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Human disturbance affects behavioural time allocation in a fiddler crab (*Austruca annulipes*) in Southern Thailand

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Abstract Human disturbances affect the macroinvertebrate populations in coastal regions. They respond to disturbances by altering their density and behaviour. Therefore, many of them are used as bioindicator species of human disturbance. Here, we pioneer the use of fiddler crabs to examine whether they alter their behaviour under human disturbance. Male fiddler crabs possess one large claw used for courting (waving) and fighting, and one small feeding claw, whereas females have two feeding claws. They show several surface activities. This study investigates (1) the effects of human disturbance on density and sex-ratio, and (2) the effects of human disturbance, and sex on behavioural time allocations in *Austruca annulipes.* Their density, sex-ratio, and time allocations were investigated in human-disturbed area (DA) and nondisturbed area (NDA). They showed feeding, feeding and walking, walking, running, standing/vigilance, inside burrows, burrowing, grooming, fighting, and waving. The results showed that crab density was higher and the sex ratio was more male biased in NDA than in DA. Human disturbance and sex affected time allocations but their interaction had no effect. Crabs in DA spent more time running, standing, and inside burrows but less time walking, burrowing, fighting, and waving than crabs in NDA. Between sexes, males spent more time standing, burrowing, grooming, and fighting but less time feeding, and walking than females. This indicates that human disturbances force the crabs to spend more time on anti-predator and escape behavior (standing/vigilance, running, inside burrows) rather than courting (waving) and constructing burrows (mating/breeding sites), which are important for breeding.

Keywords: Fiddler crabs, human-induced disturbance, coastal region, time budget, animal behaviour

1. Introduction

Currently, human-related disturbances are increasing in coastal regions because of the important ecosystem services in these regions (Davenport and Davenport 2006; Halpern et al 2008; Barbier et al 2011). Unfortunately, these disturbances will continue to increase in the future since the number of people is increasing in coastal regions (Vitousek et al 1997; Davenport and Davenport 2006; Halpern et al 2008). Animals, especially macroinvertebrates living in these regions, have already started to show their response towards these human disturbances. For example, ghost crab (*Ocypode quadrata*) populations respond by reducing their actual/burrow density (Neves and Bemvenuti 2006; Hobbs et al 2008; Suciu et al 2018; Gül and Griffen 2018a, b) and body/claw sizes (Hobbs et al 2008; Gül and Griffen 2018b; Gül and Griffen 2020). Moreover, their burrow morphology, fidelity, longevity, and distribution are highly affected by human disturbances (Gül and Griffen 2018a; Gül and Griffen 2019). Other crustacean species, such as sandhoppers (*Atlantorchestoidea brasiliensis*) and mole crabs (*Excirolana braziliensis*), are also sensitive to human disturbances, and their densities are negatively correlated with human impacts (Cardoso et al 2016; Suciu et al 2018). Fiddler crab (*Afruca tangeri*) density and body size have a negative relationship with human disturbances (Oliveira et al 2000; Numbere 2020).

Since macroinvertebrates in coastal ecosystems respond to human-related disturbances and signal changes in their ecosystems, many of them are used as bioindicator species to assess the ecological impacts of those disturbances. Using bioindicators is a quick and cost-effective technique for assessing human disturbances (Carignan and Villard 2002; Spellerberg 2005; Cortes et al 2013). The species that is selected as an indicator should have the ability to represent the ecological changes in a given area (Carignan and Villard 2002; Siddig et al 2016). In coastal regions, several macroinvertebrates such as ghost crabs (Gül and Griffen 2018a, b, 2020), mole crabs, sandhoppers (Cardoso et al 2016), fiddler crabs (Yáñez-Rivera et al 2019), and clams (Laitano et al 2022), are used as bioindicator species to assess the effects of human-related disturbances. Generally, the presence/absence, abundance, age and body size of bioindicator species are widely used as indicators during assessments of human disturbances in nature (Carignan and Villard 2002; Spellerberg 2005; Cortes et al 2013; Siddig et al 2016). However, animal behaviours could also be used as bioindicators of human disturbances because the first

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response of an animal to an altered environment is the modification of its behaviour (Tuomainen and Candolin 2011; Wong and Candolin 2015). Several studies have found that animals modify their daily activities under altered habitat conditions (Sih et al 2010; Sih 2013; Fontúrbel et al 2015; Wong and Candolin 2015; Costa et al 2019). For example, although the abundance of some crab populations is generally used as a bioindicator of several human disturbances (Cannicci et al 2009; Wildsmith et al 2009; Jonah et al 2015; Schlacher et al 2016), some of these populations modify their burrow construction behaviour in human-disturbed areas (Weis and Perlmutter 1987; Culbertson et al 2007; Gül and Griffen 2018a; Bartolini et al 2009) which could also be taken into account as a bioindicator. Therefore, it can be predicted that in human-disturbed area, animals may alter their behaviour or time allocations for different daily activities (i.e., time budget), which could also be used as bioindicators of human disturbances in a given area.

The amount of time animals allocate to perform different essential daily activities is limited. Time allocated for one activity takes time away from conducting another important activity that could be important for survival or reproduction (Rauter and Moore 2004; Dunbar et al 2009). In most cases, animals maximize their time allocation for feeding and gaining energy (Masman et al 1988; Tina et al 2016, 2018a, 2020). However, they also need time to allocate for anti-predation (i.e., standing/vigilance), escape (i.e., running/jumping), reproductive (i.e., courting, burrow/nest construction, mating), and social behaviours (i.e, fighting) (Loughry 1993; Dangles et al 2006; Dunbar et al 2009; Barros et al 2010; Tina et al 2016, 2018a, 2020). Therefore, animals face constraints on how much time they can allocate for each activity. Their decision to optimize time allocation for different activities depends on many factors, such as age (Ruckstuhl et al 2003; Gélin et al 2013), sex (Prates and Bicca-Marques 2008; Tina et al 2016, 2018a, 2020), body size (Tina et al 2018a, 2020), group size (Dunbar et al 2009; Lashley et al 2014), physiological status (Fenner and Bull 2008; Witter et al 2012), and environmental factors (Dunbar et al 2009). Animals are sensitive to any ecological, social, or environmental changes in their habitats, and they adjust their time allocation to the current situation (Schoener 1971; Mangel and Clark 1986). Consequently, behavioural ecologists study the time budgets of animals to investigate the ecological or social influences on their behaviour.

This study examines whether fiddler crabs (*Austruca annulipes*) alter their density, sex-ratio, and time allocations for daily activities under human disturbances and whether their behaviour could be used as a bioindicator of human disturbances. There are several reasons for choosing fiddler crabs as a model species in this study. They are abundant in coastal systems and are considered indicators of their habitat quality (Amaral et al 2009). They transfer energy to both terrestrial and marine habitats since they are consumed by a large number of fish, birds, and invertebrates (Skov and Hartnoll 2001; Litulo 2004). They act as effective ecosystem engineers in coastal systems through their feeding and intensive burrowing activities (Kristensen 2008; Smith et al 2009, Holdredge et al 2010). They are also known as key organisms because of their deposit-feeding and sediment modification activities, which have impacts on sediment characteristics and primary production (Kristensen and Alongi 2006; Kristensen 2008; Smith et al 2009, Holdredge et al 2010). Finally, they are highly social animals and show several surface activities (e.g., feeding, walking, running, standing, burrowing, etc.) those can easily be studied under natural conditions (Tina et al 2016, 2018a, 2020). In these crabs, females have two small feeding claws, whereas males have one small feeding claw and another extremely large claw that is not used for feeding but is used for courting females and fighting with other males (Crane 1975; Callander et al 2013; Tina et al 2016, 2020; Tina and Muramatsu 2020, 2021, 2022). Original major claws can be autotomized for several reasons, for example, during escaping a predator, and after autotomy, a new claw is regenerated that is visibly distinguishable from the original major claw (Yamaguchi 1973; Hopkins et al 1999). Regenerated claws are less robust, slenderer, and lighter than the original claws (Backwell et al 2000). In fiddler crabs, burrows are important resources since they serve as refuges from predators and environmental extremes, and are sites for moulting and breeding (Crane 1975; Christy 1982; Genoni 1991; Keeratipattarakarn et al 2020).

Our research objectives are to test (1) the effects of human disturbance on density and sex-ratio, and (2) the effects of human disturbance, sex, and their interaction on the time allocations for surface activities in *Austruca annulipes*. We predict that crab density, sex-ratio, and time allocations of males and females on their surface activities would be different between human-disturbed and nondisturbed areas.

2. Materials and methods

2.1 Selection of human-disturbed and nondisturbed areas

We studied the behaviours of *Austruca annulipes* on a muddy sandy flat in Mod Tanoi beach (7°18'33.2"N 99°24'57.9"E), Mod Tanoi village, Kantang district, Trang province, southern Thailand. The studied *A. annulipes* population was located at an approximately 145 m length x 25 m width site, and no other fiddler crab species was observed at this site. Mangrove vegetation was observed at this site. Some areas of this site are utilized by people, especially by fishermen. They have their houses there and most of the families farm chickens. However, some areas are not utilized by people, and thus, they are kept in their natural state.

In our study site, two different areas (each was 300 m^2 (20 m length x 15 m width)) were selected based on the presence or absence of houses, people, and chickens. One area was determined to be disturbed, and another was determined to be nondisturbed. There were 5 small fishermen houses in the human-disturbed area and no house in the nondisturbed area. In the disturbed area, people and chickens were found to walk frequently inside the crab population, disturb the crabs and destroy their burrows (personal observation by Chumsri A.). People and chicken numbers were counted in both areas for 3 consecutive days from 9 am to 3 pm, and it was observed that in the disturbed area, the mean (±SE) number of people was 9.66 ± 1.76 per day (i.e., 6 hours). Chickens were counted every 2 hours (from 9 am to 3 pm) for the same 3 consecutive days, and their mean number (±SE) was 6.50 ± 0.28 per 2 hours. No people or chickens were observed in the nondisturbed area during these 3 days (the researchers who collected data were not included). This study was conducted from March-April, 2023 during low tide.

2.2. Biology of the fiddler crab Austruca annulipes

Austruca annulipes is a dominant fiddler crab species and is widely distributed in mangrove ecosystems (Macintosh 1988***)***. Male *A. annulipes* use their major claws to court females and to fight with other males (Backwell and Passmore 1996; Backwell et al 1998, 1999). Males build breeding burrows and try to attract females towards their burrows. Females select males mostly based on breeding burrow characteristics (Backwell and Passmore 1996). Underground mating and egg incubation take place inside males' breeding burrows (Mokhlesi et al 2011). In tropical and subtropical regions, *A. annulipes* breeds throughout the year, but its peak breeding period is mostly in the summer season (Litulo 2005; Mokhtari et al 2008), which is from February to May in southern Thailand.

2.3. Measuring the density and sex-ratio of surface-active fiddler crabs (Austruca annulipes)

This study used a photography method to measure the density and sex ratio of surface-active fiddler crabs (Keeratipattarakarn et al 2021). The photography method is nondestructive and environmentally friendly and can be used effectively to estimate surface-active fiddler crab density and sex ratios (Keeratipattarakarn et al 2021). Fifteen 0.25 m^2 (0.5 m × 0.5 m) quadrats were placed in disturbed as well as in nondisturbed areas to examine the crab density and sex ratio. After placing each quadrat, a small piece of white paper written with the area code (for disturbed area 'D' and for nondisturbed area 'ND') and quadrat's number was placed inside the quadrat. Then, we waited for 10-15 min for the crabs to come out of their burrows. Afterward, we took four photographs of each quadrat by using cameras (iPhone 14 Pro Max, and Canon EOS M100) within the next 15 minutes. Photos were taken from a distance of 1-1.5 m, and the photographer did not change his/her position because a small movement of the photographer could force the crabs to enter their burrows. Once fiddler crabs get disturbed, they enter their burrows and come out of their burrows after several minutes (personal observation by Tina F.W.). The reason behind taking several photographs was to capture as many crabs as possible on the photographs (Keeratipattarakarn et al 2021).

Upon transferring the captured photographs to a computer, they were subsequently accessed for analysis. Initially, all four photographs obtained from a single quadrat were opened, and among them, the photograph that provided the clearest visibility of the crabs was selected for determining the sex of crabs and counting their numbers. It is easy to determine the sex of fiddler crabs based on the absence/presence of their major claws. After determining sex, the numbers of male and female crabs were recorded accordingly. Subsequently, the remaining three photographs were reviewed, and in the event of any additional crabs being observed, their presence was also documented.

2.4. Behaviour observation of the surface-active fiddler crabs (Austruca annulipes)

We randomly selected 40 crabs per area (disturbed area: 20 males and 20 females; nondisturbed area: 20 males and 20 females) and video recorded their activities using a Canon EOS M100 camera. During selection, only large crabs were selected based on the visual observation to avoid the effect of body size on crab behaviour (Tina et al 2016, 2020). Each day, video recordings were conducted in an unbiased manner so that both sexes were recorded equally or nearly. Each focal crab was video recorded for 7 min and then captured to measure its carapace width (CW) using digital Vernier callipers to confirm its size. A crab carapace width >9 mm was considered large (Tina et al 2016). If the crab was not in the expected size range, the data was discarded and the same procedure was conducted again. In the case of males, their major claw originality (e.g., original or regenerated claws) was also checked.

All videos were checked and crab activities were classified into ten behaviours, based on Nobbs (1999), Weis and Weis (2004), and Tina et al (2016, 2020): (1) feeding (using feeding claws to take small amounts of sediments and put them into their mouths), (2) feeding and walking (feeding while walking), (3) walking (only moving), (4) running (moving faster), (5) standing (vigilance, or doing nothing), (6) inside burrows (staying inside burrows, and not visible), (7) burrowing (digging a burrow), (8) grooming (males use their small claw to remove particles of sediment from their bodies and claws, and females use their minor claws to clean off eye stalks and/or mouth parts), (9) fighting (aggressive and defensive), and (10) waving (males moving major claws towards females). No surface mating was observed in this species. Afterward, the amount of time (i.e., minutes) each fiddler crab spent on each activity was analysed by watching the recorded videos, and the percentage of time that each crab spent on each activity was calculated (Tina et al 2016, 2018a, 2020).

2.5. Data analysis

Parametric statistics were used when normality or other assumptions of parametric tests were met. The percentage data of time allocation for different activities were arcsine transformed (in degrees) (Sokal and Rohlf 1981) to achieve the normality of the data. Differences in the sex ratio (the number of males versus number of females) of the crabs as well as differences in claw originality (the number of original claws versus number of regenerated claws) were determined by using a two-way contingency table (cross-tabulation) with Pearson's chi square test. A multivariate analysis of variance (MANOVA) test was used to analyse the effects of area (disturbed and nondisturbed), sex (males and females) and their interaction on time allocation for different activities. If the results were significant, two-way ANOVA was used to determine their effects on time allocation for each activity. In MANOVA and two-way ANOVA, male activity only (i.e., waving) was not included. Independent sample *t* tests were used to determine the differences in (1) crab density, (2) body size (i.e., carapace width) and (3) time allocation on waving in males between disturbed- and nondisturbed areas. Data are reported as the mean ± standard error (SE). All significance tests were two tailed, and tests were considered statistically significant at $\alpha = 0.05$.

3. Results

3.1. Density and sex ratio of surface-active Austruca annulipes

Independent sample *t* test showed that crab density was significantly lower in disturbed area than in nondisturbed area (Table 1). A similar result was observed in the case of male density, but female density was not different between the two areas (Table 1).

Pearson's chi square test showed that the sex ratio was significantly different between disturbed- and nondisturbed areas (Table 1). A higher number of males was observed in the nondisturbed area (Table 1).

Table 1 Density (crab numbers/0.25 m^2) and sex ratio of surface-active *Austruca annulipes*.

Density/0.25m^2	Disturbed area	Nondisturbed area	Statistical tests
Crab density	3.27 ± 0.34	6.13 ± 0.31	$t_{28} = -6.22$, $P < 0.001$
Male density	1.87 ± 0.27	4.67 ± 0.39	$t_{28} = -5.91$, $P < 0.001$
Female density	1.40 ± 0.21	1.47 ± 0.35	$t_{28} = -0.16$, $P > 0.05$
Sex-ratio (male: female)	28: 21	70: 22	$\chi^2_1 = 5.41$, $P < 0.05$

3.2. Body size and claw originality of focal Austruca annulipes in disturbed and nondisturbed areas

The carapace width of the focal crabs (those were video recorded) was not different between disturbed- and nondisturbed areas (disturbed area: 15.57 ± 0.38 mm; nondisturbed area: 15.24 ± 0.30; $t_{78} = 0.69$, $P > 0.05$). In the case of claw originality, 20% of the crabs in the disturbed area had regenerated major claws (the ratio of original to regenerated claws was 16:4), and 10% of the crabs in the nondisturbed area had regenerated claws (the ratio of original to regenerated claws was 18:2). The ratios of original to regenerated claws were not significantly different (Pearson's $\chi^2_1 = 0.78$, $P > 0.05$) between disturbed- and nondisturbed areas.

3.3. Effects of area, sex and their interaction on the time allocation of Austruca annulipes for different activities

Area and sex had significant effects on the amounts of time *A. annulipes* spent on different activities (MANOVA: area: Wilks' Lambda = 0.44, $F_{9, 68} = 9.33$, $P < 0.001$; sex: Wilks' Lambda = 0.52, $F_{9, 68} = 6.86$, $P < 0.001$). However, the interaction of these two factors did not show any effect (area*sex: Wilks' Lambda = 0.82, $F_{9, 68} = 1.62$, $P > 0.05$).

3.4. Effects of area, and sex on the time allocation of Austruca annulipes for each activity

In the case of time allocation on feeding, area did not show any effect ($F_{1, 76} = 0.77$, $P > 0.05$). However, females allocated more time on feeding than males ($F_{1, 76} = 20.10$, $P < 0.001$) (Figure 1a).

Time allocation on feeding and walking was not different between disturbed- and nondisturbed areas ($F_{1, 76} = 0.02$, $P > 0.05$) or between sexes ($F_{1, 76} = 1.31$, $P > 0.05$) (Figure 1b).

Both area and sex showed effects on the time allocation for walking. Crabs spent less time walking in disturbed area than in nondisturbed area ($F_{1, 76} = 14.05$, $P < 0.001$). On the other hand, females spent more time walking than males ($F_{1, 76} = 6.16$, $P < 0.05$) (Figure 1c).

In the case of running, crabs spent more time running in disturbed area than in nondisturbed areas ($F_{1, 76} = 10.83$, $P < 0.005$), whereas sex did not show any effect on time allocation on running ($F_{1, 76} = 0.69$, $P > 0.05$) (Figure 1d).

Both area and sex showed effects on time allocation for standing. Crabs spent more time standing in disturbed area than in nondisturbed area ($F_{1, 76} = 24.23$, $P < 0.001$). On the other hand, males spent more time standing than females ($F_{1, 76} = 13.68$, $P < 0.001$) (Figure 1e).

During the allocation of time to stay inside burrows, crabs in disturbed area stayed longer inside burrows than the crabs in nondisturbed area ($F_{1, 76} = 8.54$, $P < 0.01$). However, sex did not show any effect on time allocation for staying inside burrows ($F_{1, 76} = 1.11$, $P > 0.05$) (Figure 1f).

During burrow construction, crabs in nondisturbed area spent more time on burrow construction than crabs in the disturbed area ($F_{1, 76} = 7.86$, $P < 0.01$). On the other hand, males allocated more time on burrowing than females ($F_{1, 76} = 5.37$, $P < 0.05$) (Figure 1g).

In the case of grooming, area did not show any effect ($F_{1, 76} = 1.61$, $P > 0.05$), however, between sexes, males allocated more time on grooming than females ($F_{1, 76} = 21.94$, $P < 0.001$) (Figure 1h).

During fighting, crabs in the nondisturbed area spent more time fighting than the crabs in the disturbed area ($F_{1, 76} = 4.06$, $P < 0.05$), whereas, between sexes, males spent more time fighting than females ($F_{1, 76} = 5.36$, $P < 0.05$) (Figure 1i).

In the case of major claw waving of males towards females, males in the nondisturbed area spent more time on waving than the males in disturbed area ($t_{38} = -2.89$, $P < 0.01$) (Figure 1j).

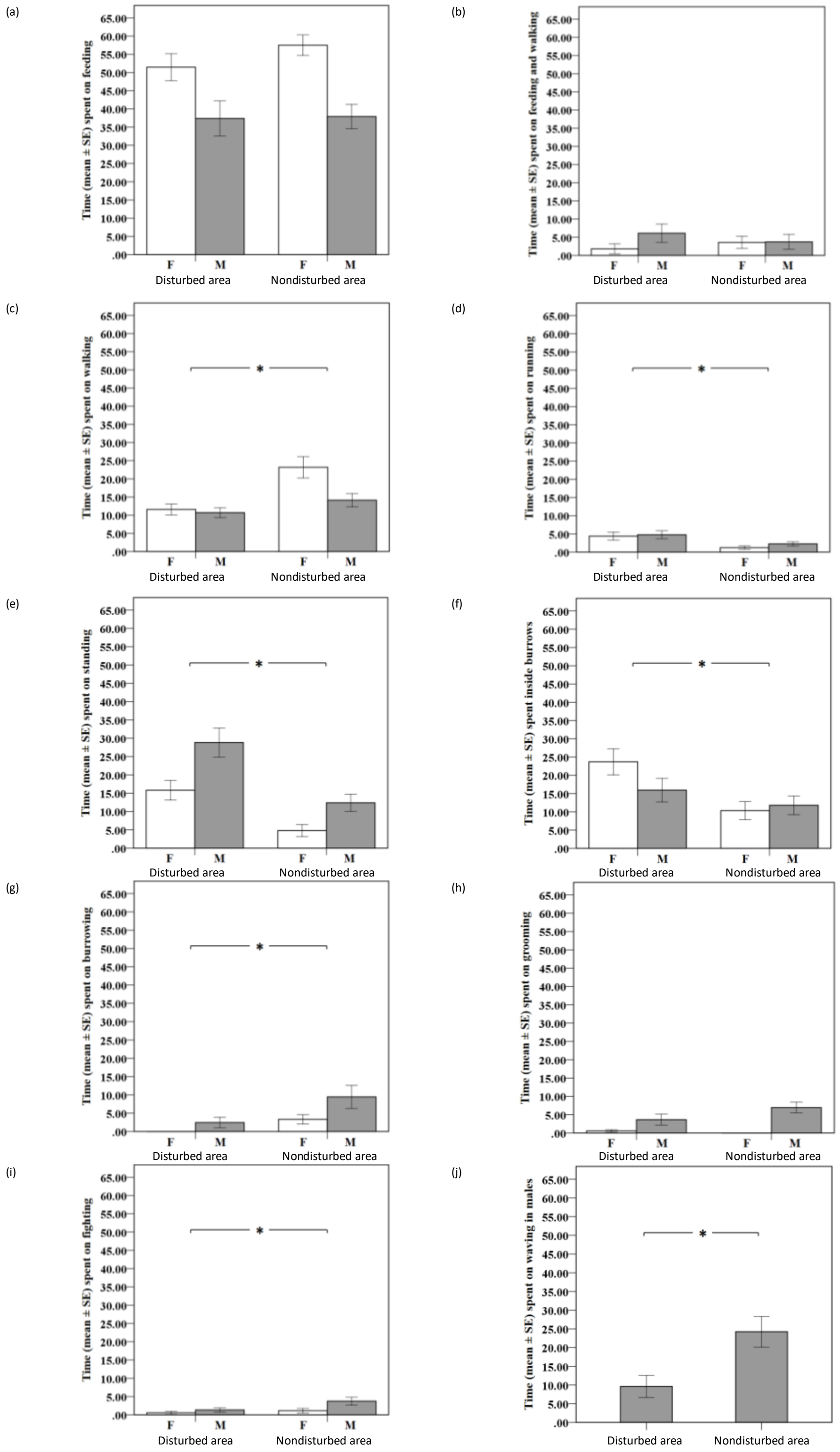

Figure 1 Time spent (arcsine transformed, degrees) by *Austruca annulipes* females (F, white bars) and males (M, gray bars) on different activities in disturbed- and nondisturbed areas: (a) feeding, (b) feeding and walking, (c) walking, (d) running, (e) standing, (f) inside burrows, (g) burrowing, (h) grooming, (i) fighting, and (j) waving; '*' indicates significant differences ($P < 0.05$) between disturbed- and nondisturbed areas.

4. Discussion

It was observed that crab density, especially male density was significantly lower in the human-disturbed area than in the nondisturbed area. This finding aligns with previous research on bioindicator species such as fiddler crabs (*Afruca tangeri*) and ghost crabs (*Ocypode quadrata*), which have exhibited a pronounced decline in burrow density in response to human disturbances (Oliveira et al 2000; Neves and Bemvenuti 2006; Maccarone and Mathews 2007; Hobbs et al 2008; Schlacher et al 2016; Gül and Griffen 2018a, b, 2019). The burrow density of crabs can be considered their actual density (Schlacher et al 2016). Several factors may explain the low crab density observed in disturbed areas, including crab mortality, limited food availability, and a scarcity of suitable foraging habitats. Observations indicate that in the disturbed area, people, particularly children, enjoy catching crabs, especially males, due to their visually appealing large claws, often taking them home for recreational purposes. Additionally, chickens were also found to disturb fiddler crabs and destroy their burrows. These disturbances could result in crab mortality or their preference for relocating to nondisturbed areas. Changes in food abundance or quality could also contribute to the decline in fiddler crab populations. Fiddler crabs primarily feed on benthic algae and vascular plant detritus (Crane 1975; France 1998). Mangroves produce leaf litter and detritus from the leaves of mangrove trees which are valuable sources of food for fiddler crabs and other animals in coastal waters. Moreover, mangroves provide essential foraging grounds for various organisms, including fish, birds, and aquatic invertebrates (Macintosh et al 2002). The destruction of mangrove trees and the subsequent reduction in leaf litter and detritus production caused by human activities, such as construction, may limit the availability of food and foraging habitats for crabs and other mangrove-dwelling animals. However, it is important to note that this study did not estimate the food abundance in disturbed and nondisturbed areas. Therefore, it is not possible to determine whether food shortage directly influenced the density of fiddler crabs in disturbed areas. Therefore, this question remains an avenue for further research and investigation.

This research study also reveals that crabs exhibit distinct behaviour patterns in the disturbed area compared to the nondisturbed area. Specifically, crabs in the disturbed area spend more time engaging in standing, running, and seeking refuge inside burrows. These behaviours are considered anti-predator responses, allowing animals to avoid or escape potential threats (Loughry 1993; Layne et al 2003; Hemmi 2005a, b; Barros et al 2010). When predators approach or intrude upon their habitat, prey animals typically display anti-predator behaviours such as standing or vigilance, running, and returning home. Standing or vigilance plays a critical role in the survival of animals, as it involves complex information-processing mechanisms aimed protecting themselves and their habitats from predators or intruders (Kim et al 2010). It has been reported that fiddler crabs can detect objects and estimate the distance of an intruder from their burrow entrance (Yu and Kim 2012). Upon detecting an object, fiddler crabs promptly cease their activities and remain motionless, exhibiting a state of vigilant standing. This behaviour allows the crabs to gather information about potential predators or intruders and assess the associated risks (Hemmi 2005b). The second stage in the crabs' response sequence is running toward their burrows. Although running incurs higher costs than standing, returning home provides them with safety. Once they are at their burrow entrance, they can assess the risk from a relatively secure zone. The third stage involves escaping or entering the burrow, effectively eliminating predation risk (Hemmi 2005b), particularly for *A. annulipes*, which construct deep burrows (Tina et al 2018b). Since fiddler crabs in the disturbed area of the present study were continuously disrupted by human and chicken activities, they showed more anti-predator and escape behaviours than the crabs in the nondisturbed area.

Crabs in disturbed area walked less than crabs in nondisturbed area. Crabs usually walk for searching of foods and mates (deRivera 2005; Nordhaus et al 2009). They tend to walk less when they need to minimize the predation risk (Lima and Dill 1990). Since there were people and chickens in the disturbed area, the crabs felt disturbed and tended to walk less. This finding indicates that crabs modify their walking behaviour due to human disturbance and thus their walking behaviour could be used as a potential bioindicator of human disturbance in mangrove regions.

In disturbed area, crabs exhibited a decreased time allocation for burrow construction compared to crabs in nondisturbed area. Burrow construction holds significant importance for fiddler crabs, as burrows serve as sites for moulting, breeding, and refuge from predators and environmental extremes (Crane 1975; Christy 1982; Genoni 1991; Keeratipattarakarn et al 2020). In many fiddler crab species, including *A. annulipes*, males construct breeding burrows, which females subsequently utilize for underground mating and egg incubation. Thus, constructing high-quality breeding burrows, characterized by greater length, depth, width, strength, and suitable temperature regulation for egg incubation, is crucial for male fiddler crabs. The process of building such burrows requires significant time and energy. If adequate time is not provided for burrow construction and if burrows are not strong enough, they may flood and collapse easily during breeding, ultimately impacting the reproductive success of female fiddler crabs (Christy and Salmon 1984). Therefore, it is essential to examine the effects of human disturbances on burrow characteristics and burrow temperature in fiddler crabs.

The fighting behaviour of crabs was found to be influenced by human disturbance. Animals typically fight to acquire or maintain possession of valuable resources, such as food, mates, or nests/burrows (Craig 1921; Morrell et al 2005; Tina et al 2017). In fiddler crabs, fights occur over territory ownership (Morrell et al 2005; Tina et al 2017) since burrows are important resources for fiddler crabs. Both males and females defend their burrows, but aggressive interactions primarily occur among males. Wandering males, who have lost their burrows either through eviction by another male or by ceding their breeding burrow to a female for egg incubation after mating, must find a new burrow. This requires fighting with resident males or females to acquire an unoccupied burrow or excavate a new burrow (Jennions and Backwell 1996). Conversely, resident males fight to protect their burrows from intruders. In the present study, crabs in disturbed area allocated less time on fighting than those in nondisturbed area. Similar observations have been made in other animal species, such as Nile tilapia (*Oreochromis niloticus*) (Almeida et al 2009), zebrafish (*Danio rerio*) (Xia et al 2010), and hermit crabs (*Pagurus bernhardus*) (Cunningham et al 2021), where aggression or social behaviour was reduced or modified in response to contaminants such as cadmium, nonylphenol, and microplastic pollution, respectively. As animal aggression is closely linked to territory defence, reducing aggressive behaviour may also diminish their ability to defend territories, which is crucial for their reproductive success and survival.

The waving behaviour of male fiddler crabs was found to be affected by human disturbance, as they allocated less time on this behaviour. Similar findings were observed in *Leptuca pugilator* males in a human-disturbed salt marsh region (DiNuzzo et al 2020). Male fiddler crabs signal or attract females by waving their major claws (Tina and Muramatsu 2020, 2021, 2022), a crucial mate acquisition tactic for males. In species where visual courtship behaviour is prominent, male display rate and duration are commonly considered common sexual traits of female choice (McDonald 1989; Backwell et al 1999; Reaney 2009; Andersson 1994). Female fiddler crabs are also attracted to males based on their claw-waving behaviour (Reaney et al 2008; Reaney 2009), as producing waves requires substantial energy expenditure (Matsumasa and Murai 2005), and only highly energetic males can sustain waving for longer durations. Since male waving display directly influences female mate choice, and attracting females is already challenging for males, reducing waving time due to human disturbances may pose additional challenges for males in courting females, potentially influencing females' mate choice and mating decisions. Environmental disturbances can impact different stages of mate choice in animals, subsequently affecting individual fitness, population dynamics, and community structure (Candolin and Wong 2019). Modification in the signalling system of animals can have important fitness consequences (Rosenthal and Fox 2012; Candolin 2019). Further research could be conducted on how human disturbances affect mate choice in fiddler crabs and its consequences for both ecological and evolutionary processes.

In terms of sexual dimorphism, male fiddler crabs spent more time engaging in courting/breeding behaviours such as grooming and burrowing, as well as in standing/vigilance, but less time on feeding and walking compared to females. Grooming, specifically cleaning their major claws, can be considered a breeding behaviour of males since they groom to keep their major claws as bright as possible, as females tend to prefer males with brighter claws (Bergey 2007). Additionally, males may require less energy to wave a major claw covered with less mud than one covered with more mud. Previous studies conducted on *A. annulipes* have also reported that males groom more than females (Tina et al 2016), and this pattern is observed in other fiddler crab species, such as *Tubuca rosea* (Tina et al 2018a, 2020).

In *A. annulipes*, there is a notable difference in burrow construction behaviour between males and females. Males typically spend more time constructing burrows than females (Tina et al 2016 and the present study). This discrepancy arises because males construct higher-quality breeding burrows, which are longer, deeper, and wider compared to burrows constructed by females (Lim and Diong 2003; Tina et al 2018b). Female fiddler crabs utilize these male burrows for underground mating and egg incubation (Christy 1983, 1987; Christy and Schober 1994). The quality of male burrows directly influences the reproductive success of females. The quality of a burrow depends on several characteristics, such as its length, depth, and width. Longer and deeper burrows help to minimize the temperature fluctuations within the burrow, providing a stable and suitable environment (Powers and Cole 1976; Keeratipattarakarn et al 2020), which is crucial for a constant embryonic development (Christy and Salmon 1984; Christy 1987). Burrow width determines the duration of egg incubation and the timing of larval release, both of which are vital for the survival of planktonic larvae upon release (Christy 2003; Reaney and Backwell 2007). Consequently, receptive females visit multiple male burrows and eventually select a high-quality breeding burrow for underground mating and egg incubation (Backwell and Passmore 1996). In contrast, females construct smaller-sized refuge burrows that are shorter, shallower, and less wide (Tina et al 2018b). These refuge burrows serve as temporary shelters for females (Christy 1982). As males need to construct longer and deeper burrows than females, they invest more time in burrowing behaviour to ensure the quality of their burrows.

The study revealed that male fiddler crabs spent more time engaging in standing behaviour than females. In fiddler crabs, males signal females by waving their major claws (Tina and Muramatsu 2020, 2021, 2022), making them more conspicuous to predators and hindering their escape (Magnhagen 1991). Consequently, males face an increased risk of predation and must be more vigilant. Increased vigilance may compensate for their heightened vulnerability to predation (Martín and López 1999, 2003). On the other hand, females were observed to spend more time feeding than males. This behaviour may be driven by the need to increase the number of eggs/clutches (Caravello and Cameron 1987) and the number of clutches per year (Salmon and Hyatt, 1983). Another contributing factor may be that males allocate more time to breeding-related activities such as grooming, waving, and burrowing, which leaves them with less time for feeding. Typically, males exhibit increased feeding during the nonbreeding period (Caravello and Cameron 1987) to store energy for the breeding period. Since this study was conducted during the breeding period of *A. annulipes*, males may have dedicated less time on feeding thus they could allocate more time on breeding activities.

Furthermore, females allocated more time on walking than males. This behaviour can be attributed to the mate-searching behaviour of females. Since the quality of male burrows directly affects the reproductive success of females, they need to find the best-quality male burrows carefully. Finding a suitable male that owns a high-quality breeding burrow requires an extensive search for females. Receptive females leave their burrows and wander to wave males. They visit several male burrows before selecting the best one. For instance, one *Leptuca crenulata* female visited 106 burrows within 65.7 minutes of her 22 m search (deRivera 2005). Therefore, searching for suitable male and good-quality breeding burrows provides a good reason why females need to walk more.

Our research findings demonstrate that human disturbance significantly alters the behaviour of fiddler crabs, leading to an increased allocation of time towards anti-predator, avoiding or escaping behaviours such as standing, running, and seeking refuge inside burrows. Conversely, there is a reduced amount of time allocated to breeding behaviours such as waving, burrowing and territorial defence behaviours such as fighting. These behavioural shifts indicate that human disturbance may have more far-reaching detrimental effects on marine organisms than currently recognized. Consequently, we propose that the time allocation behaviour of fiddler crabs could serve as a valuable bioindicator of human disturbance in coastal regions. Bioindicators are commonly utilized to quantify the responses of animals to specific disturbances (Holt and Miller 2011). Our study reveals that fiddler crabs are sensitive to human disturbance and they modify their behaviour in areas affected by human activities. Previous studies have employed fiddler crabs as bioindicator species to assess metal contamination (Capparelli et al 2016, 2017, 2019; Yáñez-Rivera et al 2019), microplastic and organophosphate pesticide contamination (Villegas et al 2021), and rare-earth elements (Lavezzo et al 2020). To the best of our knowledge, the use of fiddler crab behaviour as a bioindicator of human disturbance in coastal regions has not been explored extensively. However, DiNuzzo et al (2020) suggested the potential use of fiddler crab waving behaviour as a bioindicator of human disturbance in salt marsh regions, as males exhibited a decreased waving display in human-disturbed areas. Our study highlights the significance of investigating the effects of human disturbance on animal behaviour and time allocation in coastal regions, particularly as human populations in these areas continue to grow.

Future studies should investigate the consequences of human disturbances on animal communication, sexual selection, individual fitness, population dynamics, and community structure. This knowledge could be applied to the conservation management of fiddler crabs worldwide, particularly in polluted and human-disturbed areas, where their populations face significant challenges.

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Ethical considerations

Not applicable.

Conflict of interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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