table 3. The fitted general linear model revealed a significant effect from bird model repeated exposure on crab response ($F_{2,62} = 9.60$, $p < 0.001$), and explained a substantial proportion of variance in the response variable ($R^2 = 0.729$).

Table 3

Male Uca heteropleura density and morphometrics at El Agallito Beach. Density is expressed as the number of individuals per square meter, while carapace width and length (CW, CL) and major claw height and length (ChH, ChL) are given in millimeters.

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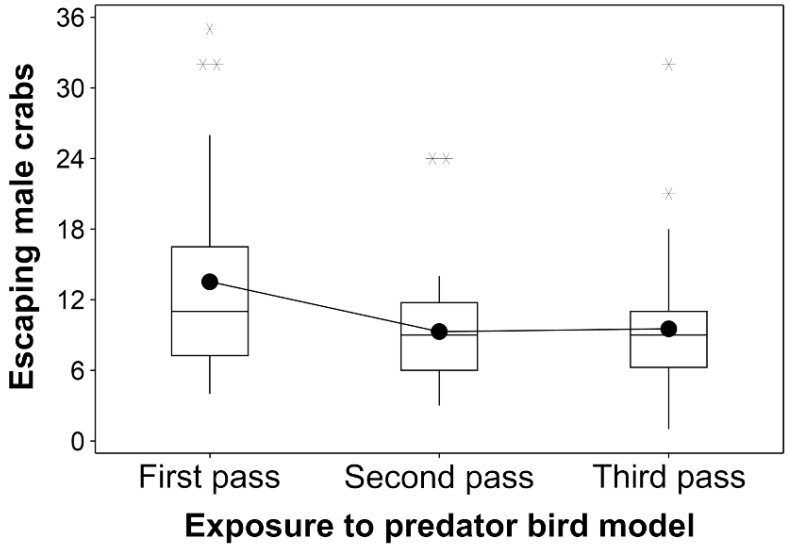
Date	Density	CW	CL	ChH	ChL
○ Full moon - April 13	14.5	17.5 ± 2.3	12.2 ± 2.5	12.0 ± 3.1	25.4 ± 6.4
◐ 1st quarter - May 17	6.2	17.1 ± 3.1	12.4 ± 2.3	9.9 ± 2.2	23.3 ± 5.8
◑ 3rd quarter - June 7	2.2	14.4 ± 3.1	9.3 ± 1.9	7.4 ± 2.0	15.8 ± 5.8
◑ 3rd quarter - June 17	6.9	14.2 ± 2.1	10.3 ±1.6	9.8 ± 2.6	18.0 ± 7.7
● New moon - July 22	11.2	17.9 ± 6.2	9.7 ± 4.1	8.4 ± 3.9	18.8 ± 9.9

Quadrat also contributed significantly to variation in the response ($F_{31,62}$ = 4.76, p < 0.001). The mean number of crabs that escaped decreased after the first simulated predator exposure (1st: 13.53 ± 8.23; 2nd: 9.28 ± 4.91; 3rd: 9.53 ± 6.03). Tukey *post hoc* comparisons indicated that the number of escaping crabs after the first pass of the predator bird model, differed significantly from both the second (*t* = -3.90, p = 0.001) and third passes (*t* = -3.67, p = 0.001), whereas no difference was detected between second and third (*t* = 0.23, p = 0.971; Fig. 2).

Figure 2

Habituation following three successive bird predator model exposures in Uca heteropleura males from El Agallito Beach, Panama Pacific.



In single-pass trials, mean density across all sampling dates was 8.2 ± 4.7

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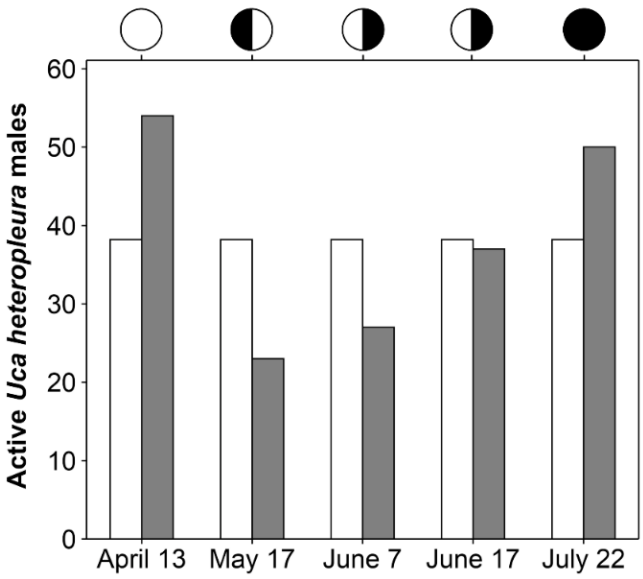
indiv. m^2, while the number of active individuals among sampling dates varied significantly (χ^2 = 19.55, df = 4, p = 0.001). To further evaluate these patterns, subgroup comparisons were conducted. No significant differences were detected between crab counts during full and new moon phases (χ^2 = 0.15, df = 1, p = 0.69), both of which exhibited higher abundances of surface-active crabs (Fig. 3). Likewise, no significant differences were observed among crab counts during quarter moons (May–June; χ^2 = 3.58, df = 2, p = 0.16).

Figure 3

Number of active Uca heteropleura males across sampling dates at El Agallito Beach, Pacific coast of Panama. Differences were assessed using a chi-square test.



Note: *White bars represent expected counts and gray bars denote observed individuals counts on the surface during each sampling date. Upper x-axis indicates the corresponding moon phase.*

Baseline surface activity, measured prior to bird predator model trials, showed significant crab count differences between lunar phases (*t* = 3.37, df = 33, p = 0.002), with greater surface activity during full and new moon relative to quarter moons (Fig.

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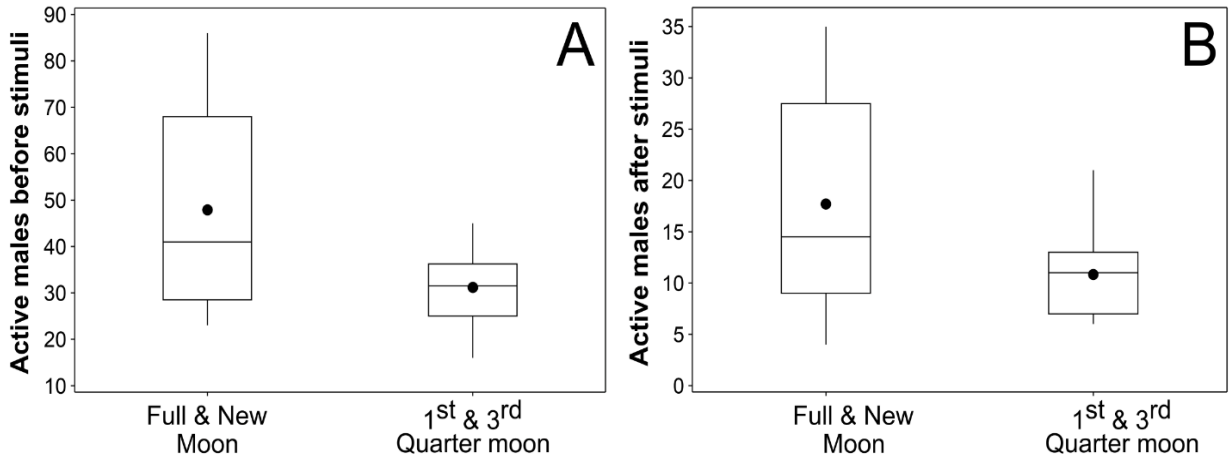
4A). A similar pattern was detected after predator stimuli (t = -2.79, df = 24, p = 0.010), with higher activity during full and new moon phases (Fig. 4B). Major claw waving frequency also differed significantly between lunar phases (t = 5.07, df = 67, p < 0.001), with higher waving rates recorded during full and new moon phases. Major claw waving frequency showed a slight but significant decrease with increasing carapace width (Linear regression; $F_{1,377}$ = 7.99, p = 0.005; R^2 = 0.02). Carapace width differed significantly among sampling dates (Welch's ANOVA; $F_{4, 22.97}$ = 29.66, p < 0.001). Games-Howell *post hoc* comparisons indicated that individuals sampled during quarter moon dates were significantly smaller than those from full or new moon, while no difference was detected between full and new moon dates (Table 4). Crabs from third quarter moon (June 7) were also significantly smaller than those from first quarter (May 17). In contrast, individuals from new moon (July 22) were significantly larger than those from quarter moon dates (May-June).

Figure 4

Uca heteropleura male response to bird model predator stimulus form single-pass trials at El Agallito Beach, panamanian Pacific.



Note: *(A) Crabs on the surface across moon phases before trials. (B) Corresponding counts by moon phase after predator model exposure.*

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Table 4

Pairwise comparisons of carapace width among sampling dates using the Games-Howell post hoc test following Welch's ANOVA.

Pairwise comparison	Difference of means	95% C.I.	*t*	p
May 17 ◐ *vs.* ○ April 13	-5.11	(-7.06, -3.16)	-7.49	**< 0.001**
June 7 ◑ *vs.* ○ April 13	-8.21	(-10.60, -5.82)	-10.20	**< 0.001**
June 17 ◑ *vs.* ○ April 13	-7.69	(-12.03, -3.36)	-6.25	**0.002**
July 22 ● *vs.* ○ April 13	0.35	(-4.63, 5.33)	0.21	1.000
June 7 ◑ *vs.* ◐ May 17	-3.10	(-5.33, -0.87)	-4.19	**0.004**
June 17 ◑ *vs.* ◐ May 17	-2.58	(-6.92, 1.76)	-2.17	0.295
July 22 ● *vs.* ◐ May 17	5.46	(0.53, 10.38)	3.37	**0.026**
June 17 ◑ *vs.* ◑ June 7	0.51	(-3.86, 4.88)	0.41	0.993
July 22 ● *vs.* ◑ June 7	8.55	(3.52, 13.59)	5.11	**0.001**
July 22 ● *vs.* ◑ June 17	8.04	(2.28, 13.80)	4.20	**0.004**

Note: *Mean differences and 95% confidence intervals (C.I.) are reported in millimeters. Significant comparisons are indicated in bold.*

The probability of escape in response to the predator stimulus decreased significantly with increasing carapace width (Binary logistic regression; β = -0.2976, X^2 = 16.61, p < 0.001). The odds ratio derived from the model ($e^{-0.2976}$ = 0.742) indicated that the odds of escape (1 - 0.742) decreased by approximately 26% per 1 mm increase in carapace width (Fig. 5).

Carapace width differed significantly between crabs that escaped into their burrow (13.67 ± 2.16 mm) and non-responsive individuals (16.46 ± 3.35 mm), with non-responsive crabs being larger (t = -3.93, df = 68, p < 0.001; Fig. 6A). Non-responsive individuals recorded during the quarter moon (17.50 ± 3.11 mm) were larger (t = -4.19, df = 38, p < 0.001; Fig. 6B) than those measured during full and new moons (13.35 ± 1.65 mm).

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Figure 5

Male Uca heteropleura escape probability following single-pass bird predator model stimulus at El Agallito Beach, Panama Pacific.

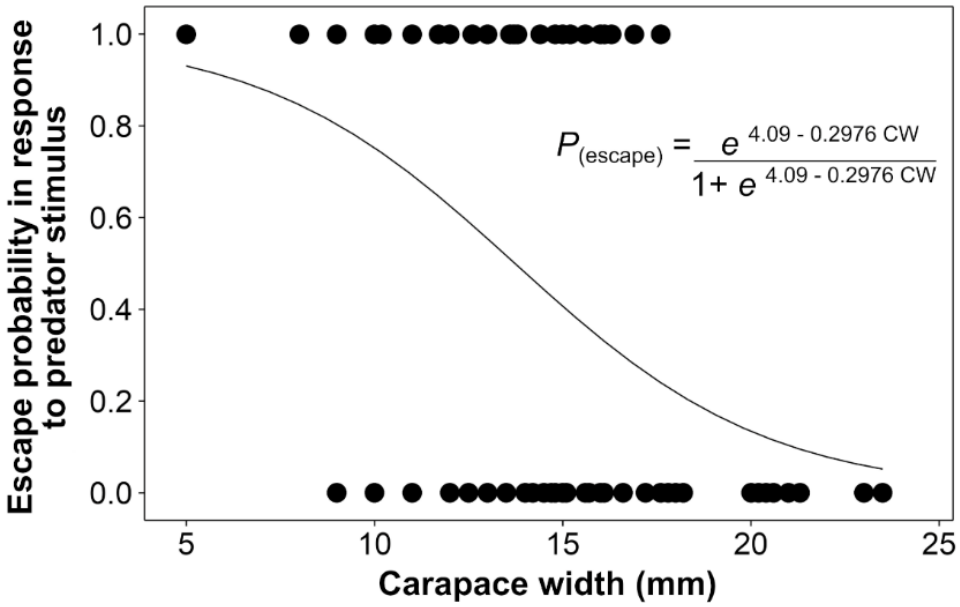
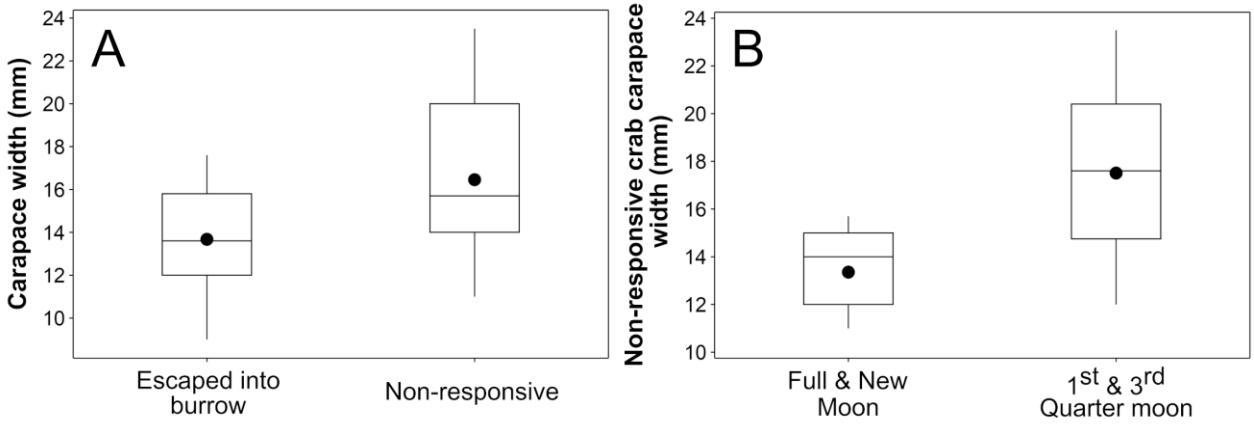


Figure 6

Carapace width in relation to simulated predator stimulus in Uca heteropleura males from El Agallito Beach, panamanian Pacific.



Note: *(A) Carapace width comparison between responsive and non-responsive individuals. (B) Carapace width distribution of non-responsive individuals across moon phases.*

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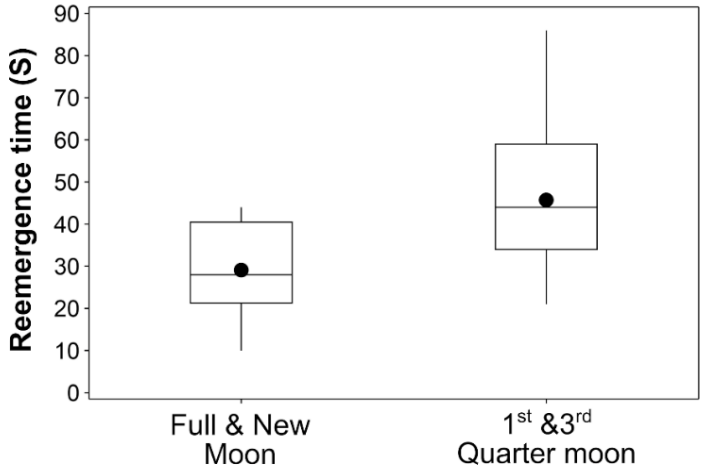
The reemergence time of crabs after exposure to the bird model (single-pass trials) varied with lunar phase. During full and new moons, crabs reemerged more rapidly (29.10 ± 11.14 s) from their burrows, whereas during quarter moons (45.73 ± 18.28 s), emergence time was significantly longer (t = -2.57, df = 23, p = 0.017; Fig. 7).

Figure 7

Reemergence time following simulated predator exposure in Uca heteropleura males from El Agallito Beach, Panama Pacific.



Discussion

Fiddler crabs can assess predation risk and modulate multistage escape decisions accordingly (Hemmi, 2005a). In the present study, repeated exposure to the predator bird model significantly reduced the escape response in *U. heteropleura* males. This decline is consistent with habituation, a fundamental form of behavioral plasticity that allows animals to filter non-threatening stimuli and avoid energetic and opportunity costs (Rankin et al., 2009; Blumstein, 2016). Similar patterns have been documented in *Gelasimus vomeris* (Hemmi, 2005b; Hemmi & Merkle, 2009), while comparable forms of short- and long-term habituation have also been described in other brachyuran crabs such as *Neohelice granulata* (Maldonado et al., 1997; Tomsic et al., 2009), suggesting that this plasticity represents a conserved

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mechanism underlying antipredator response. In this context, habituation in *U. heteropleura* may reduce the costs of lost feeding and mating opportunities associated with repeated, unnecessary retreats.

By separating habituation and single-pass trials, we were able to establish baseline antipredator responses independent of repeated exposure. In single-pass trials, surface activity varied significantly across lunar phases, with consistently higher numbers of active males during full and new moon. Importantly, this pattern was observed both before and after predator bird model presentations, indicating that the response to the model was consistent across quadrats.

Full and new moons correspond to spring tides, which are associated with increased tidal amplitude and are widely linked to enhanced foraging and reproductive opportunities in fiddler crabs (Christy, 1978; Morgan, 1996; Kim et al., 2004). Thus, elevated activity during these periods likely reflects increased reproductive effort, as males allocate more time to courtship and territory defense when mating opportunities are maximized (Backwell & Passmore, 1996; Reaney & Backwell, 2007). In contrast, reduced activity during quarter moon phases (neap tides) may reflect a more conservative strategy in which individuals limit exposure when ecological returns are lower, consistent with general predictions of risk-reward trade-offs in antipredator decision-making (Lima & Dill, 1990).

Differences in body size across lunar phases further suggest that temporal variation in activity is not random but structured by individual size. Males active during spring tides were significantly larger on average than those observed during quarter moons. Given the strong relationship between body size, competitive ability, and mating success in fiddler crabs (Reaney & Backwell, 2007; Backwell & Passmore, 1996), this pattern may indicate that larger, competitively dominant males preferentially emerge during periods of heightened reproductive opportunity.

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In species such as *Austruca mjoebergi*, larger males achieve higher mating success through enhanced signaling performance and female preference (Reaney & Backwell, 2007), while in *Austruca annulipes*, female choice is strongly influenced by both male size and burrow characteristics (Backwell & Passmore, 1996). Alternatively, the observed pattern may reflect size-dependent access to optimal territories, as larger males are more successful in acquiring and defending high-quality burrows that enhance mating success (Backwell et al., 2000; Backwell & Passmore, 1996). In contrast, the presence of smaller individuals during quarter moon sampling dates may reflect either reduced competitive ability or a shift toward lower-risk temporal niches when dominant individuals are less active.

Lombardo (2025b) documented size-dependent activity linked to reproductive effort (waving) and temporal allocation in *U. heteropleura*; though, responses to predator stimuli were not evaluated. However, in the present study, escape responses were strongly influenced by individual size, with larger males escaping less frequently and showing a lower propensity to retreat in response to the simulated predator. This suggests that risk-taking may be size-dependent in this system. Similar state-dependent patterns have been documented in fiddler crabs, where males adjust surface activity and courtship effort in relation to reproductive opportunity and competitive ability (Backwell & Passmore, 1996).

More broadly, escape behavior in fiddler crabs is highly flexible and context-dependent, varying with environmental conditions, perceived risk, and individual state (Hemmi, 2005a, 2005b; Hemmi & Merkle, 2009). However, the influence of body size on risk-taking may not be universal across fiddler crab species or behavioral contexts. For example, in *Leptuca pugilator*, some measures of boldness such as reemergence latency are unrelated to body size, while others vary with sex and behavioral context (Pratt et al., 2005; Decker & Griffen, 2012). These findings suggest that size-dependent risk-taking should be interpreted as a context-specific outcome shaped by the interaction between individual state, ecological conditions,

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and the particular behavioral metric considered (DeJaegher, 2025), consistent with state-dependent risk models (Magnhagen & Löf, 2006).

A complementary pattern emerged when considering signaling behavior alongside antipredator responses. In *U. heteropleura*, waving frequency increased under spring tides but showed a weak yet significant negative relationship with body size, indicating that smaller males contributed disproportionately to the observed high-frequency signaling. A similar pattern was reported by Lombardo (2025b), where elevated waving rates during new moon phases were driven primarily by smaller males, while larger males showed no clear relationship between size and waving frequency. Together, these results suggest that size-dependent reproductive strategies involve differential allocation among signaling effort, competitive behavior, and risk exposure.

Smaller males, typically at a disadvantage in direct contests, may compensate by increasing courtship signaling intensity to enhance their attractiveness to females, particularly under conditions of high competition or late reproductive opportunity (Milner et al., 2011; Lombardo, 2025b). In contrast, larger males appear to rely more heavily on territorial defense, prolonged surface activity, and persistence in courtship once initiated, reflecting their advantage in male-male competition and burrow ownership (Hayes et al., 2013; Backwell, 2019). Importantly, the exaggerated major claw, which can represent a substantial proportion of body mass (Crane, 1975), may impose biomechanical or energetic constraints on display performance, potentially limiting the maximum frequency or efficiency of waving in larger males. As a result, large males may prioritize display persistence, spatial dominance, and sustained visibility, whereas smaller males adopt a strategy based on elevated signaling effort to offset reduced competitive ability (Dennenmoser & Christy, 2013; Backwell, 2019).

This behavioral divergence is consistent with the broader framework of

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semilunar reproductive synchrony in fiddler crabs, where peaks in male courtship activity are tightly aligned with female receptivity and tidal cycles (Christy, 1978; Greenspan, 1982; Morgan, 1996). Male signaling effort is known to increase during periods of maximal mating opportunity and can be modulated by ecological factors such as food availability and environmental conditions (Kim & Choe, 2003; Kim et al., 2004). In particular, Murai & Backwell (2005) showed that males of *Austruca perplexa* adjust their courtship investment across the mating period, with peak mating occurring immediately before new and full moons and males reducing courtship duration as female receptivity increases.

Additionally, synchronous courtship and coordinated signaling behavior have been documented across multiple fiddler crab species, reinforcing the idea that reproductive effort is both temporally structured and socially mediated (Backwell et al., 1998; Backwell, 2019). Within this context, the presence of large, relatively inactive *U. heteropleura* males during quarter moon phases, despite reduced overall activity, may reflect alternative reproductive tactics (Morgan, 1996), such as early territory establishment or prolonged occupancy, rather than increased signaling effort. Future studies may examine this activity pattern to determine the actual nature of large male activity during quarter moon (neap tides) and how it correlates to reproductive investment. Overall, these findings indicate that risk-taking, signaling, and activity represent partially decoupled behavioral axes, and that reproductive strategies in fiddler crabs may emerge from a dynamic balance between individual state and temporally structured ecological opportunities (Lima & Dill, 1990).

Finally, variation in reemergence time supports predictions from optimal hiding theory (Jennions et al., 2003), which proposes that individuals balance predation risk against the costs of lost opportunities. During neap tides, when feeding and reproductive opportunities are reduced, crabs tended to remain longer in their burrows following disturbance, consistent with a more risk-averse strategy. In contrast, during spring tides, individuals reemerged more rapidly, suggesting a

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higher risk-taking behavior when ecological opportunities are temporally concentrated.

Conclusions

Taken together, our results indicate that antipredator behavior in *U. heteropleura* is shaped by the interaction between predictable environmental cycles and individual state (size). At the population level, activity and signaling seem to peak during spring tides, when reproductive opportunities may be higher, leading to increased exposure to predators and elevated risk-taking. At the individual level, body size modulates how that risk is expressed, with larger males consistently adopting bolder strategies. The persistence of higher activity levels before and after predator exposure during full and new moon further suggests that these patterns reflect stable behavioral responses rather than transient effects of disturbance. This coupling of environmental context and individual state highlights the dynamic nature of risk-taking behavior, where crabs continuously adjust their responses to balance predation risk against reproductive and foraging benefits.

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