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Plasticity of Foraging Strategies Adopted by the Painted Ghost Crab, *Ocypode gaudichaudii*, in Response to *in situ* Food Resource Manipulation Experiments

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The feeding strategies of *Ocypode gaudichaudii* at two sandy beaches, Culebra Beach (CB) and Playa Venao (PV) in Panama, were studied via three experiments. Two separate manipulative *in situ* experiments were conducted to determine how the densities of food resources and the size of the supplemented food offered to the crabs can affect their diet and food handling behavior. The third experiment, a transplantation study, was also conducted to determine the plasticity of the feeding behavior of the displaced crabs. In the first experiment, freshly-emerged crabs showed different feeding modes when washed-sediment was seeded with different densities of diatoms and rove beetles, which suggests that they are optimal foragers. Crabs hoarded food in the second experiment when food augmentation was performed, in which small and large food pellets were placed around the burrows at the beginning and end of the crabs' feeding cycle. All freshly-emerged crabs from both sites foraged on the small pellets outside their burrows and did not cache food; when pellets were provided at the end of the feeding cycle, crabs from CB fed on some of the small pellets and returned to their burrows with the uneaten pellets left on the surface, whereas crabs at PV picked up all the small food pellets and transferred them into their burrows over several trips before plugging their burrow entrances. Only the crabs from PV carried the large food pellets supplemented at the start and end of the feeding cycle into their burrows. In contrast, the crabs at CB often left behind the partially-eaten pellets on the sand surface, probably due to the increased risk of predation associated with the prolonged handling time of the large food pellets. Excavation of the burrows of the crabs that hoarded food showed that all the pellets were deposited at the bend of the burrows, indicating that they were not consumed immediately. Crabs that fed in droves at PV stopped droving and foraged around their burrows after being transplanted to CB. This is the first documentation of food hoarding in a sandy beach macroinvertebrate at a resource-impoverished habitat. The plasticity of feeding strategies adopted by the painted ghost crab in response to different densities of food resources in the habitat could be an adaptation to the dynamic sandy beach environment.

Key words: Food caching, Functional response, Opportunistic scavenger, Optimal Foraging Theory, Transplantation experiment.

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BACKGROUND

Natural environments are inherently heterogeneous in time and space. Hence, there is no single trait that is optimized throughout the life history of an organism (Levins 1968). For that reason, natural selection will favour organisms that can modify their behavior to suit the environment (Brown 1996). Animals with phenotypic plasticity exhibit variations in their behavior (Zhang et al. 2016), physiology (Tomlinson et al. 2015) and morphology (Todd 2008) in response to varying environmental conditions. While physiological and morphological changes can be gradual and permanent, behavioral changes are immediate and usually reversible (West-Eberhard 1989). There is a diverse range of behavioral adaptations, and the plasticity of feeding behaviors is one of the key factors for organisms to survive in variable environments (McLachlan and Brown 2006).

Sandy beaches are highly dynamic environments, and intertidal organisms face predictable (*e.g.*, diurnal cycles) and unpredictable fluctuations (*e.g.*, storms) in the environment. The availability of marine organic materials (*i.e.*, microphytoplankton and beach wrack), which serve as the primary food source for sandy beach fauna vary temporally and spatially due to the interactions of wave action, changing tides and moving sand (McLachlan and Hesp 1984; Veloso and Cardoso 2001). Intertidal beach organisms often exhibit plasticity in response to the changing conditions in the beach environment (Brown 1996). For example, most beach animals are opportunistic feeders (Lastra et al. 2006) with diverse diets that correspond to the food available in the habitat. Some animals, like talitrid amphipods (Duarte et al. 2010) and ghost crabs (Lucrezi and Schlacher 2014), also exhibit trophic plasticity, as their diets consist of food from different trophic levels (*e.g.*, diatoms, insects, dead plant matter and carrion). To determine the mechanisms underlying the evolution of adaptive feeding behavior (see McLachlan 1988), it is essential to understand how foraging behaviors change in the natural environment. However, there are currently few field studies on the feeding behaviors of sandy beach macrofauna as most are small and inconspicuous or feed below the sand surface (*e.g.*, amphipods, see Olabarria et al. 2009).

Ghost crabs (genus *Ocypode*) can be good model organisms for studies on plasticity in feeding behavior because they feed on the sand surface and have a repertoire of feeding behaviors that can be easily differentiated (Crane 1941). These large semi-terrestrial crabs have five feeding modes—deposit-feeding, predation, cannibalism, scavenging and feeding on macrophytes—that can be easily differentiated in the natural environment (Lucrezi and Schlacher 2014). However, there is little information on the mechanisms behind their food preference, with conflicting reports on their trophic roles. For example, at a beach in Florida where mole crabs and coquina clams were dominant, Wolcott (1978) observed that the two types of macrofauna comprise 90% of the diet of *Ocypode quadrata*, with scavenging accounting for less than 10% of the diet, whereas this species was reported to be scavengers previously (see Cowles 1908). In addition, two studies reported that *O. gaudichaudii* scavenges on dead plants and animals (see Koepcke and Koepcke 1953; Trott, 1988), but Crane (1939 1941) highlighted that they were not attracted to animal carcasses. She observed that large colonies of *O. gaudichaudii* ignored the carcasses of fish and birds in their midst and preferred to deposit-feed instead. Trott (1988) proposed that the different feeding behaviors of *O. gaudichaudii* from various geographical locations were attributed to phenotypic plasticity, but did not substantiate his suggestion with quantitative data.

When the environmental cues are reliable, the adaptive value of a behavioral response depends on the sensory ability of the organism to detect the cues so that an appropriate behavior is developed (Windig et al. 2004). Laboratory and field experiments showed that the ghost crabs, *O. quadrata* and *O. gaudichaudii*, can differentiate the nutritive quality and quantity of food via contact chemoreception at the chelipeds and dactyls of legs (see Trott and Robertson 1984; Trott 1987 1999). Furthermore, *O. gaudichaudii* was able to detect food gradients within a short distance (Trott 1987). The droving behavior of *O. gaudichaudii* provides further evidence of their ability to detect and respond to a food gradient, as Sherfy (1986) reported that the crabs at sandy beaches with low levels of nutrients formed feeding aggregates at the nutrient-rich patches on the shore.

Animals from diverse taxonomic groups have been reported to hoard food in response to food shortages due to fluctuations in the available food resources and energy requirements (Vander Wall 1990). Rong et al. (2013) observed that the European Red Squirrel employs different hoarding strategies based on food availability. Food hoarding, is thus, is an adaptive strategy that allows organisms to control the availability of food in time and space (Vander Wall 1990). The behavior of caching excess food for later consumption as a strategy to cope with unpredictable food availability was also reported in kangaroo rats and four species of sigmodontine rodents (see Jenkins et al. 1995; Giannoni et al. 2013). In addition, food-hoarders have a competitive advantage over non-food hoarders. For example, MacGregor's bowerbirds that cache food can spend more time attending to their bower to increase mating opportunities than they would if they foraged (see Pruett-Jones and Pruett-Jones 1985). Harvester ants that store seeds during summer when conditions are favorable for foraging would have food to sustain the colony when conditions at the ground surface were unfavorable for foraging (Willard and Crowell 1965).

It is evident that food hoarding is well documented across diverse taxonomic groups in vertebrates as well as terrestrial invertebrates, but not so for aquatic invertebrates (see Vander Wall 1990). There are currently only a few studies that suggest the possibility of food storage in mangrove crabs, *e.g.*, *Dotillopsis brevitarsis*, and two species of fiddler crabs, *Austruca lactea* and *Gelasimus vocans*—previously *Uca lactea* and *U. vocans*, respectively (see Salmon 1984; Wada 1985; Kim 2010; Shih et al. 2016). In a manipulative field experiment at an intertidal sandy mudflat in Japan, *A. lactea* carried nutrient-enriched sediment and carrion into their burrows and most probably stored the food for later consumption (Kim 2010). These behaviors were less commonly observed in another population of *A. lactea* from a muddier habitat in Korea (see Kim and Choe 2003) and suggest that food hoarding in *A. lactea* is related to the scarcity of food in the habitat (Kim 2010). To date, there is no record of beach fauna hoarding food except for anecdotal accounts that *O. quadrata* and *O. kuhlii* carried food into their burrows (see Cowles 1908; Evans et al. 1976). This lack of empirical studies has resulted in a limited knowledge around the ecological impact of food hoarding on the energy flow in the beach ecosystem.

Ocypode gaudichaudii is the only species that undergoes an ontogenetic diet shift, *i.e.*, the juvenile crabs prey on small crustaceans and insects but the adults mainly deposit-feed on diatoms and rarely feed on small crustaceans, insects, worms, seaweed and wood (Crane 1941; Lim et al. 2016). However, two reports described the adult crabs in Costa Rica and Peru as deposit-feeders, opportunistic scavengers and predators (see Koepcke and Koepcke 1953; Trott 1988). Crane (1941) pointed out that *O. gaudichaudii* was only distributed at sheltered shores in Panama, but Koepcke and Koepcke (1953) argued that *O. gaudichaudii* were also found on moderately-exposed shores. According to the swash hypothesis, species richness, abundance and biomass increase along the physical gradient from reflective to dissipative sandy beaches (see McLachlan et al. 1993). Therefore, the density of food resources at the moderately-exposed Peruvian beaches (see Koepcke and Koepcke 1953) might be lower and could have resulted in more adult crabs scavenging for food. There are currently no quantitative studies to determine the relationship between the different levels of food resources and the plasticity of feeding behaviors of ghost crabs.

The feeding behaviors of *O. gaudichaudii* at two sandy beaches—Culebra Beach (CB) and Playa Venao (PV)—in Panama with different levels of wave exposure were distinctly different (AYPY personal observation). The two crab populations differed in the areas that they fed, when they fed, what they ate and how they fed. *Ocypode gaudichaudii* at the more exposed shore appeared to have two feeding strategies to cope with the low availability of food. During the day, most of the adult crabs left the nutrient-impoverished burrow zone to form feeding droves at the nutrient-rich sand flats. The crabs also carried food (*e.g.*, seedpods) that they encountered on the sand surface into their burrows. It is uncertain whether the crabs adopted this strategy to conceal the food from conspecifics or to store the food for future consumption (see Jones 1972; Trott 1988). Hence, two separate *in situ* feeding experiments and a transplantation study were conducted in Panama during daytime hours to investigate the diurnal feeding behaviors of *O. gaudichaudii*. The objectives of this study on *O. gaudichaudii* were to determine the effects of different food densities on its 1) feeding modes, 2) food hoarding behavior, and 3) plasticity of feeding strategies. We hypothesized that 1) the feeding mode would correspond to the type of food in greater abundance, 2) food hoarding would occur when food was scarce in the habitat, and 3) the feeding strategy would be adjusted and be dependent on the level of food availability in the habitat.

MATERIALS AND METHODS

The abundance and distribution of food resources at the study sites

The study was conducted from July 2012 to October 2013 at CB (8°54'45"N, 79°31'48"W) and PV (7°25'54"N, 80°11'29"W) along the Pacific Coast of Panama. CB is a sheltered sand beach on the eastern side of the Pacific entrance to the Panama Canal, whereas PV is a moderately-exposed sandy beach on the south-eastern coast of the Azuero Peninsula. Observations of the foraging crabs were carried out at both beaches during the day and night using a hand-held video camera (Sony Handycam DCR-SR62). Field observations and gut content analyses of *O. gaudichaudii* from both beaches indicated that the crabs fed on three types of invertebrates (*i.e.*, rove beetles, isopods and amphipods), diatoms and detritus (AYPY unpublished data). During the day, the crabs at CB predominantly fed on diatoms and rove beetles, whereas detritus and rove beetles constituted the main diet of the crabs at PV. Nocturnal foraging was only observed for *O. gaudichaudii* at CB. The abundance and distribution of the different types of prey and diatoms during the day were determined by sampling the organisms at the zones in which the ghost crabs foraged. Each prey type was collected by the appropriate sampling methods and their distributions compared using kite diagrams as described in Yong and Lim (2019). A *t*-test was carried out to test for the difference in density of the prey between the two sites.

The abundance of diatoms deposited on the shore was estimated by measuring the chlorophyll *a* content in surface sediment. Approximately 5 g of surface sediment (top 1 mm layer) was collected from the unforaged areas at the upper (CB: 3.5 m to 4.6 m above the mean lower low water (MLLW); PV: 2.5 m to 3.2 m above MLLW) and lower shore levels (CB: 2.4 m to 3.5 m MLLW; PV: 2.1 m to 2.5 m above MLLW) where *O. gaudichaudii* deposit-fed. The sediment was stored at -80°C until analysis using the methods described in Brito et al. (2009). Acetone was used as the solvent for the chlorophyll extraction and the mean chlorophyll *a* content in the sediment at each shore level was calculated based on the method in Lorenzen (1967). A *t*-test was carried out to test for the difference in mean chlorophyll *a* content between the two shore levels. The same procedure was carried out to compare the difference in mean chlorophyll *a* content in the sediment samples from PV.

The total organic carbon (TOC) content present in the surface sediment collected from the upper and lower shore levels where *O. gaudichaudii* deposit-fed were determined. Sediment samples were stored at -20°C until analysis using the method described by Lim and Wong (2010). A *t*-test was used to compare the mean sediment TOC from the two shore levels at CB. The procedure was repeated for the sediment from PV.

Experiment 1: Effects of the different densities of diatoms and rove beetles on the feeding modes of *O. gaudichaudii*

An *in situ* experiment was carried out at CB in December 2013 to determine the effects of different densities of diatoms and rove beetles on the two predominant feeding modes (*i.e.*, deposit-feeding and scavenging) of *O. gaudichaudii* at CB. Diatoms of the genus *Aulacodiscus* were collected by sampling the greenish-brown film of diatoms deposited on the sediment surface at CB when the tide receded. The diatoms were cultured in filtered seawater enriched with a media for algae growth (Proline F/2 Algae Food, Pentair Aquatic Eco-systems, Inc.) at 27°C under continuous fluorescent light for five days. Diatom suspensions at two different concentrations (high and low) were prepared for the experiment. The high concentration treatment was the undiluted stock culture of diatoms ($\approx$ 82000 diatoms ml^{-1}) and the low concentration was prepared using a dilution factor of 9:1 with filtered seawater.

Sediment within the burrow zone at CB was collected and washed with distilled water over a Wentworth grade sieve with a mesh size of 500 µm to remove organisms such as rove beetles and isopods. To remove the diatoms, the sediment was further washed with distilled water over a stack of two Wentworth grade sieves with mesh sizes of 125 µm and 63 µm. Sediment retained on each sieve was oven-dried at 80°C until achieving a constant weight, at which point the dried sediment was examined under a stereomicroscope to ensure that there were no diatoms. The fine sediment grains that passed through the sieves with the diatoms were removed with a pair of forceps and pooled with the rest of the clean and dry sediment.

Rove beetles were collected as described in Yong and Lim (2019) and stored at -18°C until the day of the experiment. Table 1 gives the different densities of diatoms and rove beetles that were seeded for each treatment (set-up see Fig. 1). The densities of diatoms that were added to the feeding area were based on the ratio of the number of sand grains to the number of diatoms of the sediment collected at the uppermost and lowest foraging zone of CB. For treatments with high densities of diatoms, the density of diatoms (*i.e.*, number of sediment grains:number of diatoms was < 2:1) that were seeded was higher than that in the sediment collected at the lowest foraging zone, where the density of diatoms was the highest. The number of sediment grains:number of diatoms for treatments with low densities of diatoms was > 4:1.

The moisture content of the sediment in each treatment was adjusted such that it was similar to that at the intertidal zone ($\approx$ 20% of water). Ten and 40 dead rove beetles that were stored in the freezer were added to the plates of sediment for the treatments with low and high densities of beetles, respectively. The burrow diameter (BD) for each crab was measured and the carapace width (CW) was estimated by extrapolating the BD using the regression equation CW = 1.02BD + 0.95 obtained from the regression of the variable 'CW' against 'BD' of the crabs from both sites (AYPY unpublished data). Freshly-emerged crabs (CW 1.2 cm to 3.1 cm) were selected from the entire burrow zone for the experiment (Fig. 1). Six replicates of the nine treatments were placed over the burrow entrance of the freshly-emerged crabs when the crabs were in their burrows. The plates remained in the field until the crabs stopped feeding for the day and returned to their burrows, just before the rising tide inundated the area. Only the data obtained from the crabs that fed within the feeding plate throughout the experiment were used. At the end of the experiment, the number of remaining rove beetles as well as the presence or absence of pseudofecal pellets were recorded. The mean number of beetles consumed for each treatment was calculated. Data analyses were carried out using recursive partitioning with the rpart package in R version 3.5.2 (R Core Team 2018). Recursive partitioning is a nonparametric statistical analysis that uses a classification tree or regression tree to split up the dataset based on the homogeneity of data. A classification tree is used to identify the main predictors in a categorical dataset. In comparison, a regression tree is used to determine the main predictors when the response variable is continuous.

Experiment 2: Behavioral response of *O. gaudichaudii* to supplemented food

This *in situ* study was conducted in October 2013 at PV and in December 2013 at CB to test for food preference when food resources were presented in different food types and at different densities. *Ocypode gaudichaudii* at the two sites usually started feeding about an hour after they emerged from their burrows during the day. Small pellets of a commercial crab food (Hikari Tropical Crab Cuisine Kyorin Co. Ltd.) and large pellets of a commercial cat food (GATUCO Bioalimentar Cia. Ltda.) were used as food supplements. At each site, 20 freshly-emerged crabs of various sizes at different shore levels were chosen for the experiment. The diameter of the burrow opening of each crab was measured. Twelve small food pellets were scattered within a 10-cm radius of the burrow opening of 10 crabs. Two large cat food pellets were placed within a 10 cm radius from the burrow opening of the 10 remaining burrows. All the food pellets were supplemented when the freshly-emerged crabs were in their burrows. There was no control experiment to substitute the food pellets with non-food items because the crabs never carried non-food items into their burrows. Conspecifics and hermit crabs nearby were often seen to go near the crabs with the large food pellets with some of them attempting to snatch the food pellets. When this was observed, the experiment was discarded and repeated on another freshly-emerged crab with a similar burrow diameter.

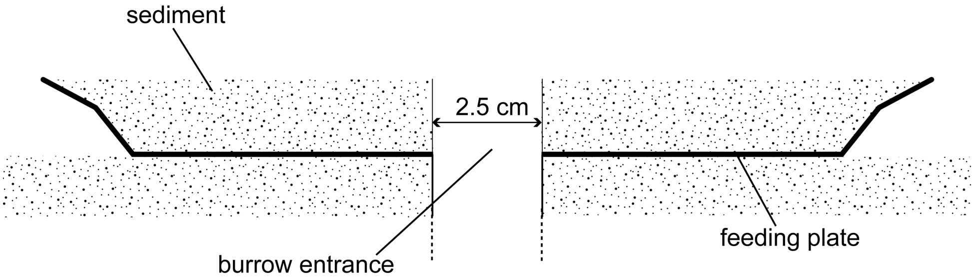

Fig. 1. Feeding plate placed over the burrow entrance of *Ocypode gaudichaudii*.

Table 1. Experimental treatments with the densities of diatoms and rove beetles added to each set-up (*n* = 6 per treatment). Density of diatoms: High, the number of sediment grains:number of diatoms was < 2:1; Low, the number of sediment grains:number of diatoms for treatments with low densities of diatoms was > 4:1, density of beetles: High, 40 beetles; Low, 10 beetles

Treatment	Density of diatoms	Percentage of stock diatoms suspension (%)	Density of beetles	Number of beetles
1	High	100	High	40
2	High	100	Low	10
3	High	100	0	0
4	Low	10	High	40
5	Low	10	Low	10
6	Low	10	0	0
7	0	0	High	40
8	0	0	Low	10
9	0	0	0	0

All 40 crabs were observed from a distance ca. 5 m with a pair of binoculars. The number of food pellets that were eaten and carried into the burrows was recorded. Burrows that were likely to contain food pellets were excavated at the end of the experiment (*i.e.*, when the burrow entrances were sealed with a plug of sand or when the crabs had stayed in the burrow for 15 min). The experiment was repeated at the end of the feeding cycle of another 20 crabs that had foraged for a substantial period (*i.e.*, at least an hour). Crabs that were deposit-feeding and approaching the end of the feeding cycle could be easily identified by the numerous pseudofecal pellets around the foraging area. The crabs that scavenged or preyed on live animals would be probing the sediment around their burrows and fed for at least an hour.

Recursive partitioning in R was used to identify the main predictors (*i.e.*, location of the study site, period of feeding cycle, the number of pellets that were carried into the burrow and burrow diameter) that were associated with the mean number of small food pellets eaten and cached. Hence, this analysis was designed to also indicate the mean number of small food pellets that were consumed by the crabs for each variable.

Experiment 3: Transplantation study to determine the plasticity of feeding behavior in *O. gaudichaudii*

A transplantation experiment was carried out to determine if the droving behavior of *O. gaudichaudii* was habitat-dependent. Forty-four droving adult *O. gaudichaudii* were captured at the sand flats of PV. The crabs were tagged with colored tape glued on the carapace with cyanoacrylate glue and released at CB during the diurnal low tide on 25 November 2013. Feeding behaviors of the tagged crabs were monitored during the diurnal low tides for 14 days. The foraging behavior of the transplanted crabs from PV and the crabs from CB were compared. Crabs from CB were not transplanted to PV because the crabs' foraging range at PV is about 10 times greater in area, too extensive to monitor the location of individual crabs.

RESULTS

Abundance and distribution of the prey of *O. gaudichaudii*

Rove beetles were the only prey found at PV. Isopods and rove beetles at CB was distributed throughout the zones sampled (Fig. 2). The mean density of rove beetles across the zones at CB was significantly higher than that at PV ($t = 6.07$, $d.f. = 193$, $p < 0.05$; 129 ± 18 individuals $m^{-2} > 66 \pm 4$ individuals m^{-2}; mean ± S.E. respectively).

Abundance and distribution of diatoms

The mean chlorophyll *a* content in sediment at the lower shore of CB where the crabs deposit-feed was significantly higher than that at the higher shore ($t = -10.02$, $d.f. = 2$, $p = 0.010$; 23.37 ± 0.34 mg^{-1} sediment $> 12.21 \pm 1.1$ mg^{-1} sediment; mean ± SE, respectively) indicating that the biomass of diatoms at the lower shore of CB was higher than that at the upper shore. In contrast, the lower and upper shore of PV (where deposit-feeding occurred) did not differ significantly in chlorophyll a content ($t = -2.77$, $d.f. = 1$, $p = 0.22$.; 0.74 ± 0.06 mg^{-1} sediment $\approx 0.31 \pm 00.15$ mg^{-1} sediment; mean ± SE, respectively). The mean chlorophyll *a* content at the lower shore of CB was ≈ 32 times higher than that at PV (23.37 ± 0.34 mg^{-1} sediment cf. 0.74 ± 0.06 mg^{-1} sediment, respectively).

Total organic carbon content in the sediment from the areas with deposit feeding *O. gaudichaudii*

The TOC content in the sediments from the foraging areas at the two shore levels of CB were not significantly different ($t = -0.07$, $d.f. = 4$, $p = 0.949$; $0.280 \pm 0.067\% \approx 0.285 \pm 0.036\%$; mean ± SE, respectively). In contrast, at PV, the TOC content in sediments from a foraging zone at the upper shore was significantly lower than that at the foraging zone at lower shore (sand flat) ($t = -10.11$, $d.f. = 4$, $p = 0.001$; $0.043 \pm 0.025\% < 0.394 \pm 0.023\%$; mean ± SE, respectively. The mean sediment TOC at the sand flat was approximately 1.4 times higher than that at the lower shore of CB.

Experiment 1: Effects of the different densities of diatoms and rove beetles on the feeding modes of *O. gaudichaudii*

Feeding occurred in 37 out of the 54 plates that were laid out in the experiment. Deposit-feeding only occurred in 14 out of the 36 plates with diatoms. A higher percentage of crabs deposit-fed in the treatments with high densities of diatoms (Treatments 1, 2 and 3) than the treatments with low densities of diatoms (Treatments 4, 5, and 6). In comparison, all the crabs in the treatments (Treatments 1, 2, 4, 5, 7 and 8) with beetles fed on the beetles regardless of the beetle densities. All the crabs in the treatments with both diatoms and beetles (Treatments 1, 2, 4 and 5) fed on beetles, but not all of them consumed diatoms. While all the crabs in the treatments (Treatments 1 and 5) with similar densities of diatoms and rove beetles (*e.g.*, high density of diatoms and high density of beetles) fed on beetles, only 50% of the crabs in Treatment 1 consumed diatoms. None of the crabs in Treatment 5 fed on diatoms. The mean number of rove beetles consumed corresponded with the densities of beetles at the start of the experiment (Fig. 3).

Mode of feeding

A classification tree was used to split up the dataset of the occurrence of deposit-feeding based on the homogeneity of data. The classification tree showed that the density of diatoms was the main predictor that was associated with the occurrence of deposit-feeding (Fig. 4). Burrow diameter did not emerge as one of the main predictors, indicating that the feeding mode is not size-dependent. Out of the 37 feeding plates on which there was feeding, the crabs on 23 of the plates only scavenged on the dead beetles and out of these 23 crabs, 19 scavenged when the density of diatoms was low or absent (Fig. 4). Eleven out of the 14 crabs with deposit-feeding foraged when the density of diatoms was high (Fig. 4), indicating that most crabs would deposit-feed when the density of diatoms was high.

Beetle density

Since the response variable 'number of beetles eaten' was continuous, it was possible to fit a regression model to the target response variable using each of the predictor variables (*i.e.*, burrow diameter, beetle density, diatoms concentration). After recursive partitioning, a constant value of the response value was predicted. Rove beetles were only present in 31 out of the 37

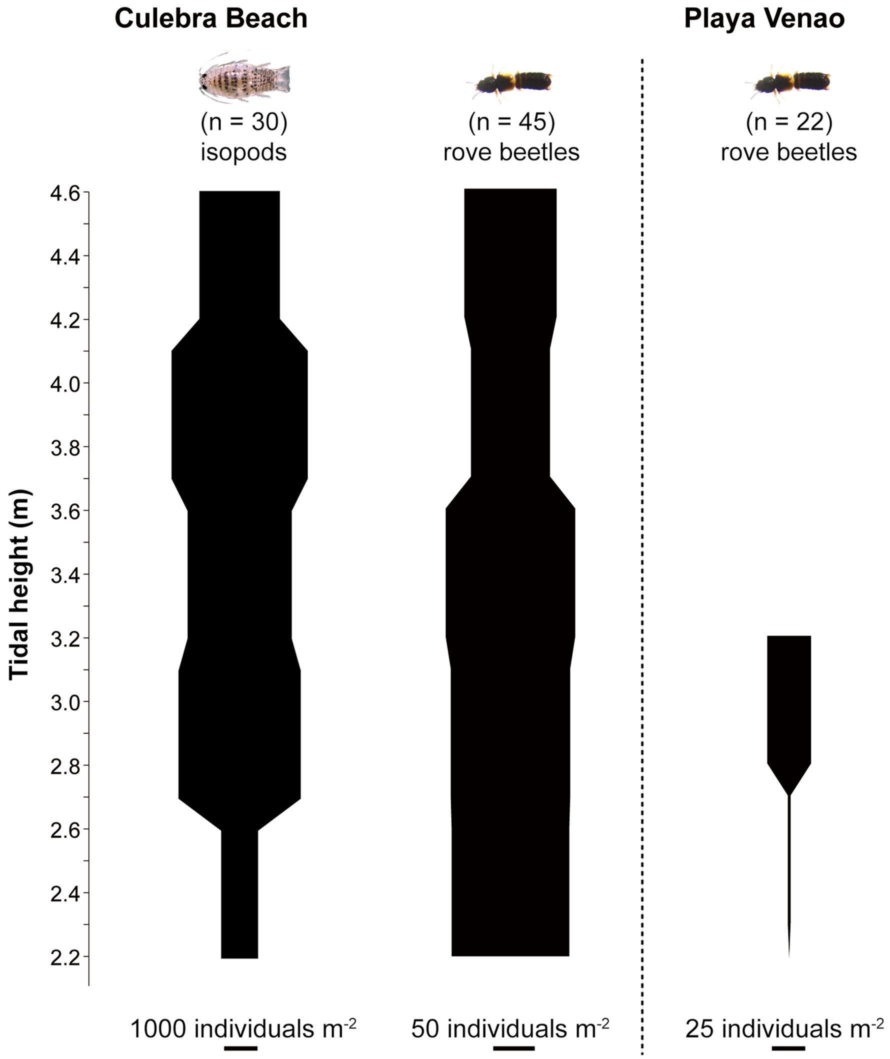

Fig. 2. Kite diagrams showing the distribution of isopods and rove beetles at Culebra Beach and Playa Venao during the day.

plates with feeding activity. Results of the analysis showed that the density of beetles at the start of the experiment was the main predictor that was associated with the mean number of beetles consumed. The mean number of beetles consumed by the 31 crabs was 16.5 beetles (Fig. 5). Out of the 31 crabs, 14 of them were supplemented with low density of rove beetles, and the mean number of beetles that were eaten was 6.8 beetles. Crabs exposed to the remaining 17 plates that were seeded with high densities of rove beetles consumed a mean of 24.6 rove beetles (Fig. 5).

Experiment 2: Behavioral response of *O. gaudichaudii* to supplemented food

Upon excavating the burrows in which the crab occupants were observed to hoard food, food pellets were found at the bend of the 29 burrows (Fig. 6, Table 2). The total number of food pellets in all 29 burrows tallied with the number of pellets that were brought into the burrows. All 40 freshly-emerged crabs at both sites fed on the small food pellets outside their burrows and no hoarding behavior was observed at CB (Table 2). When the small pellets were supplemented at the end of the feeding cycle, the crabs at CB fed on two to five of the 12 pellets. In contrast, the crabs from PV often placed the first pellet they encountered at the mouthparts before carrying the uneaten food into the burrow. The crabs usually emerged from their burrows almost immediately and moved towards another food pellet. Upon encountering the small food pellet, the crabs would carry the food and dash into their burrows (see video S1). The process was repeated until the crab had to plug its burrow just before the tide inundated

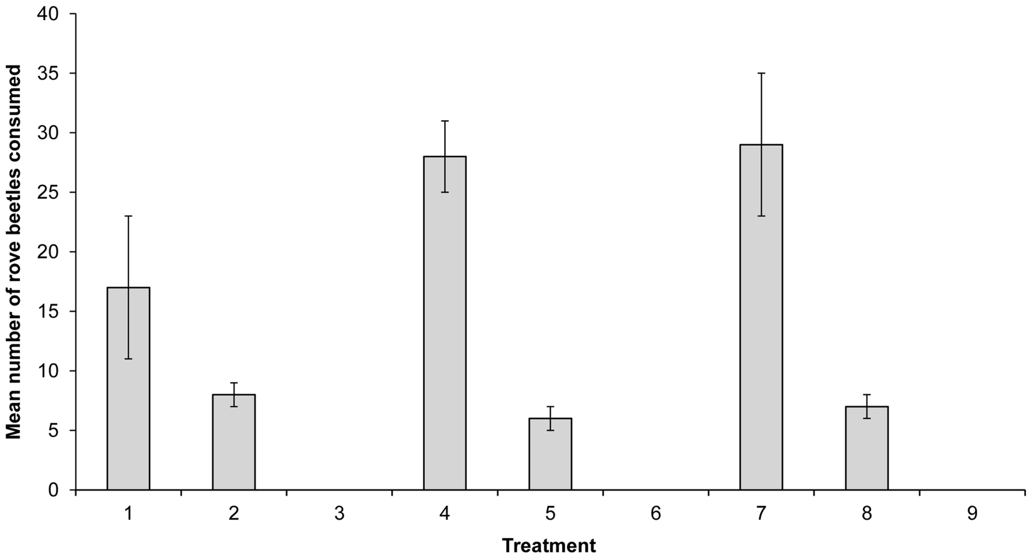

Fig. 3. Mean number of rove beetles consumed (± SE) by *Ocypode gaudichaudii* in each treatment. Treatment 1, high density of diatoms and high density of beetles; Treatment 2, high density of diatoms and low density of beetles; Treatment 3, high density of diatoms only; Treatment 4, low density of diatoms and high density of beetles; Treatment 5, low density of diatoms and low density of beetles; Treatment 6, low density of diatoms only; Treatment 7, high density of beetles only; Treatment 8, low density of beetles only and Treatment 9, no diatoms and no beetles.

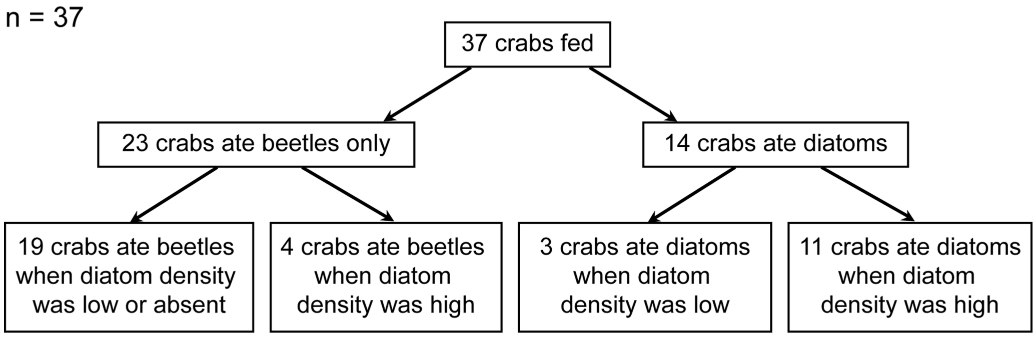

Fig. 4. Classification tree showing the feeding modes of *Ocypode gaudichaudii* at low and high densities of diatoms.

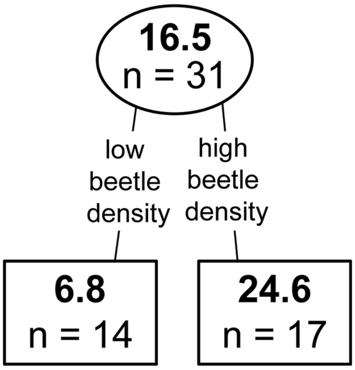

Fig. 5. Regression tree showing the mean number of rove beetles that were eaten by *Ocypode gaudichaudii* in set-ups with different densities of rove beetles. The mean number of beetles that were eaten under each category of treatment are in bold.

the area. Crabs were observed to carry up to three small food pellets (*i.e.*, a small food pellet between the mouthparts and a pellet in each chela). Three crabs excavated their burrows after having carried a few small food pellets into their burrows. After the excavations, more food pellets were carried into their burrows.

The regression tree (Fig. 7) indicated that the period of the feeding cycle at which the food pellets were supplemented was more important than the study site of the experiment in determining the mean number of food pellets that were eaten. A higher mean number of small food pellets were eaten when they were supplemented at the beginning of the crabs' feeding cycle (beginning of feeding cycle cf. towards the end of the feeding cycle: seven compared to two small food pellets) (Fig. 7). All the crabs that had food

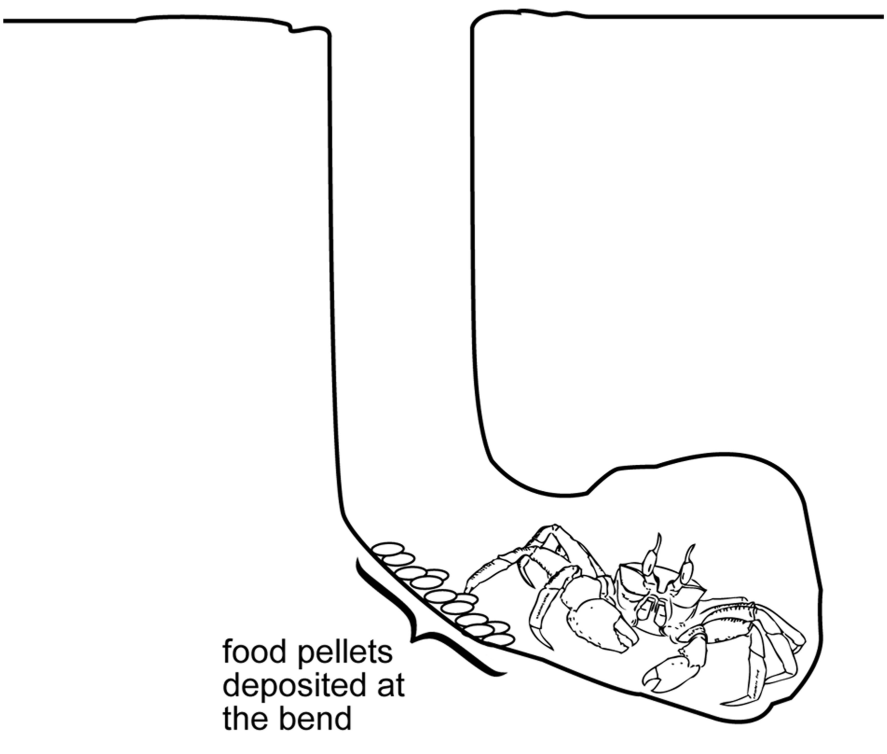

Fig. 6. Region in burrow where *Ocypode gaudichaudii* deposited the food pellets.

Table 2. Percentage of the hoarding of supplemented food pellets at Culebra Beach and Playa Venao during different periods of the feeding cycle of *Ocypode gaudichaudii*. (*n* = 10 per treatment)

Period of feeding cycle that food pellets were supplemented	Percentage of hoarding (%)			
	Culebra Beach		Playa Venao	
	Small pellets	Large pellets	Small pellets	Large pellets
Beginning	0	0	0	90
Towards the end	0	0	100	100

supplemented at the beginning of their feeding cycle were categorized into two size categories based on the results of the regression partitioning—crabs residing in burrows ≥ 1.7 cm and those residing in burrows < 1.7 cm. The larger crabs (BD ≥ 1.7 cm) consumed a higher mean number of pellets than the smaller individuals (BD < 1.7 cm) (Fig. 7). When small pellets were supplemented towards the end of the feeding cycle, none of the crabs at PV consumed the pellets that they encountered (Fig. 7). Hoarding of the small food pellets occurred for all the crabs at PV (Table 2).

The crabs at CB fed on the large food pellets that were scattered at both the beginning and at the end of the feeding cycle outside their burrows. None of the crabs at CB carried food into their burrows (Table 2). At PV, the large pellets were brought into the burrows by all the freshly-emerged crabs except for one crab that consumed the two food pellets at the surface (Table 2). All the crabs also carried the large pellets into their burrows towards the end of the feeding cycle. Unlike the larger crabs that could carry two large food pellets, the smaller crabs only carried one of the two large pellets into their burrows before they plugged the burrow entrances. The large food pellets were usually wider than the burrow entrances and three out of the four juvenile crabs had to enlarge the burrows to fit the large pellets.

Experiment 3: Transplantation study to determine the plasticity of feeding behavior in *O. gaudichaudii*

Only six out of the 44 crabs transplanted from PV were observed on the sand surface at CB during the two weeks even though there was no predation by birds. However, birds did fly across the burrow zone. The six crabs did not drove but fed around their burrows instead. All the crabs left behind pseudofecal pellets in radial arrangements like the other deposit-feeding crabs at CB. These crabs either remained at the burrow entrance or in their burrows when they were not feeding.

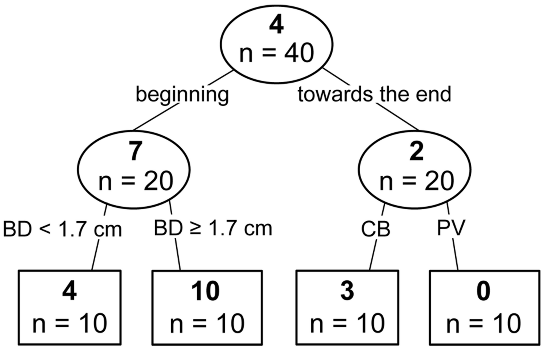

Fig. 7. Regression tree showing the mean number of small food pellets that were eaten by *Ocypode gaudichaudii* at Culebra Beach and Playa Venao with different burrow diameters at different periods of the feeding cycle. Beginning, beginning of feeding cycle; Towards the end, towards the end of the feeding cycle; CB, Culebra Beach; PV, Playa Venao; BD, burrow diameter. The mean number of pellets that were eaten by the crabs under each category are in bold.

DISCUSSION

Ocypode gaudichaudii demonstrated evident feeding plasticity in response to the different densities and distribution of food in the environment. Deposit-feeding was observed as the predominant feeding mode at CB even though high densities of rove-beetles occurred across the foraging zones. This could be due to the higher encounter rate of diatoms deposited on the sand surface as compared to live rove beetles. Since less effort is probably needed to search and handle the diatoms as compared to searching and handling the live rove beetles which can burrow, the foraging efficiency of crabs that deposit-feed would be optimized.

In the first experiment, *O. gaudichaudii* exhibited functional responses to the increasing densities of diatoms and rove beetles (*i.e.*, the consumption of diatoms and rove beetles increased in response to the increased densities of diatoms and rove beetles respectively; see Figs. 2, 3, 4). Feeding on the food that is present in greater abundance would maximize foraging efficiency as it means a higher chance of encountering the food resource. However, regardless of the densities of diatoms and rove beetles present at the start of the experiment, rove beetles were consumed (Fig. 3): this could possibly be due to the different energetic and nutritive values of diatoms and beetles. The foraging effort would likely be maximized if beetles were a more profitable food source. However, further studies need to be done to verify this hypothesis. The results of Treatments 2 and 5 (Fig. 3) also suggest that switching from scavenging to deposit-feeding is dependent on the density of diatoms available with respect to a threshold density of diatoms. A crab that switched to deposit-feeding could have detected that the density of diatoms was above a critical density and consumed diatoms instead of rove beetles (see Stephens and Krebs 1986).

The preference for rove beetles that was observed in *O. gaudichaudii* in the first experiment seems to contradict the prevalence of deposit-feeding observed in the field. This difference could be due to the constraints of using dead rove beetles in the experiment. In a meta-analysis of 134 studies on optimal diet theory (ODT), Sih and Christensen (2001) highlighted that in general

ODT worked well with immobile prey but not with mobile prey. As dead rove beetles were used in the experiment, it was uncertain if the results would differ if live beetles were used instead. Ghost crabs can detect substrate vibrations (Popper et al. 2001) and may rely on vibrational cues to detect the moving prey during predation. There is a possibility that the smaller crabs were feeding on more live rove beetles because they were more sensitive to vibrational cues and hence more efficient in capturing the moving insects than the larger adults. Further experiments with live rove beetles are necessary to substantiate these hypotheses. In addition, results of the first experiment also provide new evidence that there is a lack of ontogenetic variation in the feeding mode of *O. gaudichaudii*. Previous studies (Crane 1941; Lim et al. 2016) reported that juvenile crabs are not capable of deposit-feeding, but the results from this study and field observations (AYPY personal observation) show that both the juvenile and adult crabs are capable of using all feeding modes. Thus, the prevalence of rove beetles in the juveniles and diatoms in the adults were likely due to the distribution of food in the microhabitats.

The crabs in the second experiment had similar behavioral responses to supplemented food as *O. kuhlii* (see Evans et al. 1976). *Ocypode gaudichaudii* were able to locate the food pellets more efficiently once they had encountered the first pellet. This behavior implies that the crabs could have located the food pellets by learning the search image of the food they just encountered (see Evans et al. 1976). The sequestered food pellets were probably deposited at the bent portions of the burrows (Fig. 6) so that the crab inhabitants could excavate sand from the burrow ends to create more space to hoard more food without disturbing the pile of food collected (see video S2). This is the first report of food hoarding in ghost crabs.

The experiment was conducted during the rainy season, and *O. gaudichaudii* did not forage when there was heavy rain. Hence, food hoarding could be a feeding strategy for the population at PV to meet their energy demands during adverse periods (*e.g.*, rainy days). However, more studies need to be conducted during the non-rainy season to ascertain if food hoarding is, indeed, a seasonal behavior. The crabs at PV had different behavioral responses when food pellets were supplemented at different periods in their feeding cycle. A possible reason why none of the small food pellets were hoarded when they were supplemented at the beginning of the feeding cycle is that the freshly-emerged crabs were hungry. Since only a short handling time was required to consume the small food pellets, they were quickly consumed on the sand surface. In contrast, the small food pellets that were offered towards the end of the feeding cycle were hoarded. Assuming that *O. gaudichaudii* were satiated at the end of the feeding cycle, the crabs that hoarded food could be storing the excess food for inclement weather.

The crabs at PV also displayed different behavioral responses when food pellets of different sizes were supplemented at different periods of their feeding cycle. When the large food pellets were offered, all except one crab hoarded the large food pellets regardless of the feeding period. Since a longer handling time was required to consume the large pellets, crabs consuming the large pellets on the exposed beach would be subjected to increased predation risk and competition (*i.e.*, hermit crabs or conspecifics). Hence, food hoarding could be a strategy for *O. gaudichaudii* to feed on food reserves in the safety of their burrows when conditions outside the burrows were unfavorable for foraging. The ecological implication that food hoarding has on energy flow in sandy beach ecosystems is currently unknown, and further work is required to establish it.

In the third experiment, the transplanted crabs from PV showed plasticity in their behavioral responses to the higher densities of food in the new environment (*i.e.*, CB). Instead of droving, the transplanted adult crabs fed around their burrows like their conspecifics at CB. The results were expected since the burrow zone at CB is nutrient-rich and droving usually occurs at sandy beaches with low densities of food only (see Sherfy 1986). Moreover, with the lower density of crabs at CB (unpublished data), the crabs could not form large aggregates to attain safety in numbers. The success rate of the transplantation experiment in this study is very low and could possibly be due to the stress the crabs encountered during the translocation. Hence, the current results are preliminary and provide an indication of how the environment can affect the foraging strategies. Further work is therefore necessary to verify the results.

Ghost crabs have good vision and are sensitive to visual cues (see Crane 1939 1941). At PV, the crabs that formed droves appeared to be watching the movements of the neighboring crabs (see Christy and Wada 2015). Once a few crabs started to head down-shore towards the sand flats, other crabs would follow suit within seconds to form feeding aggregates that could range from dozens to hundreds of crabs (unpublished data). Droving could possibly be a learned behavior as ghost crabs are capable of associative-learning (see Evans et al. 1976). The crabs could have learned from past experience and associated the *en masse* down-shore movement with foraging at the nutrient-rich sand flats. However, more experiments are necessary to test if droving is indeed a learned behavior. An additional point to note is that the six transplanted crabs, which were previously feeding in droves on the exposed sand flats at PV, largely remained at their respective burrow entrances at CB. The crabs could be sensitive to predator cues (*e.g.*, the shadow of an avian predator) and adjusted their foraging and anti-predatory behaviors in the new environment (see Land and Layne 1995).

The radial arrangements of the pseudofecal pellets deposited by the transplanted crabs indicated that the crabs fed systematically along radial paths around their burrows. In comparison, crabs in the burrow zone at PV fed in random paths and often wandered away from their burrows to feed (AYPY personal observation). The difference in foraging patterns was likely associated with both the different densities and distribution of food patches and the predation pressure at the two beaches. Since there was abundant food around the burrows at CB, *O. gaudichaudii* could reduce the search time and travelling time to obtain food. Moreover, a crab was less likely to feed in an area that it previously foraged when it fed systematically (see Zimmer-Faust 1990). However, since the risk of predation by birds is higher at CB, the crabs could optimize the net resource yield and seek quick refuge in the burrow during systematic foraging near their burrows. As the burrow zone of PV had low densities of food, the crabs had to spend more time in search of the nutrient-rich food patches in the habitat. Since there was a lower risk of predation by birds at the burrow zone at PV, the crabs could search for food in areas further from their burrows.

It is evident from these three experiments that *O. gaudichaudii* shows short-term behavioral plasticity to the unpredictable changes in food availability (see Brown 1996). The crabs also showed long-term behavioral plasticity to the predictable changes, *e.g.*, diurnal and tidal cycles (see Brown 1996). For example, the population at CB fed on diatoms and rove beetles during the day but switched to preying on isopods and amphipods at night because diatoms and rove beetles were diurnally active (AYPY personal observation). Our current findings provide strong quantitative evidence that agree with Trott's (1988) passing statement that phenotypic plasticity could account for the variations in feeding behaviors of *O. gaudichaudii* from different geographical locations.

Behavioral plasticity is one of the key factors behind the resilience of sandy beach organisms under stressful conditions in dynamic sandy beach ecosystems (Brown 1996). To further understand the evolution of behavioral adaptations of *O. gaudichaudii*, more comparative studies with other populations in more diverging environments are necessary (see Scapini 2014). While the present study provides evidence that the feeding responses are habitat-dependent, future work should investigate the possible genetic contributions or the interactions between the genotype and environment to understand the mechanistic underpinnings of plasticity. It is also important to consider how learning and ontogeny can influence the plasticity of behaviors.

CONCLUSIONS

In conclusion, *O. gaudichaudii* is an opportunistic omnivore that uses short-term and long-term feeding strategies to cope with the spatial and temporal variations in food availability and maximize the energy gained during foraging. As the top benthic predator in sandy beach ecosystems, the switching of foraging modes and the use of different feeding strategies can have top-down effects on the predator-prey dynamics and interaction strength of food webs in the sandy-shore ecosystem. The various foraging behaviors that *O. gaudichaudii* exhibited in response to the spatial and temporal fluctuations in environmental conditions (*e.g.*, food availability) are likely associated with the trade-offs between the cost and benefits of foraging plasticity. However, further work is required to determine the adaptive value of plasticity before the cost and benefits of foraging plasticity can be ascertained.

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

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Supplementary materials

Video S1. (download)

Video S2. (download)