

Unique Behavioral Strategies Adopted by Gravid *Ocypode gaudichaudii* to Overcome Dehydration Stress while Minimizing Predation Risks

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Semi-terrestrial crabs require continual access to water to maintain life-sustaining processes such as circulation and feeding. When they emerge from their burrows during low tide to forage, they face the problem of dehydration as they leave the dampness of their burrows. While foraging above ground, water uptake is elicited through capillary action via the hydrophilic setae near the base of the crab's body. Extruded eggs that are borne on the abdominal flap of females tend to obstruct the contact of the setae with the wet sediment. The behavioral adaptations of how the gravid female painted ghost crab, *Ocypode gaudichaudii*, overcomes dehydration stress and minimize predation risks at a sandy shore Playa Venao, Panama was studied by field observations. Comparison of the morphometric measurements of setal tufts between 30 male and 30 female crabs were made to determine if there are morphological adaptations. Analysis of the water uptake behavior from video footages, showed that gravid crabs spent a longer duration on water uptake than crabs that do not carry eggs. Masquerading behavior of a gravid *O. gaudichaudii* to minimize the detection by predators through freezing movement next to a stone enroute to the lower shore during the day was observed for the first time. There was no sexual dimorphism in the length and width of the setal tufts between the male and female adult crabs. The results of this study provide the first evidence that the water-uptake behavior in gravid *O. gaudichaudii* is dependent on behavioral adaptations as setal tuft morphology does not differ between the sexes.

Key words: Behavioral adaptation, Masquerade behavior, Setal tufts, Trade-off, Water uptake.

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BACKGROUND

To survive, animals need to ensure that they have adequate food, water, and oxygen, as well as a reliable shelter in order to reproduce successfully to propagate the species. When animals experience stress, they exhibit proximate and ultimate adaptations. The immediate response involves behavioral adaptations (*e.g.*, avoiding or alleviating the source of stress, etc.) and responses may differ from individual to individual. The ultimate success of survival of an individual, however, is limited by characteristics that have been selected for over generations. Generally, these traits that are genetically controlled constitute morphological and physiological adaptations.

Crabs belonging to the Ocypoididae, are semi-terrestrial crabs. The transition from an aquatic medium to a terrestrial environment presents both benefits and problems for crabs (Combs et al. 1992). Although there may be more new resources to exploit on land, and oxygen would be more readily available, there are certain morphological, physiological, and behavioral strategies necessary to overcome problems associated with terrestrial living such as dehydration, circulatory and osmotic adjustments (Burggren and McMahon 1988). In addition, predation risks are higher as they are preyed upon by larger land predators as well as avian predators (Koepcke and Koepcke 1953; McCullough et al. 2019; Yong and Lim 2022). A continual availability of water is crucial for life-sustaining processes such as circulation and feeding. Previous studies (*e.g.*, see Wolcott 1976, 1984; Mercier and Wilkens 1984; Burggren and McMahon 1988; Thompson et al. 1989; Matsuoka and Suzuki 2011) have documented that water uptake involves two mechanisms: (1) the generation of low relative hydrostatic pressure in branchial chambers—through the forward beating of the scaphognathite such that the hydrostatic pressure in the branchial chambers is less than that of the external surrounding—thereby drawing water from the moist substrate to circulate across the gills, and (2) the capillary action between adjacent hydrophilic setae surrounding the Müller's aperture—an opening near the base of the crab's body, which leads to the branchial chambers (see Maitland 1990)—located between the second and third pairs of walking legs (Fig. 1). The Müller's aperture is an opening near the base of the crab's body, which leads to the branchial chambers (Maitland 1990). Hence, an efficient system of uptake of water through the combined effects of the low relative pressure in the branchial chambers and the capillary action of hydrophilic setal tufts surrounding the Müller's aperture works to keep the crabs sufficiently hydrated. Water that enters the Müller's aperture is then circulated through the branchial chambers and out via the exhalant apertures located near the mouthparts.

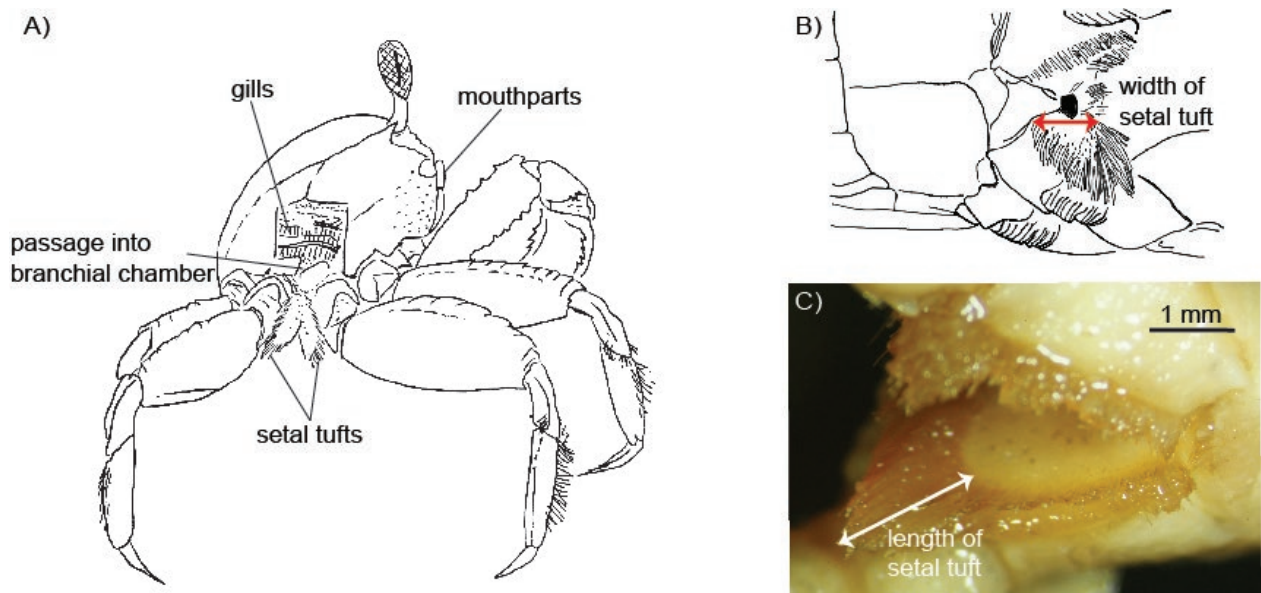


Fig. 1. A, *Ocypode gaudichaudii* with portion of carapace cut away showing relative portions of structures involved in water uptake (adapted from Wolcott 1976); B, width of setal tuft (adapted from Wolcott 1984); C, length of setal tuft.

During deposit-feeding, sediment is brought to the mouthparts by the chelae, where specialized setae at the maxillipeds help to dislodge organic matter from the surface of sediment particles (Miller 1961; Crane 1975). The organic matter is then flushed using respiratory water pumped into the buccal cavity—known as ‘flotation’ process—and eventually enters the stomach (Miller 1961). In contrast, the heavier inorganic particles are collected at the base of the mouthparts and rolled into moist boluses known as feeding pellets and left on the sediment surface (see Crane 1975). Hence, continual access to water is integral for the procurement of food to crabs that deposit-feed; it is therefore logical to infer that a crab that is heavily engaged in deposit-feeding exhibits more frequent and/or longer bouts of water uptake and circulation.

Semi-terrestrial crabs generally emerge from their burrows during ebb tide when the intertidal shore is exposed, to feed and engage in other activities, such as defence of burrow and courtship (Crane 1975). To maximize the limited time available for surface activity while the tide is out, it would be more efficient to conduct water uptake directly from the surface of the substrate rather than interrupt foraging and courtship opportunities by making frequent trips back into the burrows or to the water’s edge for rehydration (Miller 1961; Crane 1975). Wolcott (1976) described the behavior exhibited by the Atlantic ghost crab, *Ocypode quadrata*, during water uptake: the desiccated crabs in his experiments sat down on the damp sand and brought the tufts of setae into close contact with the sand surface by moving side to side, until the tufts became saturated with water. To study the water uptake process further, he conducted experiments to measure the branchial chamber pressure as well as manipulated the setal tufts to impede capillary action (*e.g.*, gluing on rubber flaps as a loose cover, and matting the setae with lacquer).

Continual reproductive success in a species is crucial to the sustainability of viable populations. In semi-terrestrial brachyuran crabs, mating, which involves internal fertilization, may occur either above ground or in burrows. After copulation, the fertilized eggs are extruded and carried on the female's pleopods, partially protected by the abdominal flap. Females with extruded eggs are more conspicuous when wandering around on the shore due to the large egg mass. It is well established that burrows of ocypodoid crabs are used as a refuge from predators, extremes of temperature, desiccation—providing water for physiological needs—as well as serving as a site for molting, copulation, and reproduction (see Hughes 1973; Christy 1982). For example, gravid females of the sand fiddler crab, *Uca pugilator* has been reported to sequester in burrows and incubate their eggs in safety for about 12–14 days before releasing their eggs during a spring tide (see Christy 1982).

In recent years, the diet of juveniles and adults, foraging strategies as well as niche partitioning of the two life stages of the painted ghost crab, *Ocypode gaudichaudii*, has been studied in detail (see Lim et al. 2016; Yong and Lim 2019; Yong and Lim 2021; Yong and Lim 2022). *Ocypode gaudichaudii*, the painted ghost crab, is one of the largest semi-terrestrial crabs that deposit feeds, and its behavior after emergence at ebb tide is easily observed. The adults of this species of ghost crabs are bright red in color, which makes them highly conspicuous on a sandy shore (see Crane 1941). A 14-month field ecological study of two populations of *O. gaudichaudii* in Panama (Culebra Beach and Playa Venao) showed that hardly any gravid females wandered around the shore to forage during daylight hours as there were avian predators at the two sites (AYPY personal observation). In addition, there is a nocturnal predator, *Hoplocypode occidentalis*, a sympatric ghost crab that preys upon crabs that emerged at night at Playa Venao. The situation at this surf beach is exacerbated due to the crab population being concentrated in a narrow stretch of foreshore, thereby making space at the beach, a prime resource. Water at the bottom of burrows at the high shore tend to drain out faster due to the lowering of the water table during low tide. When population densities are high, invariably there may be some gravid *O. gaudichaudii* which have to occupy burrows on the high shore due to overcrowding. In this paper, we examined how gravid female *Ocypode gaudichaudii* overcomes the dehydration stress caused by living high up on the shore with behavioral adaptations to minimize predation risks.

MATERIALS AND METHODS

The study was conducted in 2012–2013 at Playa Venao, PV, (7°25'54"N, 80°11'29"W) along the Pacific Coast of Panama. PV is a moderately-exposed surf beach at the south-eastern coast of

the Azuero Peninsula. The data collected for this paper were part of a larger study on the ecology of *Ocypode gaudichaudii* in Panama. In total, thousands of crabs were observed and the general surface activities of these crabs were documented during day and night-time sessions using a hand-held video camera (Sony Handycam DCR-SR62). Excerpts of the video recordings of the diurnal and nocturnal activities of these crabs which involve water uptake in gravid females and adult crabs that did not carry eggs were extracted and analyzed. The duration of water uptake was defined as the duration in which a crab lowered either one (video 1) or both sets (video 2) of setal tufts to the surface of the sediment until it lifted its carapace off the substrate.

As *O. gaudichaudii* is not sexually dimorphic, the observed adult crabs that were not laden with eggs could have consisted of both female and male crabs. Morphometric measurements of the setal tufts of 30 dead male and 30 dead female crabs of various sizes were measured to determine if there was sexual dimorphism in the setal tufts. The second and third left walking legs were pushed apart to separate the flaps with the setae. An image processing system that comprised a Zeiss Stemi SV11 stereomicroscope, a Canon digital camera EOS 450D, and Canon Utility image capturing software was used to photograph the setal tuft on the third left walking leg of each. Length and width of the setal tuft (Fig. 1) were measured from the 1200 dpi digital photographs in the image processing software ImageJ.

We used ANCOVA with 'Length of setal tuft' or 'Width of setal tuft' as the response variable, 'Sex' as the factor, and 'Carapace width' as the covariate to compare the patterns of morphometrics of setal tufts between sexes. All data were tested for homogeneity of variance with Levene's test before an ANCOVA was carried out. The ANCOVAs for length and width of the setal tufts in males and females were performed to determine whether the sexes differ in the pattern of morphometrics of setal tufts with increasing size. If slopes did not differ significantly, a test of intercepts was carried out. All statistical analyses were done using MINITAB software (MINITAB, Inc., Release 14, 2003).

RESULTS

In the 14-month ecological study period, although 25 gravid crabs were observed, only three gravid crabs (one during the day, one at night and one at dawn) were recorded on video as they were the only ones that exhibited water uptake. The gravid *O. gaudichaudii* that was observed at low tide during the day exhibited a unique behavior that has never been reported before. The crab relocated from a burrow at the upper shore to excavate another burrow near the water's edge. Enroute to the lower shore, the crab initially had to rapidly traverse a stretch of open beach area and

was therefore vulnerable to predation. Once it crossed into a zone on the beach where there are stones and pebbles, it made stops next to stones and pebbles in an attempt to disguise itself to minimize predation risk. It moved between stones and pebbles on the shore, seeking ‘protection’ through association with similar-looking objects (*i.e.*, the stones) as its carapace. While it crouched stationarily beside the stone/pebble, it hydrated itself by lowering one side of its carapace to contact the damp sediment such that the setal tufts can uptake water through capillary action (video 3). No feeding activity was carried out during this relocation journey to the lower shore. The female that was observed at dawn also sat on one side of its carapace during water uptake; however, the gravid female that emerged at night did both modes of water uptake, one sided as well as sitting down squarely on the damp sediment.

The duration of water uptake when the gravid crabs sat one-sidedly on the sediment was 2.6 times longer than when a gravid crab sat squarely on the sediment surface with both sets of setal tufts on the right and left in contact with the damp sand (31.0 ± 5.2 s *cf.* 12.0 ± 0 s respectively; Fig. 2). A total of 43 crabs that were not carrying eggs were randomly recorded in the process of water uptake; of these, 40 crabs sat on one side of the carapace for a mean duration of 4.7 ± 0.4 s while three crabs had the setal tufts on both sides of the carapace in contact with the sediment surface for 8.4 ± 6.9 s.

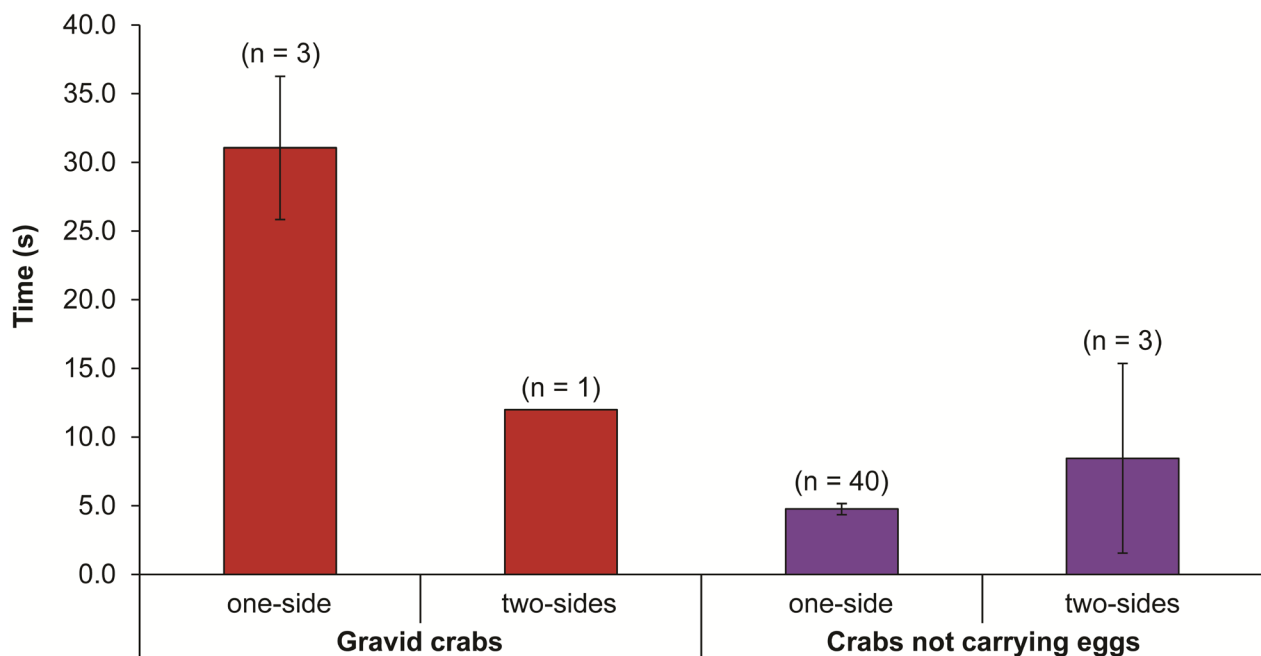


Fig. 2. Time taken for water uptake using setal tuft(s) on one-side and on both sides of carapace in gravid and non-gravid *Ocypode gaudichaudii*. ■, female; ■, mixed sexes.

The length and width of the setal tufts increased with an increase in crab carapace width (Females: Setal tuft length = $0.11 \text{Carapace width} - 0.30$, $R^2 = 0.70$; Setal tuft width = $0.20 \text{Carapace width} - 0.46$, $R^2 = 0.85$; Males: Setal tuft length = $0.09 \text{Carapace width} + 0.15$, $R^2 = 0.71$; Setal tuft

width = 0.21Carapace width – 0.32, $R^2 = 0.82$) (Fig. 3A and B). ANCOVA results of the setal tuft morphometrics shows that there was no significant difference ($p > 0.05$) between the slopes or the intercepts of regression lines of males and females for the length and width of the setal tufts in relation to carapace width (Table 1; Fig. 3A and B).

Table 1. Results of ANCOVA testing slopes and intercepts of regression equations estimating relationships among morphological variables in *Ocypode gaudichaudii*

Source	df ₁ , df ₂	F	<i>p</i>	Inference	
A) Length of setal tuft					
Sex	1, 56	1.48	0.229	n.s.	Intercepts not different
Carapace width	1, 56	132.40	0.000		
Sex × Carapace width	1, 56	1.61	0.210	n.s.	Slopes not different
B) Width of setal tuft					
Sex	1, 56	0.07	0.796	n.s.	Intercepts not different
Carapace width	1, 56	2.36	0.000		
Sex × Carapace width	1, 56	1.36	0.703	n.s.	Slopes not different

A: length of setal tuft in males vs females; B: width of setal tuft in males versus females. n.s., not significant; sig., significant at $p = 0.05$.

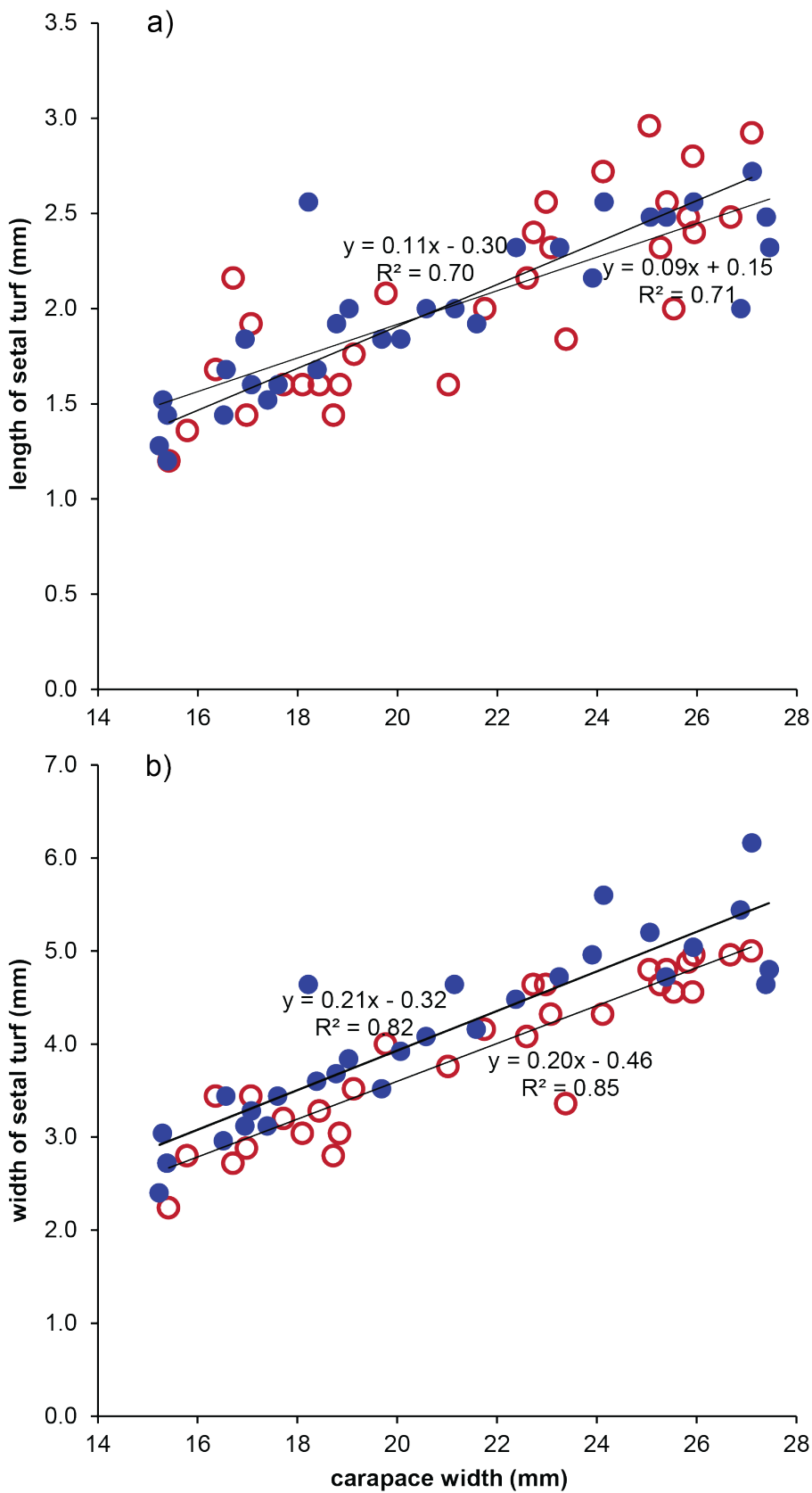


Fig. 3. Scatterplots of the A) length and B) width of setal tuft in relation to carapace width of *Ocypode gaudichaudii*. ●, male; ○, female. —

DISCUSSION

Our morphometric results showed that there is no sexual dimorphism in the length and width of the setal tufts in female and male adult *O. gaudichaudii*; this validates that the mean duration of water uptake time of all the crabs without eggs (combined) was representative of the typical water uptake behavior without having to ascertain the sex of the crabs. Furthermore, it is also indicative that female crabs are not morphologically adapted to facilitate water uptake when laden with eggs, by having longer and wider setal tufts. The large protruding egg mass of gravid crabs limits the range of movement of the crabs and made it more difficult for them to keep their setal tufts in contact with the damp sediment. In addition, more water could be needed to hydrate the egg mass. Therefore, the gravid females compensated by spending a significantly prolonged period keeping their setal tufts in contact with the damp sediment than their non-ovigerous conspecifics. This behavioral adaptation is logical since females are in a dehydrated state when they risk their safety to emerge from their burrows to satisfy physiological needs. However, the sighting of water uptake in gravid crabs at the sediment surface is a rare phenomenon.

A great diversity of burrow architecture exists in the ocypodids: unbranched, straight, gently curved, spiral tubes, multi-branched, J-, U- and Y-shaped burrows have been reported for seven species of ghost crabs, viz., *O. quadrata*, *O. cursor*, *O. cordimana*, *O. stimpsoni* and *O. ceratophthalmus* (see Braithwaite and Talbot 1972; Shuchman and Warburg 1978; De 2005; Chan et al. 2006; Lim et al. 2011). However, *O. gaudichaudii*, have simple-shaped burrows (*i.e.*, straight, bow-shaped, S, half-spiral or spiral) (Schober and Christy 1993). The evaporative rate of the water in simple-shaped burrows would, presumably be higher than those of complexly shaped burrows; coupled with the location of the burrow at the upper shore, it is conceivable that the gravid females that live in this zone would be extremely dehydrated after sequestering for a period of time. It is not known if the burrows at the upper shore are deeper than those at the lower shore to reach the water table as reported for another ocypodoid, the porcelain fiddler crab, *Uca annulipes* (see Lim and Diong 2003).

It is evident that the predominant hydration behavior is to utilize one set of setal tuft to elicit water uptake through capillary action, regardless of sex and reproductive state (gravid vs non-gravid). Although a shorter duration of water uptake time can be achieved using both sets of setal tufts, perhaps this stance would render the crab more vulnerable to predation as the reaction time to run to safety would be longer since the crab must lift its carapace off the substrate before escaping. It is pertinent to note that only the gravid crab which was observed during the night adopted the two-sided water uptake mode while the other two crabs that emerged during the day and at dawn, only contacted the setal tufts on one side with the damp sediment. This suggests that the gravid crab

perceived that predation risks at low light intensity (*i.e.*, night-time) are probably lower than that in broad daylight and growing light at dawn, albeit there is *H. occidentalis* lurking around on the shore.

Besides the ‘flight’ or ‘fight’ response when predators are encountered, the first line of defence that animals use is to avoid detection by predators as far as possible. Mechanisms to achieve predator-avoidance involve camouflage, masquerade, apostatic selection, living underground or nocturnality. Being such a conspicuously colored crab on the shore, *O. gaudichaudii* usually dashes to seek refuge rapidly into burrows whenever a threat is perceived (SSLL and AYPY personal observations) since ghost crabs are renowned as the fastest crustaceans on sandy beaches (see Hafemann and Hubbard 1969).

Gravid *O. gaudichaudii*, however, used masquerade to avoid detection by a predator through freezing movement next to a stone enroute to the lower shore during the day. In the case of a severely dehydrated gravid crab in the high shore region, perhaps the crab is physiologically ‘weakened’ to such an extent that the energy to effect that quick burst in speed is lacking, or that the distance to the lower shore is too lengthy to dash to cover at one go. This is the first report of such a masquerade behavior in ghost crabs; these macrofauna on sandy beaches are known to exhibit the ‘flight’ behavior as their primary anti-predator response since they are such fast-runners. Mechanisms used for predator-avoidance have been reported to be species-specific and independent of sex. For example, Su and Lim (2016) reported that the mangrove brachyurans, *Paracleistostoma depressum* and *Haberma nanum* exhibited species-specific anti-predator behaviors, with males and females behaving in a similar manner. *Paracleistostoma depressum* used a ‘sit’ strategy instead of ‘flight’ whereas *H. nanum* reacts early in the onset of impending threat with ‘run’ as a response. However, it should be noted that the female crabs used in their experiments were all non-gravid. In our study, it would seem that male and female *O. gaudichaudii* are capable of showing differentiated anti-predator avoidance behavior, albeit only gravid female crabs exhibited masquerade behavior. Hence, future studies investigating the influence of sex in predator-avoidance behavior of crabs should consider an added dimension by including the reproductive state of female crabs.

CONCLUSIONS

In summary, this study provides the first evidence of the behavioral strategies that gravid *Ocypode gaudichaudii* undertake to alleviate dehydration stress and avoid predators. As gravid crabs are more conspicuous with a large egg mass, it is crucial that they are able to avoid predators while spending a longer time hydrating themselves on the open shore. Our study suggests that

gravid *O. gaudichaudii* benefits from its apparent masquerade as beach pebbles when it moved across the open shore. Although the proximate mechanism of the strategy remains unclear, this study sheds light on how a common beach macrofauna in a dynamic sandy beach environment balances the trade-offs of dehydration and predation.

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Competing interests: The authors declare that they have no conflict of interests.

Availability of data and materials: The data generated and analyzed during the study are available from the corresponding author.

Consent for publication: Not applicable.

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REFERENCES

- Braithwaite CJR, Talbot MR. 1972. Crustacean burrows in the Seychelles, Indian Ocean. *Palaeogeogr Palaeoclimatol Palaeoecol* **11**:265–285. doi:10.1016/0031-0182(72)90048-X.
- Burggren WW, McMahon BR. 1988. *Biology of land crabs*. Cambridge University Press.
- Chan BKK, Chan KKY, Leung PCM. 2006. Burrow architecture of the ghost crab *Ocypode ceratophthalma* on a sandy shore in Hong Kong. *Hydrobiologia* **560**:43–49. doi:10.1007/s10750-005-1088-2.

- Chen PZ, Su TL, Lim SSL. 2019. To hide or to feed: an evaluation of personality traits in the sand bubbler crab, *Dotilla wichmanni*, when responding to environmental interference. *Behav Proc* **164**:123–132. doi:10.1016/j.beproc.2019.05.002.
- Christy JH. 1982. Burrow structure and use in the sand fiddler crab, *Uca pugilator* (Bosc). *Anim Behav* **30**:687–694. doi:10.1016/S0003-3472(82)80139-5.
- Christy JH. 1983. Female choice in the resource-defense mating system of the sand fiddler crab, *Uca pugilator*. *Behav Ecol Sociobiol* **12**:169–180.
- Christy JH. 1987. Female choice and the breeding behaviour of the fiddler crab *Uca beebei*. *J Crust Biol* **7**:624–635. doi:10.2307/1548648.
- Combs CA, Alford N, Boynton A, Dvornak M, Henry RP. 1992. Behavioral regulation of hemolymph osmolarity through selective drinking in land crabs, *Birgus latro* and *Gecarcoidea lalandii*. *Biol Bull* **182**:416–423. doi:10.2307/1542261.
- Crane J. 1941. On the growth and ecology of brachyuran crabs of the genus *Ocypode*. *Zoologica* **26**:297–310.
- Crane J. 1975. Fiddler crabs of the world. Ocypodidae: Genus *Uca*. Princeton University Press, Princeton.
- De C. 2005. Biophysical model of intertidal beach crab burrowing: application and significance. *Ichnos* **12**:11–29. doi:10.1080/10420940590914471.
- Hafemann DR, Hubbard JI. 1969. On the rapid running of ghost crabs (*Ocypode ceratophthalma*). *J Exp Zool* **170**:25–31. doi:10.1002/jez.1401700103.
- Hughes DA. 1973. On mating and the ‘copulation burrows’ of crabs of the genus *Ocypode* (Decapoda, Brachyura). *Crustaceana* **24**:72–76.
- Koepcke HW, Koepcke M. 1953. Contribución al conocimiento de la forma vida de *Ocypode gaudichaudii* Milne Edwards et Edwards (Decapoda Crustacea). *Publicaciones del Museo de Historia Natural “Javier Prado” (serie A Zoologie)* **13**:1–46.
- Lim SSL, Diong CH. 2003. Burrow-morphological characters of the fiddler crab, *Uca annulipes* (H. Milne Edwards, 1837) and ecological correlates in a lagoonal beach on Pulau Hantu, Singapore. *Crustaceana* **76**:1055–1069. doi:10.1163/156854003322753411.
- Lim SSL, Yong AYP, Tantichodok P. 2011. Comparison of burrow morphology of juvenile and young adult *Ocypode ceratophthalmus* from Sai Kaew, Thailand. *J Crust Biol* **31**:59–65. doi:10.1651/10-3314.1.
- Lim SSL, Yong AYP, Christy JH. 2016. Ontogenetic changes in diet and related morphological adaptations in *Ocypode gaudichaudii*. *Invertebr Biol* **135**:117–126. doi:10.1111/ivb.12122.
- Lima SL, Dill LM. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Can J Zool* **68**:619–640. doi:10.1139/z90-092.

- Maitland DP. 1990. Carapace and branchial water circulation, and water-related behaviours in the semaphore crab *Heloecius cordiformis* (Decapoda: Brachyura: Ocypodidae). *Mar Biol* **105**:275–286.
- Matsuoka T, Suzuki H. 2011. Setae for gill-cleaning and respiratory-water circulation of ten species of Japanese ocypodid crabs. *J Crust Biol* **31**:9–25. doi:10.1651/10-3339.1.
- McCullough KL, Rainwater TT, McAlister MA, Dozier J, Platt SG. 2019. Attack and probable predation on ghost crab (*Ocypode quadrata*) by red-shouldered hawk (*Buteo lineatus*). *Wilson J Ornithol* **13**:399–402. doi:10.1676/18-151.
- Mercier AJ, Wilkens JL. 1984. Analysis of the scaphognathite ventilatory pump in the shore crab *Carcinus maenas*, i. Work and power. *J Exp Biol* **113**:55–68.
- Miller DC. 1961. The feeding mechanism of fiddler crabs, with ecological considerations of feeding adaptations. *Zoologica* **46**:89–101. doi:10.5962/p.203340.
- MINITAB, INC. 2003. MINITAB user's guide 2: Data analysis and quality tools. Release 14 for Windows. (State College, PA, USA).
- Schober UM, Christy JH. 1993. Sand disposal of the painted ghost crab *Ocypode gaudichaudii* (Decapoda: Ocypodidae): a possible role in courtship. *Mar Biol* **116**:53–60. doi:10.1007/BF00350731.
- Shuchman E, Warburg MR. 1978. Dispersal, population structure and burrow shape of *Ocypode cursor*. *Mar Biol* **49**:255–263. doi:10.1007/BF00391138.
- Su TL, Lim SSL. 2016. To flee or not to flee: characterising differentiated anti-predatory responses of two mangrove crabs. *Ethol Ecol Evol* **29**:181–192. doi:10.1080/03949370.2015.1129989.
- Thompson WE, Molinaro PJ, Grego TM, Tedeschi JB, Holliday CW. 1989. Regulation of hemolymph volume by uptake of sand capillary water in desiccated fiddler crabs, *Uca pugilator* and *Uca pugnax*. *Comp Biochem Physiol Part A Physiol* **94**:531–538. doi:10.1016/0300-9629(89)90134-5.
- Wolcott TG. 1976. Uptake of soil capillary water by ghost crabs. *Nature* **264**:756–757. doi:10.1038/264756a0.
- Wolcott TG. 1984. Uptake of interstitial water from soil: mechanisms and ecological significance in the ghost crab *Ocypode quadrata* and two Geocarcinid land crabs. *Physiol Zool* **57**:161–184. doi:10.1086/physzool.57.1.30155978.
- Yong AYP, Lim SSL. 2019. Quantitative methods for the determination of abundance of mobile prey of ghost crabs, *Ocypode* Weber, 1795 (Decapoda: Brachyura: Ocypodidae), a top predator on sandy shores. *J Crust Biol* **39**:516–521. doi:10.1093/jcbiol/ruz022.

Yong AYP, Lim SSL. 2021. Plasticity of foraging strategies adopted by the painted ghost crab, *Ocypode gaudichaudii*, in response to *in situ* food resource manipulation experiments. *Zool Stud* **60**:37. doi:10.6620/ZS.2021.60-37.

Yong AYP, Lim SSL. 2022. Coexistence of juvenile with adult *Ocypode gaudichaudii* at Culebra Beach, Panama: A temporal-spatial partitioning compromise. *Zool Stud* **61**:8. doi:10.6620/ZS.2022.61-08.