



## Phenotypic effects on male risk-taking behavior in *Leptuca beebei* from field experiments at Playa El Agallito, Chitre, Panama

### Efecto fenotípico en la toma de riesgos por *Leptuca beebei* en experimentos de campo en Playa El Agallito, Chitré, Panamá

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## Abstract

Risk-taking behavior in *Leptuca beebei* was studied through field experiments conducted at Playa El Agallito, Chitré, Panama. This study aimed to determine whether larger males or those with pillar structures take greater risks when courting females and whether female size affects male risk-taking behavior. Females exhibiting mate-searching behavior were tethered 30 cm in front of randomly selected courting males, both with and without pillars. Male behavior was observed using binoculars, recording the maximum distance traveled from their burrow and whether they intercepted the female. Results indicate that male size and pillar presence did not significantly affect the distance traveled or the likelihood of intercepting the tethered female. Males traveled an average of 18.81 cm from their burrows, but this distance was not influenced by female size. Instead, males' risk-taking behavior may have been influenced by factors such as predation risk and potential burrow loss, rather than female size. The findings suggest that the dangers of leaving their burrows outweigh the benefits of courting distant or larger females.

### Keywords

Burrow, carapace width, fiddler crab, predation, risk

## Resumen

Se estudió el comportamiento asociado a la toma de riesgos en *Leptuca beebei* mediante experimentos de campo en Playa El Agallito, Chitré, Panamá. El objetivo fue determinar si los machos más grandes o aquellos con estructuras de pilar asumen mayores riesgos al cortejar hembras, y si el tamaño de las hembras influye en este comportamiento. Hembras en búsqueda de pareja fueron capturadas y ancladas a 30 cm de machos en cortejo, seleccionados al azar con y sin pilares. El comportamiento de los machos fue observado con binoculares, registrando la distancia máxima recorrida desde su madriguera y si interceptaron o no a la hembra. Los resultados indican que ni la talla del macho ni la presencia de pilares afectaron la distancia recorrida ni la probabilidad de interceptar a la hembra. Los machos recorrieron un promedio de 18.81 cm desde sus madrigueras, sin que el tamaño de la hembra tuviera influencia. La distancia recorrida por los machos parece estar más influenciada por el riesgo de depredación y la posible pérdida de la madriguera por robo, que por el tamaño de la hembra. Estos resultados sugieren que los peligros de abandonar la madriguera superan los beneficios de cortejar hembras distantes, independientemente de su tamaño.

### Palabras clave

Ancho de caparazón, cangrejo violinista, depredación, madriguera, riesgo

## Introduction

*Leptuca beebei* (Crane, 1941) is considered a small fiddler crab species (~10 mm carapace width), inhabiting from El Salvador to northern Peru. Its carapace typically displays a blend of muted green, blue, and brown hues, and the major claw is often white, with a dark purple patch at the base of the pollex (Crane, 1975). During each semilunar cycle, approximately every 15 days before spring tides, females alternate between mating on the surface (outside their burrow) and inside male burrows (Christy, 1987, 1988a; Christy & Schober, 1994). Surface matings might be costly for females, as the increased time spent on the surface attending to courtship and evaluating male burrows increases the risk of predation (Crane, 1975; Koga et al., 1998, 2001). In contrast, the reproductive costs for males primarily involve predation risk due to their high detectability resulting from typical courtship movements and/or the color of their major claw (How et al., 2009; Murai & Backwell, 2005; Pope, 2005). This asymmetry in detectability has been demonstrated in *L. beebei* and one of its predators, *Quiscalus mexicanus*, a common bird species in Panama. The large claw and lighter colors of male fiddler crabs make them more visible than cryptic females. This



visibility allows birds to track males much more effectively than females (Koga et al., 2001). When a male fiddler crab detects a wandering female (mate-searching), it typically moves from its burrow towards the female, waving the major claw in a courtship display, and then attempts to guide her back to his burrow (Christy et al., 2002). In *L. beebei*, males move varying maximum distances (~20-40 cm) toward females. By leaving their burrow to court females, males face two key risks: losing their burrow to theft and increased predation risk (Christy et al., 2002; Koga et al., 1998, 2001; Ribeiro et al., 2019). This scenario raises questions about how males respond to risks associated with reproduction. A practical approach is to examine the distance males travel from their burrows to court females. As males venture farther from their burrows, the time to return increases, along with the associated risks (Heatwole et al., 2018; Ribeiro et al., 2019). Males generally stay near their burrows during surface activities to minimize such risks, making distance traveled an important indicator of risk-taking behavior (Heatwole et al., 2018).

Males build pillars (~15 mm high; figure 1A–D) during courtship, at the entrance of their burrows (Christy, 1987, 1988a; Crane, 1975). These structures serve as reference points, aiding males in locating their burrows after moving away to court a female (Christy et al., 2002; Ribeiro et al., 2006). This could enable males that build pillars to venture farther from their burrows to approach females compared to those without pillars (Christy et al., 2002; Heatwole et al., 2018; Ribeiro et al., 2019). This scenario poses questions such as: Are larger males takers of higher risks? Do pillar-building fiddler crabs risk venturing farther from their burrows compared to those without pillars? Male risk-taking behavior may also be influenced by female size, as larger females produce more eggs, potentially motivating males to take greater risks to gain reproductive advantages (Ens et al., 1993; Gruber et al., 2019; Heatwole et al., 2018). There is evidence males increase their courtship efforts when the potential reproductive benefits are higher (Reaney & Backwell, 2007). Since courtship and sexual selection are costly for males, they are expected to optimize the balance between costs and benefits based on the perceived value of females or expectations for future reproductive events (Heatwole et al., 2018; Reaney & Backwell, 2007). Thus, the aim

of this study was to test male risk-taking behavior as indicated by their positioning relative to their burrow and potential female mates under natural conditions.

## Materials and Methods

### Study site

The study was conducted in an unvegetated intertidal mudflat in “El Agallito” beach (17 P 565802.87 m E 884594.94 m N), Chitré, Pacific coast of Panama. The study area is a stretch of intertidal mudflat formed by silt deposits from the Parita and La Villa rivers. It features a tropical savanna climate (Aw) according to the Köppen’s climate classification (Beck et al., 2018). Temperatures range from 24°C to 30°C, with minimal seasonal variation. The rainy season is from May to November, characterized by heavy precipitation, especially in October (1,500 to 2,500 mm), while the dry season is from December to April (Instituto de Meteorología e Hidrología de Panamá, 2024).

During low tide, the surface is exposed for at least 2 km, attracting birds that almost exclusively feed on fiddler crabs. Some of the common potential predators include: Grackles (*Quiscalus mexicanus*; figure 1E), Whimbrel (*Numenius phaeopus*), Willet (*Catotrophorus semipalmatus*), Ruddy turnstone (*Arenaria interpres*), Black-bellied plover (*Pluvialis squatarola*), White ibis (*Eudocimus albus*; figure 1F), Wilson’s plover (*Charadrius wilsonia*), and Semi-palmated plover (*C. semipalmatus*) (Backwell et al., 1998).

### Tethered female protocol

Data was collected in three field trips to El Agallito in May 26<sup>th</sup>, June 22<sup>nd</sup> and July 6<sup>th</sup> 2024, during diurnal low tides. Females displaying mate-searching behavior (wandering and having entered the burrow of at least one courting male) were captured by hand, and their carapace width (CW) was measured with a Vernier caliper (0.01 mm). Females were secured to a metal nail (~8 cm length) by glueing (Loctite, ethyl cyanoacrylate) a cotton thread to her carapace (figure 1G) and tying it to the nail as a 5-cm tether. We then randomly located courting males (actively waving), alternating between those with and without a pillar.

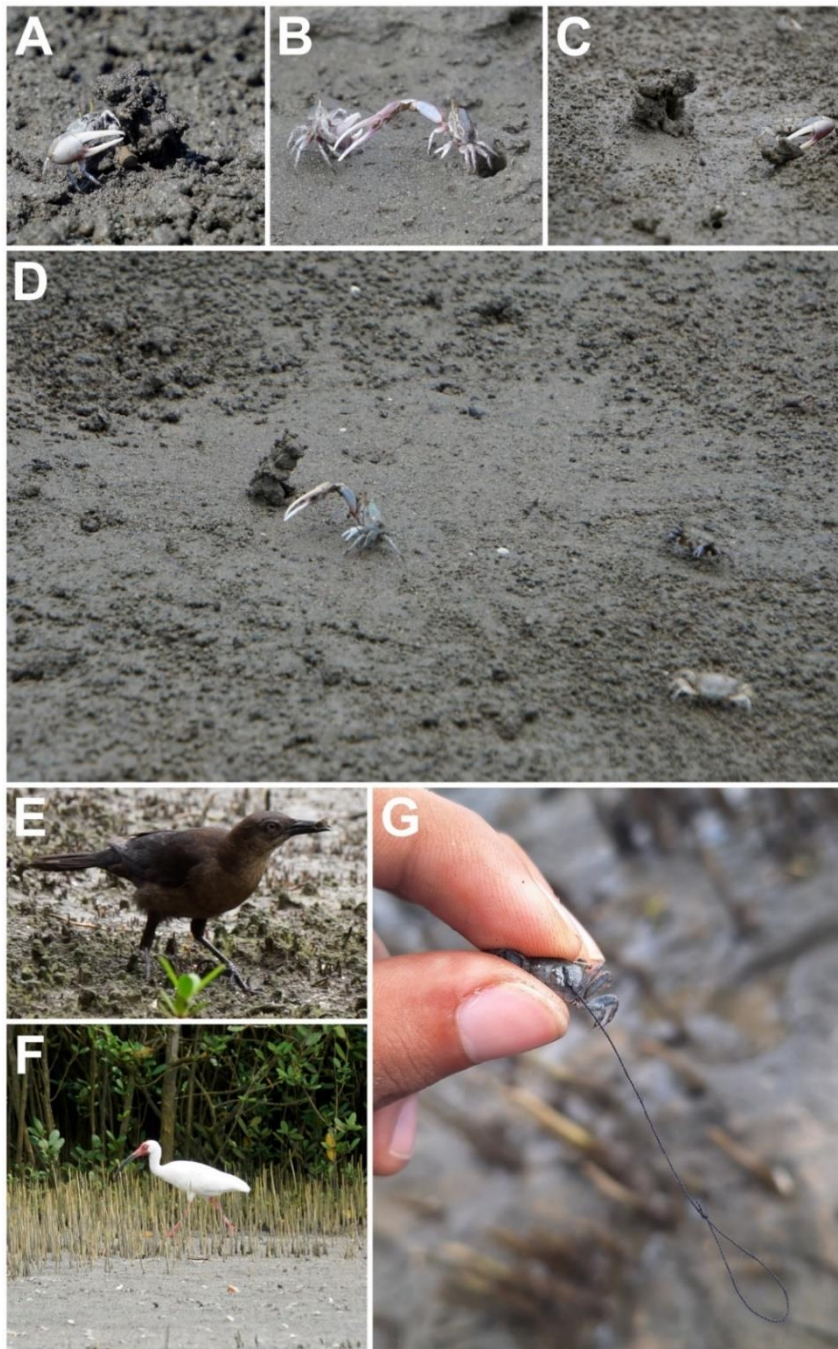
Nails were pushed into the substrate, positioning tethered females 30 cm in front of the



focal male's burrow entrance. To minimize interference, we carefully identified neighboring burrows and sealed them with cotton within a 30 cm radius. To observe *L. beebei* male behavior, we used binoculars (Bushnell 10×42 mm) at a minimum distance of three meters. The observer presence prevented birds from preying on tethered females during the study. Trials began after the focal male emerged, giving each one five minutes to respond to female presence. During this period, we recorded the maximum distance males traveled from their burrow to the female using a tape measure. This distance was marked with a stick, measuring from the front edge of the burrow. We noted whether the male successfully intercepted the female or not, the elapsed time and general behavior as well. After each trial, we captured the male to measure the width of his carapace, as well as the length of the major claw (ChL). This process was repeated for each male-female combination, ensuring consistent experimental conditions across all trials. Males and females were used only once, and after the trials, all individuals were released. Males were released into temporary burrows, while the threads attached to the females' carapaces were removed, allowing them to resume mate-searching; sealed burrows were also reopened.

### Data analysis

For the statistical analysis, the distance traveled by males (response) was compared using a general linear model in RStudio (vers. 2023.6.0.421) with pillar as a categorical factor and the sizes of both males and females and time to maximum distance from the burrow as covariates (predictors). The dependent variable of distance was transformed by squaring to ensure the resulting residuals from the model were normally distributed (Anderson-Darling test). Chi-square tests were employed to compare proportions, and two-sample t-tests were used to compare the sizes of males that did or did not reach the female during the trial. The Mann-Whitney W test was used to compare the carapace widths between intercepted and non-intercepted females.



**Figure 1.**  
***Leptuca beebei*** and common avian predators from El Agallito, Chitré, Panama. A. Male at burrow entrance with pillar. B. Male without pillar defending burrow from intruder. C. Hood-like pillar. D. Male with columellar pillar during courtship and two approaching females (lower right). E. Thread fixture on female carapace for tethering. F-G. Female grackle (*Quiscalus mexicanus*) preying on a male *L. beebei* and White ibis (*Eudocimus albus*)

## Results

Although focal individuals were randomly selected, male ( $10.38 \pm 1.32$  mm) and female ( $10.97 \pm 0.97$  mm) *L. beebei* were similar in carapace width ( $t = -1.62$ , d.f. = 22,  $P = 0.12$ ). All males involved in the trials displayed courting behavior towards the tethered females, characterized by major claw waving upon spotting the female. Courted females reacted to waving by tightening the tether orienting their body towards the male burrow. On average, males traveled  $18.81 \pm 8.73$  cm SD ( $n = 37$ ) from their burrows while courting a tethered female within the five-minute observation period; this is roughly, 18.12 times the average male CW. Although the assumptions were fulfilled (figure 2A–C), the general linear model found poor fit ( $R^2 = 0.158$ ,  $F_{(2-34)} = 3.19$ ,  $P = 0.054$ ) with significant contributions of male CW and ChL to maximum distance (figure 2D,E). For each millimeter increase in male CW, the distance increased 4.2 carapace widths, while for ChL the relationship was negative (table 1). Female CW had no effect on maximum distance (figure 2F), while male pillar presence-absence and time did not contribute to the model fit.

**Table 1. Regression parameters for distance variable as response in *Leptuca beebei* from the Parita Gulf, Panama, Pacific. Carapace width (CW), Chela length (ChL), standard error (SE) and degrees for freedom (DF).**

Source	Coef	SE Coef	t	DF	F	P
Constant	-42	115	-0.36			0.718
Regression				2	3.19	0.054
Male CW	43.50	17.20	2.53	1	6.38	0.016
Male ChL	-11.65	5.61	-2.08	1	4.32	0.045
Error				34		
Total				36		

Of the 37 females, 26 were not intercepted, while 11 were reached by the males; the difference between these proportions was significant ( $\chi^2 = 6.08$ , d.f. = 1,  $P = 0.014$ ). There was no significant difference in the approach time between males that intercepted ( $183.41 \pm 131.91$  sec.) the females and those that did not ( $92.40 \pm 113.91$  sec.) cover the full 30 cm distance ( $W = 438$ ,  $P = 0.065$ ).

Non-intercepted ( $10.88 \pm 1.05$  mm) and intercepted females ( $11.10 \pm 0.99$  mm) were not different in CW ( $W = 492.00$ ,  $p = 0.960$ ). No significant difference was observed in the size of males that did ( $10.71 \pm 1.24$  mm) or did not ( $10.25 \pm 1.36$  mm) approach the female to the 30 cm mark ( $t = -0.97$ , d.f. = 35,  $P = 0.337$ ). Within the group of males that intercepted the female, the proportion of those that built pillars was consistent with those that did not (pillar: 3, no pillar: 8;  $\chi^2 = 2.27$ , d.f. = 1,  $P = 0.132$ ).

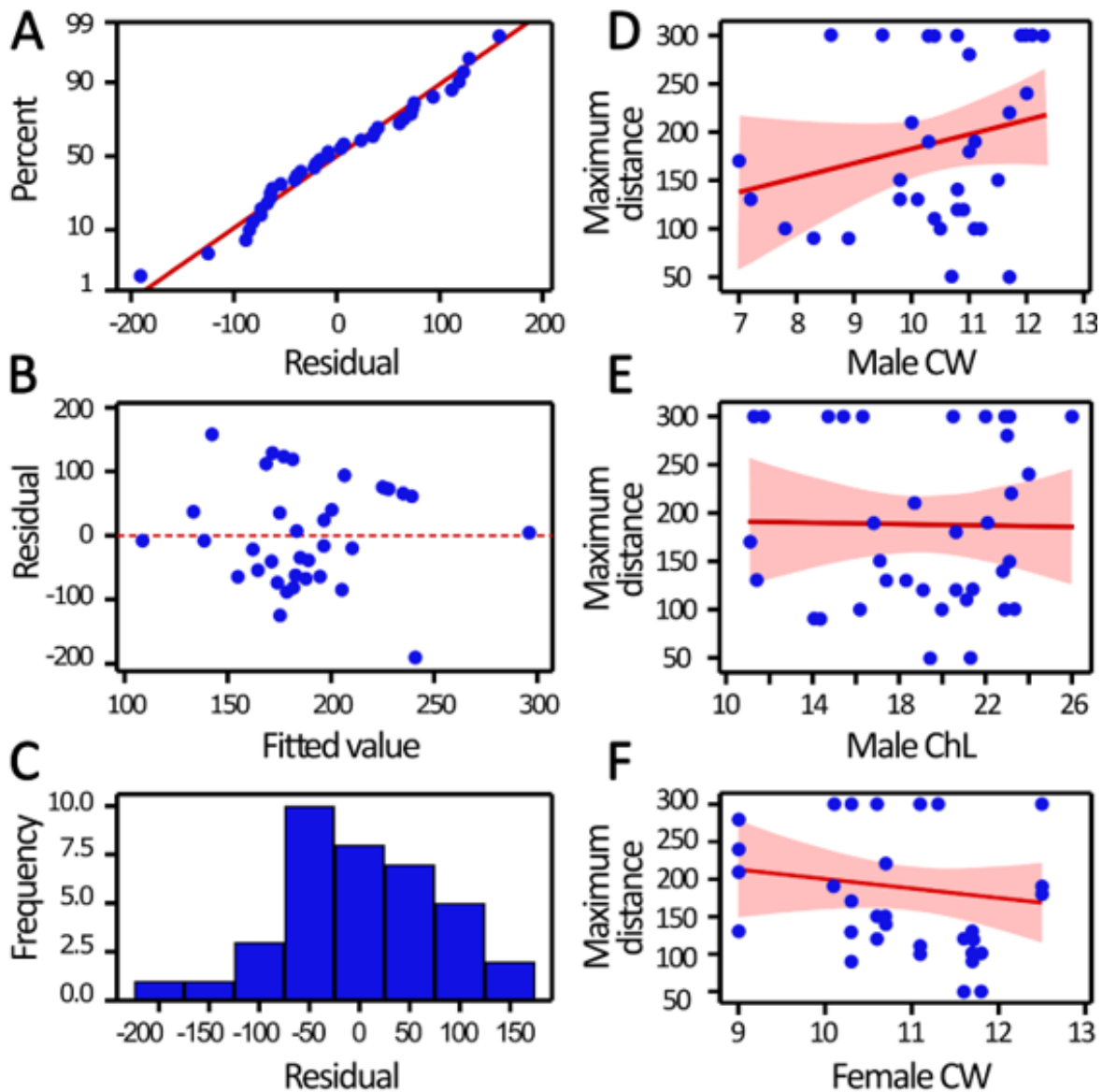


Figure 2. Confirmation of model assumptions (A–C) and response-predictor relationships (D–F) of interest for *Leptuca beebei* in El Agallito, Chitré, Panama.



The distance pillar-builders moved away from the burrows was not significantly different from that of non-builders ( $161.00 \text{ mm} \pm 88.3 \text{ mm}$  vs.  $186.30 \pm 88.6 \text{ mm}$ ;  $t = -0.96$ , d.f. = 43,  $P = 0.344$ ). The CW between males with ( $6.46 \pm 0.87 \text{ mm}$ ) and without pillars ( $5.91 \pm 0.94 \text{ mm}$ ) was not significantly different ( $t = 1.83$ , d.f. = 35,  $P = 0.075$ ). Nonetheless, male CW and ChL were correlated ( $R^2 = 0.64$ ,  $F_{(1-35)} = 60.91$ ,  $P < 0.001$ ), and the ChL of males that built pillars was longer ( $20.22 \pm 3.67 \text{ mm}$  vs.  $17.76 \pm 3.86 \text{ mm}$ ;  $t = 2.18$ , d.f. = 43,  $P = 0.035$ ).

## Discussion

In contrast to studies where larger females attract greater risk-taking behaviors from males, our results show no significant relationship between female size and the risk males were willing to take. This finding was consistent regardless of the presence of a pillar, suggesting that male *L. beebei* may prioritize other factors over female size when assessing risk. If the fitness advantages of risk-taking differ across contexts (e.g., distance from the burrow), it is expected that evolutionary forces would shape behavior to enhance fitness by adaptively modulating risk-taking behavior (Coleman & Wilson, 1998; Gruber et al., 2019; Koga et al., 1998). This phenomenon has been reported in *L. beebei* where predator presence affected the number of waving males and pillar construction as well as the number of wandering females that approached courting males (Koga et al., 1998). In this regard, Heatwole et al. (2018) reported that *L. terpsichores* males took greater risks to court larger females by going further from their burrow. However, in the present study this relationship was absent, suggesting male *L. beebei* might be constrained by high risk of predation or burrow loss associated with moving far from the entrance, which limits their willingness to take risks based solely on female size. Distance from the burrow therefore played a critical role, potentially overshadowing female size. All males advanced and waved at the tethered females, indicating that their hesitation to leave their burrow should not be interpreted as choosiness or fitness loss. This means all tethered females were considered potential mates and would likely have approached the courting males if they had not been tethered. Furthermore, one could argue that larger males, being more likely to mate, would take



higher risks (Callander et al., 2012; Christy, 1988b). Yet, in our experiments there was no difference between male size and the distance travelled to court a female.

Independence between male size, age and risk-taking has been also reported in other fiddler crab species such as *Leptuca pugilator*, *L. terpsichores* and *Austruca mjoebergi* (Callander et al., 2012; Heatwole et al., 2018; Pratt et al., 2005; Reaney & Backwell, 2007). In our trials, the proportion of males that did not reach the female was higher than those that did and attempted to guide her back to the burrow. This suggests that reproductive costs for males might be particularly high as distance from the burrow increases. Crabs caught far from their burrow almost certainly end up being eaten by birds (Backwell et al., 1998; Lombardo González, 2023). As a result, males may be hesitant to venture too far from their burrows. In this study, *Leptuca beebei* males typically stayed within an average distance of 18.81 cm from their burrows. Similarly, courting *Leptuca terpsichores* remained within 15 cm of their burrow entrance when females were nearby (Christy et al., 2002) and within 17 cm when presented with tethered females under natural conditions (Heatwole et al., 2018). Crabs assess and modulate risk based on their position relative to their burrow (Hemmi & Zeil, 2003; Zeil & Hemmi, 2006). Similarities in the response of *L. beebei*, *L. terpsichores*, and *G. vomeris* suggest that risk assessment might be similar across species. This may explain why individual size and pillars had no effect, since all females were positioned at the same distance; twice the average distance from the burrow entrance. The observed behavior of male *L. beebei* implies they are constantly aware of their position and can navigate directly back to the burrow (Murakami et al., 2017; Zeil & Hemmi, 2006).

In our experiment, the reaction of focal *L. beebei* males to nearby males was always strong, drastically reducing the distance to their burrow along with major claw and merus displays; two territorial signals (Crane, 1966, 1975). This scenario suggests the cost of burrow loss places strain on reproductive behavior. In this context, burrow theft and interference by other males during courtship may increase with population density (Zucker, 1984). In fact, risk-taking has been found to be dependent on density and predation risk in the milky fiddler crab, *Austruca lactea* (Takeshita & Murai, 2019; Takeshita & Nishiumi, 2022).



Although density and predation are factors beyond the scope of our study, they seem to have important effects strengthening or relaxing selection forces across various species of fiddler crabs, explaining why males are generally reluctant to leave their burrows to court distant females.

Forty-seven species of fiddler crab are known to construct ornamental structures outside their burrow entrance that fulfill different functions (Pardo et al., 2020). The construction of hoods or pillars by males is an important sexually selected trait that can influence female mate choice in various species such as *L. beebei* (Backwell et al., 1995; Christy, 1988b), *L. terpsichores* (Christy et al., 2002), *A. lactea* (Zhu et al., 2012) and *Leptuca leptodactyla* (Rodrigues et al., 2016). Furthermore, Ribeiro et al. (2006) showed that crabs that had built hoods next to their burrows relocated their entrance faster and effectively compared to those without. Thus, it could be hypothesized that pillars would enable males to take higher risks by moving farther away from their burrow to court females (Heatwole et al., 2018; Ribeiro et al., 2006). However, while pillar building is influenced by male body condition (Backwell et al., 1995), and the chela of pillar builders in our study was longer than that of non-builders, we found no evidence that pillar builders took greater risks by moving farther away. This lack of increased risk-taking behavior is consistent with the pattern observed in *L. terpsichores* (Heatwole et al., 2018; Kim & Christy, 2015) and yet an indication of the consistent effect of risk assessment through distance from the burrow, regardless of individual size. Crabs navigate their environment using both visual and non-visual mechanisms (Layne et al., 2003; Zeil & Hemmi, 2006). Non-visual path integration errors, which can occur when crabs become disoriented during combat or courtship, may lead to failures in burrow relocation (Layne et al., 2003; Zeil & Hemmi, 2006). Pillars can aid in relocation when disorientation results in position offsets greater than 20 cm (Ribeiro et al., 2006). However, in our study, males traveled an average of 18.81 cm when presented with tethered females, suggesting that if any non-visual orientation errors occurred, they were likely minimal within this range. As a result, the advantage pillars might offer for burrow entrance relocation is unlikely to embolden males to take higher risks within the 20 to 30



cm range (Heatwole et al., 2018; Ribeiro et al., 2006). Although our methods did not test female choice, it could play a larger role in male behavior than previously assumed (Kim & Christy, 2015). If females ultimately select mates based on traits other than risk-taking (e.g., the presence of a pillar, territory or other courtship displays), it might explain why male size and female size did not correlate with risk-taking behavior.

## Conclusions

- Risk-taking in *L. beebei*, within the reproductive context, is not influenced by male size or pillar presence. Instead, reproductive costs associated with burrow theft and predation risk significantly influence male risk-taking, as evidenced by their reluctance to leave their burrows to court distant females.
- In our trials male *L. beebei* showed they can take risks while venturing to meet tethered females. However, it was not possible to determine if such risk was taken to court larger females differentially.
- *Leptuca beebei* males may perceive the dangers of leaving their burrows as outweighing the benefits of courting larger distant females. This indicates that their risk assessment is influenced more by factors like predation risk and potential burrow loss rather than female size, especially since wandering females appear to be similar in size. Thus, males' risk-taking behavior seems to be driven more by ecological and reproductive costs than by the size of females available for courting.

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