An Acad Bras Cienc (2024) 96(3): e20230675 DOI 10.1590/0001-3765202420230675
Anais da Academia Brasileira de Ciências | *Annals of the Brazilian Academy of Sciences*
Printed ISSN 0001-3765 I Online ISSN 1678-2690
www.scielo.br/aabc | www.fb.com/aabcjournal

ANIMAL SCIENCE

Fiddler crabs from highly disturbed beaches are more sensitive to human presence

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Abstract: The presence of humans frequently modifies the behavior of animals, particularly their foraging patterns, compromising energetic demands. The fiddler crab *Leptuca leptodactyla* inhabits mangroves with high degrees of anthropogenic influence. Thus, we tested if populations living in highly anthropized mangroves respond differently from those living in more protected areas. We predict that individuals from touristy areas will be more tolerant to humans and will resume their activities sooner after disturbance. To do so, we conducted an experiment that consisted in the approach of an observer to the burrows, recording the response of individuals to the stimuli. The experiment took place in July 2022, in Ubatuba, São Paulo, Brazil. We analysed the duration and latency of various behaviors of a total of 80 adult males from two populations (high and low anthropogenic influence). Contrary to our predictions, individuals from the anthropized population were less tolerant, spending more time inside their burrows and taking longer to resume their activities. Therefore, fiddler crabs were not habituated to human presence. These results help us understand the learning process in invertebrates and their ability to select stimuli, contributing to understanding the impacts of human-wildlife interactions.

Key words: Anthropogenic disturbances, behavior, latency, time budget, *Leptuca*.

INTRODUCTION

Wildlife responses to anthropogenic disturbances are complex and influenced by several factors (Bejder et al. 2009). The exponential development of cities and urbanization have resulted in an increasing alteration of natural environments (Hamer & McDonnell 2009), increasing the frequency of interactions and conflicts between human populations and wildlife (Abrahams et al. 2018, Walton et al. 2022). With the loss of natural resources and habitat and high degrees of anthropogenic disturbances, the most sensitive species tend to disappear, while less sensitive species, depending on the level of degradation/environmental alteration, manage to resist these changes and coexist with humans (McKinney 2006). This flexibility can be observed at the behavioral level, where individuals that can adjust their behavior are more likely to tolerate human presence (Sih et al. 2011, Lowry et al. 2013, Sol et al. 2013).

On one side, animals can present the so-called habituation, a gradual reduction in responsiveness to recurrent events (Rankin et al. 2009). As the direct opposite of habituation, there is a phenomenon called sensitization (Peeke 1984), defined as the intensification of the response to stimuli. Both phenomena are related to the stimuli and how it perceived by the animal in question, low intensity and high volumes of stimuli tend to habituate, while high intensity and low volumes tend to sensitize (Blumstein 2016). These processes are relevant to be addressed given that some animals might habituate to the human presence or sensitize to it (Blumstein 2016). For instance, some species do not perceive humans as predators, becoming habituated to them (Walker 1972, MacFarlane & King 2002, Knight 2009). Such capacity demonstrates that animals can filter non-threatening stimuli from those necessary to survival, avoiding unnecessary energy expenditure (Geist 2011, Hemmi & Merkle 2009, Raderschall et al. 2011). Filtering certain stimuli allows for increased foraging time and decreased periods of alertness; thus, being an advantage to the individual (Hemmi 2005b).

Fiddler crabs comprise several genera of crabs of the Ocypodidae family that have an extensive distribution around the world, being present on all continents except Antarctica (Crane 1975, Rosenberg 2019). Due to their wide distribution (Rosenberg 2019), fiddler crabs frequently interact or reside on beaches with human presence, thus enabling studies on the effects of human presence on essential behaviors, such as feeding and fleeing (Zeil & Hemmi 2006). Studies with species worldwide have demonstrated that fiddler crabs can filter various stimuli and exhibit habituation to humans and cars (Walker 1972, Tomsic et al. 1993, Hemmi & Merkle 2009, Raderschall et al. 2011, DiNuzzo et al. 2020). However, some studies found that habituation occurred only in certain contexts (Tomsic et al. 1998, Park & Kim 2021).

The target species is *Leptuca leptodactyla*, a species commonly found along the Brazilian coast (Thurman et al. 2013), usually in high densities and in areas with low vegetation cover (Checon & Costa 2017). This species occupies mangroves, one of the most productive and threatened ecosystems, suffering acutely with the expansion of human settlements (Angelini et al. 2018, Leonardi et al. 2018), with a deforestation rate of 1 to 2% a year (Alongi 2015), emphasizing the necessity of understanding the impacts of humans on the local fauna. The present study aimed to test the hypothesis that the behavior of fiddler crabs, *L. leptodactyla*, will be modified by human presence. In the area with higher anthropogenic influence, we expect fewer individuals to respond to an observer's approach and, when they respond, they will take longer to respond, will spend less time in their burrows and take less time to resume foraging. Our study adds to the understanding of learning in invertebrates and their selection of stimuli, as well as contributes to the understanding of the influence of human populations on wildlife.

MATERIALS AND METHODS

Location of study and characterization of the beaches

The study was conducted in Ubatuba, São Paulo, Brazil, in the mangrove of Praia Dura/Rio Escuro (23°29'3" S, 45°09'5" W) (Fig. 1). We sampled two populations living in two different beaches inside this mangrove separated by approximately 160m. Populations were chosen based on observable differences in anthropogenic influence, considering access and logistical limitations. In the beach with the highest frequency of tourists, there is a bridge 75 m afar acting as a barrier for tourist passage. We used this construction to delimit one of the populations and employed the same distance to the other.

To assess the degree of anthropogenic influence, we followed the criteria of González et al. (2014), with adaptations, employing six out of seven urbanization variables proposed, namely 1) number of tourists; 2) proximity to urban centers; 3) buildings on the sand; 4) beach cleaning from vehicles; 5) solid garbage in the sand; 6) vehicle traffic on the sand. Each of the above cited variables was assigned a value of zero

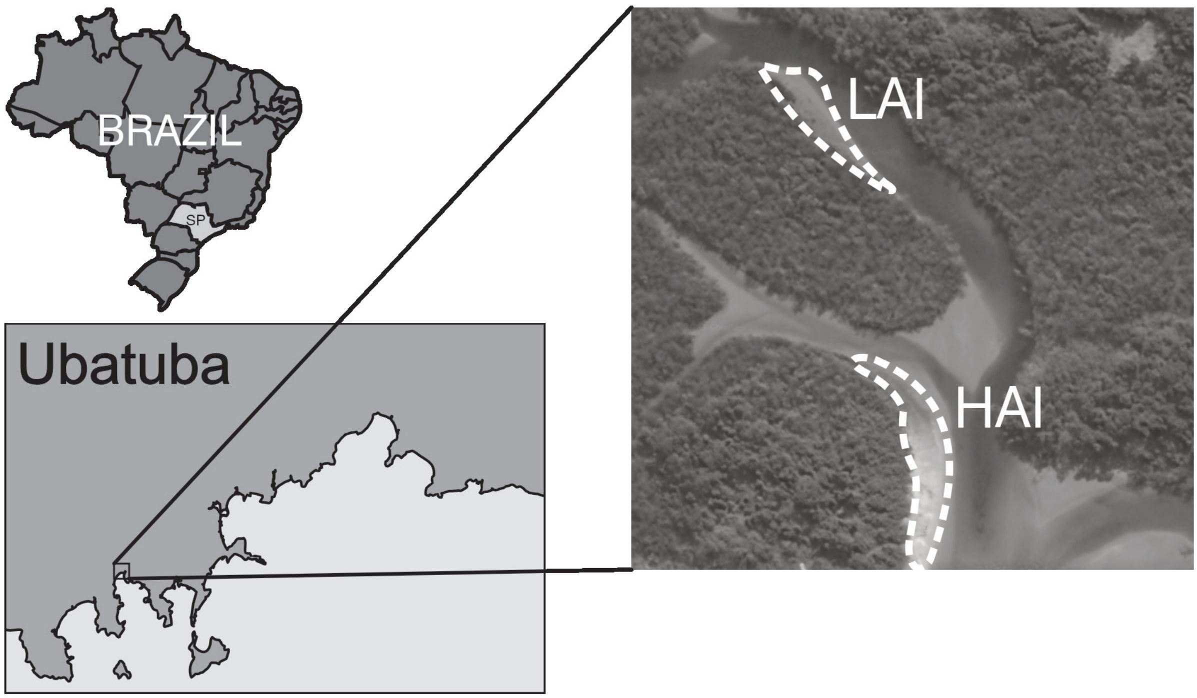

Figure 1. **Image obtained by Google Maps showing the two beaches where the study was conducted. High anthropogenic influence (HAI), Low anthropogenic influence (LAI). Source: Google Maps.**

(low) to five (high). For the number of tourists, since we did not have access to the data from local authorities, we used field observation only, considered an adequate method for counting (Morgan 2018). Field observation consisted of the manual counting of tourist numbers during the peak hours of recreational activities, considering everyone found within the 75 m radius of each fiddler crab population, following a similar rationale for the nearby buildings (see below). Proximity from urban centers was calculated with Google Maps based on the nearest residential neighbourhood. Buildings on the sand were considered those near the populations, and the bridge was the only building near these populations. Mechanical cleaning did not happen for any of the beaches. The solid garbage in the sand was quantified by two parallel transects of 30 m (4 m apart). Garbage counting happened on Monday after the weekend when the experiment was conducted. The vehicle traffic on the sand is forbidden in the area (Table I) of the values of these six variables were included in the urbanization index calculation which gives a result ranging from 0 to 1, where zero indicates beaches with lower urbanization index and 1 indicates higher urbanization index. The mangrove beach of Praia Dura/Rio Escuro presented an urbanization index of 0.3 while the other presented a value of 0.066. Based on these values, the beaches were separated into low anthropogenic influence (LAI) and high anthropogenic influence (HAI) following their urbanization index (low or high). Therefore, animals living on the beach with a higher level of anthropogenic influence would be more exposed to human presence than animals living on beaches with a lower level of influence.

Table I. Ethogram made for adult male *L. leptodactyla* living in Ubatuba, São Paulo based on van Himbeeck et al. (2019).

Behavior	Description
Feeding - pre stimuli	The crab repeatedly scrapes the substrate with the minor cheliped and puts it into his mouth
Flee	The crab runs rapidly towards his burrow direction. The flee movement ends when at least one pereopods touches the burrow entrance
Enter the burrow	The crab enters his burrow. The behavior is considered from the moment he touches the burrow entrance until he's fully out of sight
Emerge	The crab emerges from his burrow. The behavior is considered from the moment he reappears in sight, until he stays with his body parallel to the substrate (horizontally set up)
Unanchor	The crab does the unanchor movement with his pereopods from the burrow entrance and initiates his movement away from it. The behavior is considered from the moment "Emerge" behavior is finished until the complete unanchor of all pereopods
Feeding - post stimuli	Same feeding behavior as described above, however after the observer stimuli
Inside	The crab is out of sight and safely retreated to his burrow
Burrow Maintenance	The crab repeatedly pushes pellets from the substrate with help of his major cheliped away from his burrow

Study animals

Species identification followed the parameters of Crane (1975), de Melo (1996), and Rosenberg (2019), so that the study species was identified as *L. leptodactyla*. The individuals could easily be separated according to sex due to the developed heterochelia in males (Crane 1975). Adult males also have an average size of 5 mm in length, although some individuals can reach 6.5mm (Crane 1975). Crabs could also be identified individually, as each burrow was used by a single individual (Hemmi 2005a). Additionally, since crab behavior can vary according to sex (Chumsri et al. 2023), we restricted our study to adult males.

Each population (high and low anthropogenic influence) was sampled twice (two subgroups of different individuals). The two subgroups distanced themselves by about 25m. In each of these subgroups, 20 randomly selected adult males were analysed, totalling 80 animals for the study (40 per population) (Fig. 2).

Experiment

The experiment was conducted in July 2022, the winter break for the region, a month marked by an increase in the number of visitors by up to 500% (Poletto & Batista 2008). Such an increase in visitors can likely change the urbanization index and emphasize the differences between the two beaches, as seen in other sites (Asensio-Montesinos et al. 2019, Vincent & Hoellein 2017). Data collection involving the animals happened in a single day. We followed De Grande et al. (2018) protocol where the date chosen for data collection had to be sunny and not preceded by storms. Moreover, data collection should not exceed 30 minutes for each population to avoid significant environmental changes.

We ensured that there was no interference from tourists during the experiment. The experiment consisted of a single approach by an observer with 1.95m in height. A camera (iPhone 8), fixed on a tripod with a total height of 80 cm and an angle of 45° towards the

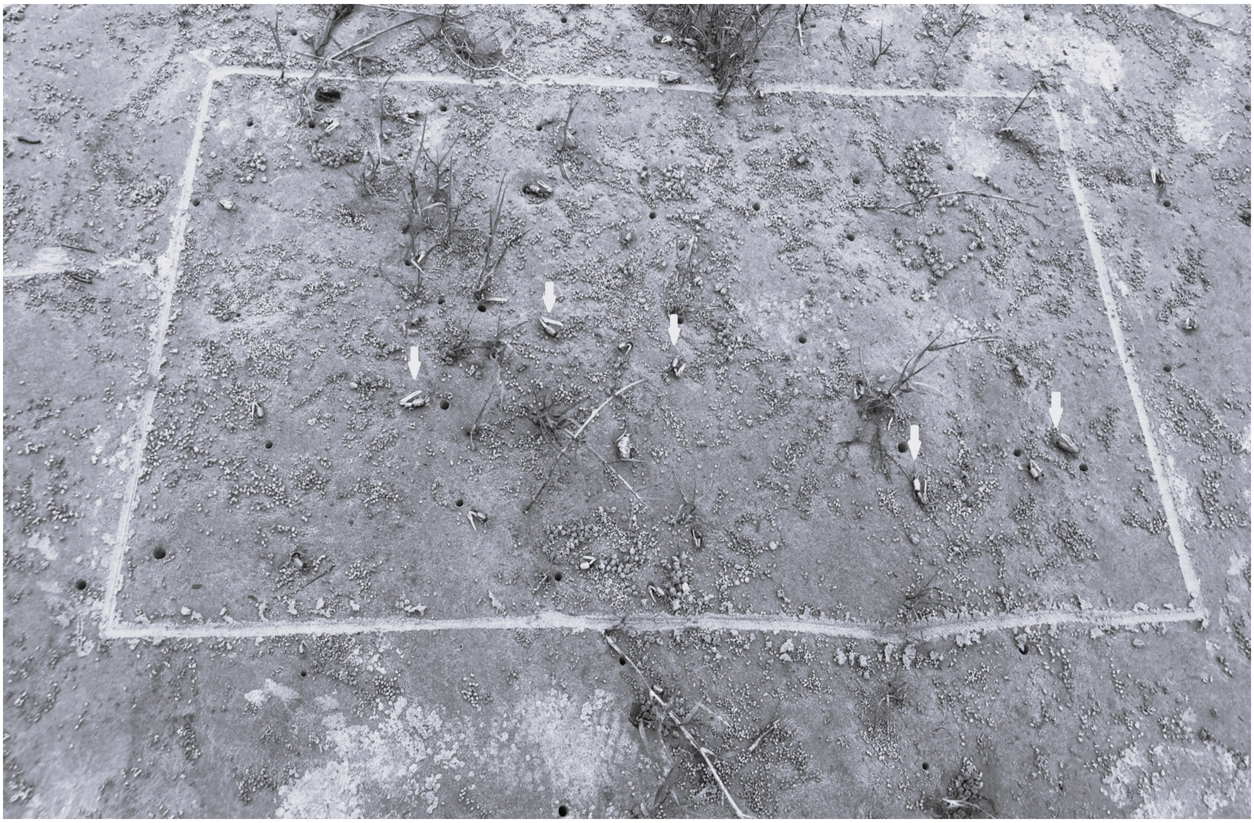

Figure 2. **Image captured during the experiment, showing the counting area (mark on the sand) and adult males of *Leptuca leptodactyla* (white arrows).**

ground, recorded an area of 1.2 m². A period of 10 minutes of acclimatization was given to the crabs to avoid possible biased responses to the camera's instalment (Hemmi & Merkle 2009).

After the recording started, the observer waited for 10 s to start the approach. The approach lengthened 10 m from the recorded areas, ending at the limits of the camera's field of view, taking 10 s to reach the end. After reaching the finishing point, the observer returned to the starting point using the same route. The observer walked at the same speed and wore the same clothing in all approaches, ensuring standardization in all experiments (Hemmi & Merkle 2009). The same protocol was used for all subgroups. The recording lasted 190 seconds, like the procedure of Hemmi & Merkle (2009).

Ethogram

Our ethogram consisted of eight categories (Table I), with six behaviors directly related to burrows, such as fleeing (to burrow), entering the burrow, inside the burrow, emerging, unanchoring, and constructing (or burrow maintenance). Additionally, feeding behavior was split between pre-stimulus and post-stimulus. This conceptual division of the same behavior enabled a more refined understanding of foraging, an activity that represents a state of normality for populations when not stimulated, and the primary behavior represented in daily activity budgets (Weis & Weis 2004).

Feeding is the main activity performed by fiddler crabs because even during different activities, they feed simultaneously (Weis & Weis 2004). Therefore, feeding behavior is crucial to understand differences between populations. Pre-stimulus foraging duration represents the time elapsed until a response is noticed to the observer's approach. Considering that all individuals were exposed to the same experiment (see below), a crab with a longer duration of pre-stimulus feeding means it tolerated the observer's approach for longer (more tolerant individuals). As for post-stimulus feeding, the latency to initiate feeding indicates when the animal resumed its normal activities. Therefore, a more intense response to the observer's approach translated into longer latency of the post-stimulus feeding behavior.

Video analysis

First, one of us (GBR) built an ethogram based on previously described behaviors (van Himbeeck et al. 2019) with adaptations (Table I). Recordings were analyzed with BORIS software (Friard & Gamba 2016). We listed the number of individuals that responded to the observer's approach (flee in the direction of their burrow), the onset of each behavior, and its duration. In addition, we also measured the distance between the fiddler crabs and their respective burrows at the moment of the approach using ImageJ software (Schneider et al. 2012). It is important to address that the camera was fixed at 45 degrees angle instead of 90 degrees as described by Hemmi (2005a, b), possibly causing some distortion in distances. Since some individuals were on the far end of the recorded frame and thus further away from the stimulus in question (approach of the observer), we separated the individuals into front and back blocks to assess whether there would be a difference in response between the two. No ethics approval was required to undertake this study.

Statistical analysis

Statistical analyses were conducted using R software version 4.0.3 (R Development Core Team 2020). First, variables were tested for normality using the Shapiro-Wilk test. Since all variables were non-normally distributed, we tested the difference in means with the Mann-Whitney U test and Dunn *a posteriori* test (FSA package). We also did a Pearson's correlation between the position of the fiddler crab and the duration of it flee movement to assess if there was a direct relationship between the distance from the burrow and the time the crab took to reach it. The mean distance of crabs from their burrows was also tested for each beach (high and low anthropogenic influence). In addition, the significance of the differences in latency means between treatments was calculated for each of the behaviors using the Mann-Whitney U test and Dunn *a posteriori* test (FSA package) with latency values rounded to 10-second blocks, and the mean latency between populations treatments was calculated to elucidate the differences between treatments better.

RESULTS

Ethogram and populations differences

All individuals responded to the stimulus (the approach of the observer) by fleeing and entering their burrows. We found differences in behavior durations between populations for six of the eight categories, except for entering burrow and construction (Dunn's Test $p<0.001$) (Table II), mostly because both behaviors were fast or rare (n=6 showed constructing behavior). The population with high anthropogenic influence spent more time inside their burrows, emerging and unanchoring, while the low anthropogenic influence population spent more time feeding (pre and post-stimulus) and fleeing.

Pearson's correlation detected a strong and positive correlation between the flee duration and the individuals' initial distance from their burrows (corr = 0.67; $p<0.001$). Therefore,

Table II. Means (and standard deviations) in seconds for each behavior and distance, given in centimeters, for each population. HAI - High anthropogenic influence. LAI - Low anthropogenic influence. The behaviors marked with a * showed a significant difference between the two populations (p < 0.05).

Behavior	HAI	LAI
	Means (SD)	
Emerge (s)*	29.4 (26.7)	17.2 (21.6)
Unanchor (s)*	9.1 (4.2)	8.5 (8.5)
Maintenance (s)*	3.9 (2.8)	9.2 (13.1)
Flee (s)	0.10 (0.1)	0.15 (0.1)
Enter the burrow (s)	3.1 (3.3)	2.7 (2.5)
Feeding - pre stimuli (s)*	9.0 (5.2)	11.2 (4.9)
Inside (s)*	92.2 (22.8)	47.0 (12.1)
Feeding - post stimuli (s)*	63.6 (32.6)	100.0 (35.2)
Initial distance from burrow (cm)*	1.7 (1.0)	2.7 (1.8)

animals that fled for longer were further from their burrows. As for latency, we did not detect differences between populations for entering the burrow (p=0.85), while all other behaviors showed similar latencies ($p<0.05$). Latencies of fleeing and entering the burrow were smaller in the high anthropogenic influence population, meaning that individuals from this population reacted sooner to the approach of the observer. Conversely, the low anthropogenic influence population had higher values of latency for emerging, unanchoring, and post-stimulus feeding, meaning that these individuals resumed their foraging activities sooner than the other population (Fig. 3).

DISCUSSION

This work investigated whether the behavior of fiddler crabs, *L. leptodactyla*, was related to distinct urbanization index. Contrary to what we expected, all individuals responded to the observer approach. Moreover, the hypothesis of the present work was not supported since the crabs from the high anthropogenic influence beach presented intense escape responses to the observer's approach and took longer to resume their pre-stimulus activities, such as foraging.

Feeding

All analyzed individuals were feeding before the stimulus, even those near the entrance of their burrows. The reaction to the approach of the observer caused the interruption of this behavior, a reaction like other fiddler crab species (Hemmi 2005a). A longer duration of pre-stimulus feeding was predicted in the HAI population, i.e., more tolerant individuals (Raderschall et al. 2011). Since the HAI population had constant interaction with humans, we expected that the approach of another human would not trigger such an intense response. Surprisingly, it was the beach with a lower urbanization index that showed higher averages of duration in this behavior (more tolerant), contesting the hypothesis of this work and the literature (Hemmi & Merkle 2009, Raderschall et al. 2011). In line with the results observed for pre-stimulus feeding, individuals from the LAI

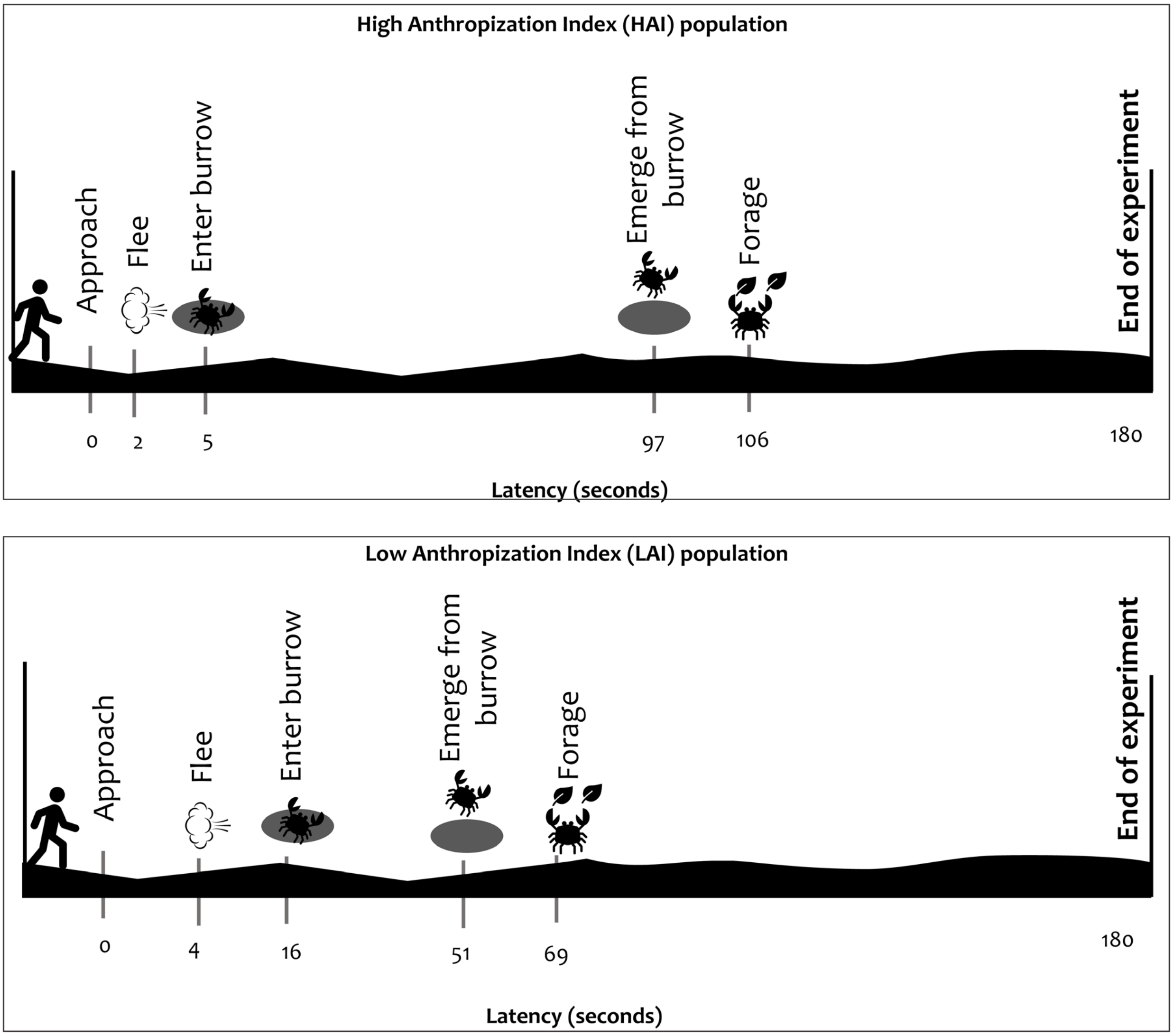

Figure 3. Comparison of mean latencies, in seconds, for the main behaviors (flee, enter burrow, emerge from burrow and forage) analysed in adult males of *Leptuca leptodactyla* living on two beaches with different degrees of anthropization in the Praia Dura mangrove in Ubatuba, Brazil.

population also showed a longer duration of post-stimulus foraging behavior.

Scape behavior (flee)

Scape behavior was the only response observed in our population. We did not call this behavior a "home run" (Hemmi 2005a, Hemmi & Merkle 2009) because the definition of this behavior required a distance of at least 3 cm travelled towards the burrow. In addition, a strong correlation was detected between the distance from the burrow and the duration of the fleeing behavior, indicating that animals farther from their burrows would run for longer. Individuals from the LAI beach showed a greater distance from their burrows and longer fleeing behavior. These results contradict the literature, as individuals farther from their burrows are expected to react more quickly to stimuli (Hemmi & Zeil 2003).

Burrow-related behaviors

There were no differences between the mean durations of the two populations during the burrow entering. Since entering the burrow is a transitional behavior between being inside and outside and should be considered an event, not a state. Similarly, emerging was also a behavior that did not show significant differences between populations and should be treated as an event.

Staying inside the burrow is closely related to the post-stimulus feeding behavior, as all animals resumed foraging after leaving their burrows. Individuals from the HAI population spent more time inside their burrows (i.e., a more intense response) in comparison with the LAI (i.e., a less intense response). These results again contradict the literature, as a more intense response to the presence of humans was expected in HAI populations (Hemmi & Merkle 2009, Raderschall et al. 2011). Since staying inside the burrow is associated with predator avoidance (Bellwood 2002, Jennions et al. 2003) then perhaps the HAI population is perceiving humans as predators.

The unanchoring behavior is not considered in other studies on fiddler crabs (e.g., Hemmi 2005a, b, Hemmi & Merkel 2009, Raderschall et al. 2011), although it showed great interpopulation variation. This behavior relates to the animal releasing its pereopods from any instance of its burrow. Hence, if animals are presenting shorter durations of this behavior, then they are distancing from their burrows more quickly. Unanchoring followed the same trend as other behaviors, where the HAI population presented more intense responses concerning the observer's approach, with a higher mean duration in this population.

Possible explanations for non-habituation

There are several possible explanations for the phenomenon reported here (Bejder et al. 2009); the effect observed here cannot be classified as habituation (Blumstein 2016); dishabituation (Leclerc et al. 2017); Harvesting as a potential selective pressure (Sadoul et al. 2021); Human presence altering selective forces), but we will discuss three of these possible explanations elucidated in the literature. The first explanation refers to the opposite effect of habituation, which is sensitization, defined as the increased response resulting from continuous exposure to repetitive stimuli (Peeke 1984). Since the time of year in which we recorded the animals may have exacerbated the number of tourists, this scenario may have contributed to the fiddler crabs exhibiting sensitization instead of habituation, thus increasing their responsiveness to anthropogenic stimuli (Bejder et al. 2009).

As another explanation is that crabs became sensitive in habitats with higher human pressure, which can be interpreted as high predation pressure. Kim et al. (2018) and Park & Kim (2021) did a study with two crab species, conducting experiments similar to ours. They assessed crab behavior under different levels of human presence. Crabs living in areas with high trampling took more time to return to surface (stayed longer in their burrows) than those living in the area where visiting was prohibited. It is important to note that surface activities include significant behaviors, such as courtship (Park & Kim 2021) and feeding (Kim & Choe 2003, Kim et al. 2008, Park & Kim 2021). Another recent study from Thailand (Chumsri et al. 2023) also detected that human disturbance affected time allocation, particularly in anti-predatory mode. Given our study was conducted during winter break, a high tourist season, increased trampling is likely to be happening in response to the higher human density. Therefore, the alteration in behavioral patterns of fiddler crabs from the HAI population could have the same explanations as these populations from Korea and Thailand.

The third possible explanation concerns past selective pressures. Such pressures – anthropogenic or not – at the individual level may have resulted in a population with individuals more responsive to humans (Bejder et al. 2009). Thus, the HAI population may be responding to human presence not due to sensitization but due to historical pressures generated by tourism and urbanization, including exposure to new chemicals (sunscreen or aerosols); water and air pollution; and higher incidence of light (by artificial means or removal of vegetation) (Sadoul et al. 2021).

Limitations of the study

There are certain limitations to the universalization of the results obtained by the research. First, habituation and sensitization take time to observe (Bejder et al. 2009), and effects of humans on crab activity can be detected a few days later (DiNuzzo et al. 2020) and a prolonged follow-up of these populations is needed. Second, although we analysed 80 individuals, they belonged to only two beaches inside a single mangrove. Therefore, including replicas from other mangroves and beaches would add more robustness to the results observed here, since some effects of anthropization, like trampling, can last six weeks (Park & Kim 2021). Third, a more detailed environmental survey can elucidate the effects of other environmental variables, obtaining a more holistic understanding of the phenomenon observed here. Some of these variables are the percentage of substrate moisture around the burrow and inside the burrow; substrate granulometry; biomass adhered to the substrate; chemical composition and physical properties of water in or around their burrows; incidence of predators; and the average size of individuals (Checon & Costa 2017), variables that influence the distribution of species, but little is known if there is any influence at the individual level (exceptions include (Hewes & Chaves-Campos 2018, Chen et al. 2019).

Our results emphasize the contrasting behavioral patterns of these two populations, where the LAI population fed for longer after the stimulus and showed a less intense response than the HAI population. Given that each population experiences distinct levels of interaction with humans, such interaction may influence not only these animals' escape behavior but also have cascade effects, with less time dedicated to foraging. However, since recording time is limited, our study does not represent the full behavioral repertoire of fiddler crabs, let alone the full extent of these effects. It is noteworthy that foraging behaviors are essential for animals as they are directly linked to caloric intake, and a calorie deficit can compromise health and reproduction (Navedo et al. 2019, Park & Kim 2021). Habituation to humans is considered a negative result of interaction with wildlife since these interactions pose several risks to animals and their populations such as dependence on human food (change in activity budget), attacks on humans and disease transmission (Orams 2002, Geist 2011). Sensitization has been proposed as a mitigating strategy to reduce human wildlife conflict (Honda et al. 2019). However, it can be costly as risk is a constant aspect of life (Blumstein 2016). The influence of human presence on wildlife, even if peaceful (as is the case with tourism), is the subject of intense research, with several consequences to wildlife such as territorial area, foraging behavior, and reproductive success (Gander & Ingold 1997, Bejder et al. 2006, Christiansen & Lusseau 2013).

Acknowledgments

A preliminary version of this paper was presented to a committee in partial fulfilment of the requirements for a Degree in Biology at Universidade Estadual Paulista. We thank the A. P. Ferreira, A. L. Arvigo and G. B. O. Machado for their contributions for species identification. We thank F. S. Búfalo for comments on early versions of this manuscript. LC receives a Research Productivity Fellowship from the Conselho Nacional de Desenvolvimento Científico e Tecnológico - CNPq (#314964/2021-5).

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How to cite

RODRIGUEZ GB, COSTA TM, CULOT L. & SOBRAL G. 2024. Fiddler crabs from highly disturbed beaches are more sensitive to human presence. An Acad Bras Cienc 96: e20230675. DOI 10.1590/0001-3765202420230675

Manuscript received on June 26, 2023;
accepted for publication on April 7, 2024

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