

Coexistence of Juvenile with Adult *Ocypode gaudichaudii* at Culebra Beach, Panama: A Temporal-spatial Partitioning Compromise

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Received 29 May 2021 / Accepted 28 January 2022 / Published 5 May 2022
Communicated by Benny K.K. Chan

The temporal-spatial resource use patterns of juvenile and adult *Ocypode gaudichaudii* were studied by comparing the zonation patterns and activity budgets of the two life stages at Culebra Beach, Panama. Burrow distribution of the crabs during the day and at night was studied over six months. Diurnal activity budgets of 46 crabs (22 juveniles and 24 adults) were determined by observing seven predominant behaviors upon emergence from their respective burrows when the burrow zone is uncovered after the tide recedes. The behaviors comprise three foraging-related activities (*i.e.*, deposit-feeding, scavenging, and probing for food), the maintenance of burrow, walking, staying within the burrow, and resting at the burrow entrance. Juvenile crabs occupied a higher intertidal zone than the adults and had a higher emergence rate at night. This temporal-spatial habitat partitioning could possibly reduce intraspecific competition between the two life stages, thereby enabling their coexistence in the habitat as well as increasing the survival rate of the juveniles, potentially raising the carrying capacity of the population at Culebra Beach. All 46 crabs—regardless of life stage—spent the highest mean proportion of time on foraging-related activities. Out of the three feeding-related behaviors, adults spent most time on deposit-feeding while juveniles spent most time probing. Only juveniles scavenged. In both life stages, a similar proportion of time was spent maintaining the burrow and staying within the burrow.

Key words: Diel activity pattern, Habitat selection, Intraspecific competition, Niche partitioning, Resource use.

BACKGROUND

In the field of community ecology, it is well established that no two interacting species can occupy similar niches, compete for the same resources, and coexist in the long term—this is known as the Competitive Exclusion Principle (see Gause 1934). However, MacArthur and Levins (1967) stated that stable coexistence is possible, up to a certain threshold of niche similarity; this was termed the ‘limiting similarity theory’. To achieve coexistence, competing species must segregate in one or more dimensions of their ecological

niche, a process known as niche partitioning (see Schoener 1974a). In his classic work on seven sympatric congeneric species of lizards in the Western Australian desert, Pianka (1969) provided evidence that resource division can be classified into three dimensions: food type, habitat, and time. Niche differentiation, thus, can be achieved through trophic, spatial, or temporal partitioning, or a combination of them, to avoid intense competition. Species may be distinctive in their resource selection (trophic differences) or in the places (spatial differences) or time (temporal differences) when shared resources are exploited.

Food resource partitioning has been extensively studied, especially in vertebrate communities (e.g., fish, birds, mammals). Most of the research has involved comparative studies of diets, e.g., prey/food type and size, through stomach content analyses (see Pianka 1969; Su and Lim 2016); food preference/selection observations (see Sushma and Singh 2006); or scat analyses (see Chillo et al. 2010). Diet data are often linked with the morphometrics of the individuals, or the species, with conclusions on food partitioning being drawn based on constraints/advantages of various morphological structures such as gape size (see Su and Lim 2016) and head proportions (see Pianka 1969).

Spatial resource partitioning occurs when two or more competing species reduce competition by occupying different areas/microhabitats within the range of occurrence of a common resource. Time is a resource axis that can be partitioned both on diel and seasonal scales. In a review on resource partitioning, Schoener (1974a) observed that temporal partitioning was markedly less common than food-type or habitat partitioning. Schoener (1974b) subsequently developed a theoretical model that predicts that temporal partitioning at the diel scale should be relatively rare as only in situations whereby there is a severe depletion of resources would it be no longer optimal to forage during the same period as competitors. Notably, there are many more papers published on seasonal temporal partitioning than diel partitioning (Schoener 1974a). However rare, temporal differences in activity patterns of competitors occur in nature, and these are discussed in a more recent review by Kronfeld-Schor and Dayan (2003).

Although niche differentiation of coexisting species is important in studies on community dynamics, there are increasing empirical studies on intraspecific resource use (see Bolnick et al. 2011). Some researchers referred to the different age-classes of a few animal taxa (e.g., crocodiles, desert scorpions, spiders) as ‘ecological species’ because the variation in resource use among the age classes were equivalent or more than that between different species (Enders 1976; Maiorana 1978; Polis 1984). For example, the different intraspecific resource use patterns in desert scorpions (Polis 1984), snakes (Shine and Wall 2007) and fishes (Marrin 1983) suggest intraspecific niche partitioning and explain the coexistence of conspecifics at different life stages (see Quevedo et al. 2009). Different resource use patterns are also evident in brachyuran crabs.

Habitat shifts (e.g., Hultgren and Stachowicz 2010) and diet shifts (e.g., Rosas et al. 1994) with the maturation of juvenile brachyuran crabs into adults have been reported, but the existing literature centres on the niche shifts in temperate sub-tidal brachyurans (e.g., *Callinectes* sp., blue crab). To date there are only three

studies on the diet shifts in semi-terrestrial brachyurans from the genera *Helice* (see Mia et al. 2001) and *Ocypode* (see Crane 1941; Lim et al. 2016), commonly known as ghost crabs. Moreover, only these two studies on ghost crabs (*Ocypode*) have been conducted in tropical regions.

Ghost crabs (genus *Ocypode*) can be good model organisms with which to study resource partitioning as their burrows are distinct (see Yong and Lim 2009) on sandy beaches (indicating habitat-use). As large beach macrofauna, their dietary preferences can be easily ascertained through behavioral observations and stomach analyses (indicating food resource use) (Crane 1941; Hughes 1966; Jones 1972), and they have been known to be diurnally and nocturnally active (indicating diel partitioning) (Barrass 1963). In addition, adult *O. ceratophthalmus* cannibalize juveniles, and the relationship between these two life stages is that of a predator-prey system (Hughes 1966). Hence, ghost crabs are excellent models for intraspecific niche partitioning investigations.

Ocypode gaudichaudii is the only ghost crab species that predominantly deposit-feeds and undergoes an ontogenetic change in claw morphology—the pointed claw tips of juvenile crabs become chisel-shaped or ‘truncated’ in the adults (see Crane 1941). Analyses of foregut contents and claw morphometrics of juvenile and adult *O. gaudichaudii* suggested that the juvenile crabs switched from a diet of small invertebrates (i.e., insects, worms, isopods) to diatoms with the onset of claw truncation as adults (see Crane 1941; Lim et al. 2016).

However, field observations of the adult and juvenile *O. gaudichaudii* at Culebra Beach—a resource-rich sandy beach in Panama—by Yong and Lim (2021) indicated no diet differentiation between the life stages, suggesting that the crabs rely on the partitioning of other resources to reduce the competition between the two life stages. How do adult and juvenile *O. gaudichaudii* differ in their utilization of resources to decrease intraspecific competition? We hypothesized that *O. gaudichaudii* show spatial and temporal variation in the resource use patterns to reduce intraspecific competition. In this study, we ascertained the diel zonation patterns and the diurnal activity budgets of juvenile and adult *O. gaudichaudii* to determine if there is intraspecific niche partitioning that could decrease competition between the two life stages.

MATERIALS AND METHODS

The study was conducted from July 2012 to October 2013 at Culebra Beach (8°54'45"N,

79°31'48"W) along the Pacific Coast of Panama. Culebra Beach (CB) is a sheltered sandy beach on the eastern side of the Pacific entrance to the Panama Canal. The burrow zone was demarcated into six 5 m wide zones across the shore and parallel to the shoreline (Fig. 1). The tidal heights of the demarcated zones at CB ranged from -0.6 m to 4.6 m, and various abiotic and biotic factors across the six zones of the two beaches were determined. According to Yong and Lim (2021), the concentration of total organic content, chlorophyll *a* and prey types (*i.e.*, isopods and rove beetles) across the burrow zones were similar.

Sediment grain size distribution in the burrow and foraging zones of *Ocypode gaudichaudii*

Granulometry of the substrate collected from the burrow and foraging zones at CB was conducted to test for sediment particle size differences across the zones. This was carried out using the methods outlined in Buchanan (1984). Data obtained from dry and wet sieving were analyzed using GRADISTAT 8 (see Blott and Pye 2001).

Abundance and distribution of juvenile and adult *Ocypode gaudichaudii*

The abundance and distribution of juvenile and adult *O. gaudichaudii* were determined from June to November 2012. Regression of the variable 'Carapace width' (CW) against 'Burrow diameter' (BD) of 86 crabs was determined following the method outlined in Lim and Yong (2015). This crab population exhibited high burrow fidelity and the smaller crabs did not colonize abandoned burrows constructed by larger conspecifics (personal observation by AYPY). The CW-BD relationship was established so that the CW, and hence the life stage of the crab occupant could be ascertained with just the BD measurement, with minimal disturbance to the crab occupant during the sampling sessions. A total of 215 juvenile crabs were

collected by examining their pleopods as described by Lim et al. (2016). The cut-off BD for juvenile crabs was based on the CW (14.3 mm) of the largest juvenile crabs collected. Extrapolation of the cut-off BD for juvenile crabs was carried out using the regression equation $CW = 1.01BD + 0.78$ ($r^2 = 0.94$) and the cut-off CW of 14.3 mm. The extrapolated BD of 13 mm indicated that adult *O. gaudichaudii* excavated burrows with BD > 13 mm. A 30 × 30 m plot across the six burrow zones was marked out as the sampling area, and the area was divided into 36 (5 × 5 m) quadrats (Fig. 2) with six replicates at each zone.

Day and night sampling sessions were conducted at low tide when the intertidal zone was exposed by the ebbing tide. During each sampling session, the burrows with crab occupants in each quadrat were identified. For each burrow, the zone in which it was located was recorded and the diameter was measured before the CW of the crab occupant was extrapolated. The burrow was then categorized as one that was excavated by a juvenile or an adult crab according to the cut-off BD of 13 mm. A boxplot was used to compare the size range of the crabs that emerged during the day and night.

All the juvenile and adult crabs in each quadrat were counted, and the percentage composition of each life-history stage was determined for each sampling session. A Chi-square test was performed to test if the mean proportions of juvenile and adult crabs that emerged during the day and night were different. The burrow density within the sampling session was calculated, and a *t*-test was used to compare the mean burrow densities at Culebra Beach during the day and night. Due to heteroscedasticity and a non-normal distribution, two separate non-parametric Kruskal-Wallis tests were performed to compare the median of the zonal burrow densities at different times of the day. A Kruskal-Wallis test was used to compare the median burrow densities between the zones. Scatterplots of the burrow densities of the juvenile and adult crabs in each sampling session were plotted against the highest high tide level and lowest low tide level for the day at

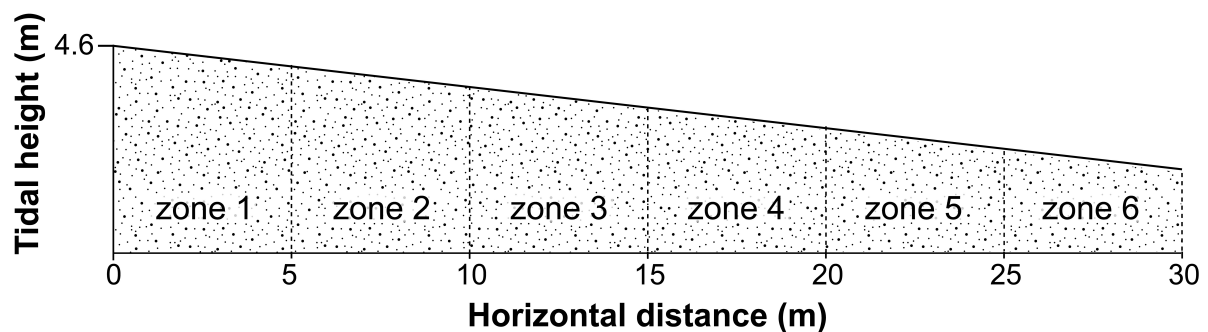


Fig. 1. Beach profile showing the burrow zones of *Ocypode gaudichaudii* at Culebra Beach.

each site. These two tide levels determine the upper and lower limits of the intertidal zone for each day and could influence the burrow densities at the site. The zonal burrow densities of the juvenile and adult crabs during each sampling day were also related to the highest high tide and lowest low tide levels during the study.

Behavioral observations of *Ocypode gaudichaudii*

Ad libitum sampling and ethogram construction

Field observations for an ethogram were conducted from June to August 2013. During the day, crabs were observed from 5 m away with a pair of binoculars (Steiner Safari 10 × 26) and a hand-held video camera (Sony Handycam DCR-SR62) to minimize the influence of human disturbance on the behavior of the animals. Night observations of the crabs were made in total darkness using a pair of night vision goggles (ATN NVG-7 CGT) within 2 m from the crabs. Preliminary observations showed that the crabs were only active at the intertidal zone for about

6 h after emergence during the day. *Ad libitum* sampling was carried out to identify the common behaviors of *O. gaudichaudii* after emergence during the day. An ethogram based on the types of behavior observed in the field was constructed.

Activity budget of *Ocypode gaudichaudii*

The diurnal activity budgets of 46 crabs (22 juveniles, 24 adults) were determined from August to December 2013. During the day, most crabs emerged from their burrows approximately half an hour after the receding tide uncovered the burrow zone. Freshly-emerged juvenile and adult crabs were randomly selected from each zone for observation. The crabs usually rested at the burrow entrance for approximately an hour upon emergence. Recording of a crab's behavior started once it moved away from the burrow entrance. The activity in which the observed crab was engaged was recorded at five-minute intervals. Every crab was observed for a minimum of an hour and for as long as possible until it was out of sight for more than 15 min. The mean total activity time between the juveniles and adults from each site were compared with *t*-tests. The

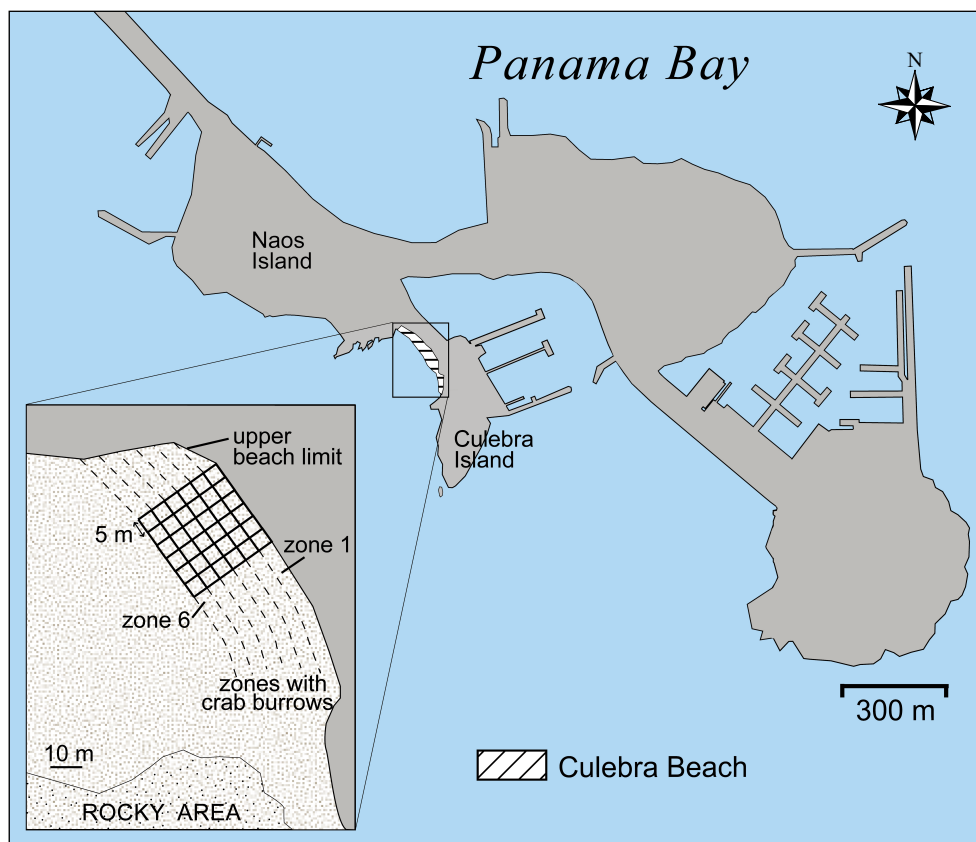


Fig. 2. Location of Culebra Beach with the inset showing a 30 × 30 m plot marked out as the sampling area across six five-metre zones (zone 1 to zone 6). The area was divided into 36 (5 × 5 m) quadrats.

mean proportion of time in which the juvenile and adult crabs were engaged in each activity was calculated and compared separately. No field observations were carried out on rainy days as the crabs did not emerge.

We used statistical methods similar to those used by Baladrón et al. (2016) to compare the activity budgets of the two life stages by first constructing a Bray-Curtis similarity/dissimilarity matrix, then performing a similarity percentage (SIMPER) procedure to examine the contribution of each behavior to the similarity within each life stage and average dissimilarity between the life stages. Non-metric multidimensional scaling based on the Bray-Curtis similarity matrix was then applied to visualize the ordination distribution between the juvenile and adult crabs. The crabs with similar activity budgets will cluster closer in the ordination plot and vice versa for the crabs with different activity budgets. In addition, a cluster analysis based on the same similarity matrix was performed to determine the occurrence of behavioral heterogeneity of the crabs at the life stages. The ordination plot was superimposed with the results of the cluster analysis at 80% similarity indicated the heterogeneity in crab behavior. A One-way Analysis of Similarities (ANOSIM) was performed to verify the behavioral heterogeneity between the juvenile and adult crabs. All multivariate statistical analyses were carried out using the PRIMER software (PRIMER-E Ltd., Version 6.1.2, 2005; see Clarke and Gorley 2001).

RESULTS

Sediment grain size distribution

The sediment had approximately 98.7% sand and 1.3% of silt and clay. Results from the analysis showed that the sediment across the zones had uniform particle grain size (well-sorted). The mean sediment grain size was $98.7 \pm 0.3 \mu\text{m}$.

Abundance and distribution of *Ocypode gaudichaudii*

All extrapolated CW > 37.0 mm and < 4.0 mm were discarded as the CW of the crabs observed throughout the study ranged from 4.0 mm to 36.9 mm. The size range of the crabs that emerged during the day and night was similar to the CW: 5.1 to 35.6 mm (Fig. 3). However, the mean CW of the crabs that emerged during the day was significantly larger than those that emerged at night ($t = 12.92$, $d.f. = 769$, $p < 0.05$; $18.8 \pm 0.1 \text{ mm} > 14.5 \pm 0.3 \text{ mm}$; mean $\pm$ S.E., respectively).

The mean proportion of juvenile and adult *O.*

gaudichaudii that emerged during the day and night were significantly different ($\chi^2 = 16.592$, $d.f. = 1$, $p < 0.05$). During the day, 32% of the crabs that emerged were juveniles, but the mean proportion increased to 58% at night. There was no significant difference in the mean burrow densities between day and night ($t = 1.23$, $d.f. = 185$, $p = 0.221$; $0.18 \pm 0.01 \text{ burrows m}^{-2} \approx 0.14 \pm 0.03 \text{ burrows m}^{-2}$; mean $\pm$ S.E., respectively). Results of the Kruskal-Wallis tests showed a significant difference in the median burrow densities between the zones during the day ($H = 241.70$, $d.f. = 5$, $p < 0.05$) and night ($H = 83.13$, $d.f. = 5$, $p < 0.05$). The burrow densities of the adult crabs were consistently higher than the juveniles during the day except on six out of the 21 days of sampling. There was no clear trend in the fluctuation of burrow densities throughout the tidal cycles.

Scatterplots of the burrow densities at each burrow zone (Fig. 4) showed the highest burrow densities of the adults mainly (16 out of the 21 sampling days) occurred between zones 3 and 4. In comparison, the highest burrow densities of the juveniles generally (15 out of the 21 sampling days) occurred between zones 1 and 2. However, on 27 September, and 9 November, 2012, the burrow densities of the juveniles at zone 3 were the highest. There is no clear trend in the results with respect to the tidal cycle. The scatterplot of zone 6 of the burrow zone was excluded due to negligible burrow densities throughout the study. Generally, the burrow densities of the adults and juveniles were the highest in zone 2 at night (Fig. 5). The only exception was on 27 September, 2012 when the burrow densities of the

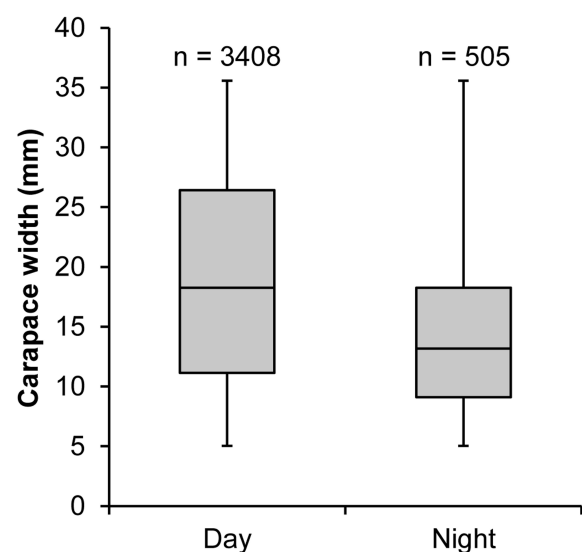


Fig. 3. Boxplots of the median carapace width and interquartile range of *Ocypode gaudichaudii* during the day and night at Culebra Beach. Dark bands represent medians, boxes represent interquartile range and whiskers represent 1.5 times the interquartile range.

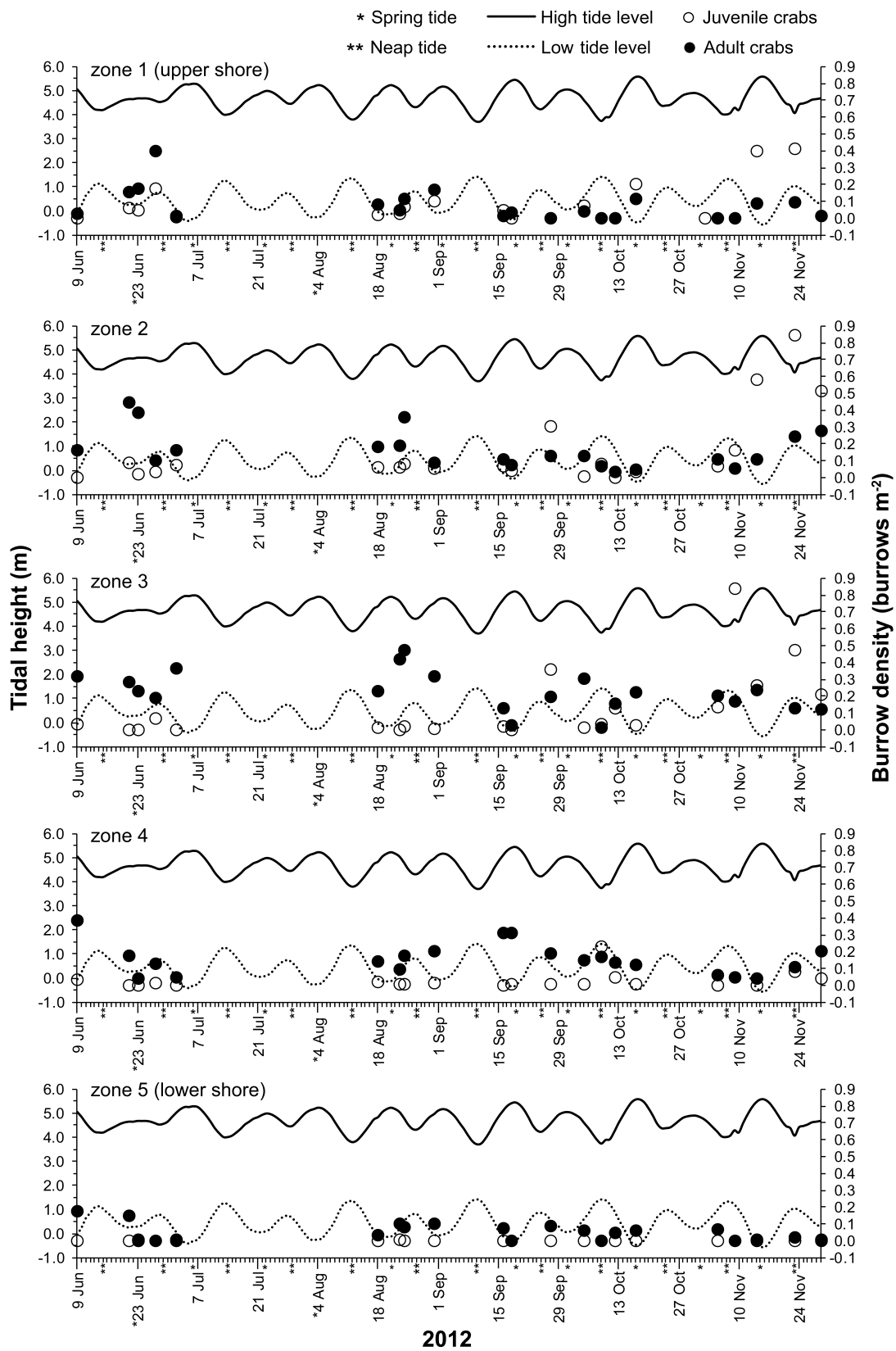


Fig. 4. Burrow densities of the juvenile and adult *Ocypode gaudichaudii* at zones 1 to 5 of Culebra Beach during the day with respect to the high and low tide levels from 9 June to 29 November, 2012.

adults and juveniles in zone 3 were the highest, which is similar to the trend observed during the day.

Behavioral observations of *Ocypode gaudichaudii*

Ad libitum sampling and ethogram construction

Seven distinct behaviors in juvenile and adult *O. gaudichaudii* were observed over the month-long period of *ad libitum* sampling (Table 1). *Ocypode gaudichaudii* spent a large proportion of time foraging when the

intertidal zone was exposed at low tide. Three out of the seven common behaviors—deposit-feeding, probing, and scavenging/predation—observed in the crabs were related to foraging (Table 1).

Activity budget of *Ocypode gaudichaudii*

Juvenile crabs usually emerged before the adults when the tide receded. As a result, all the juvenile crabs that were observed were engaged in the observed activities before the adult crabs. The juveniles spent a significantly lower mean total activity time than the

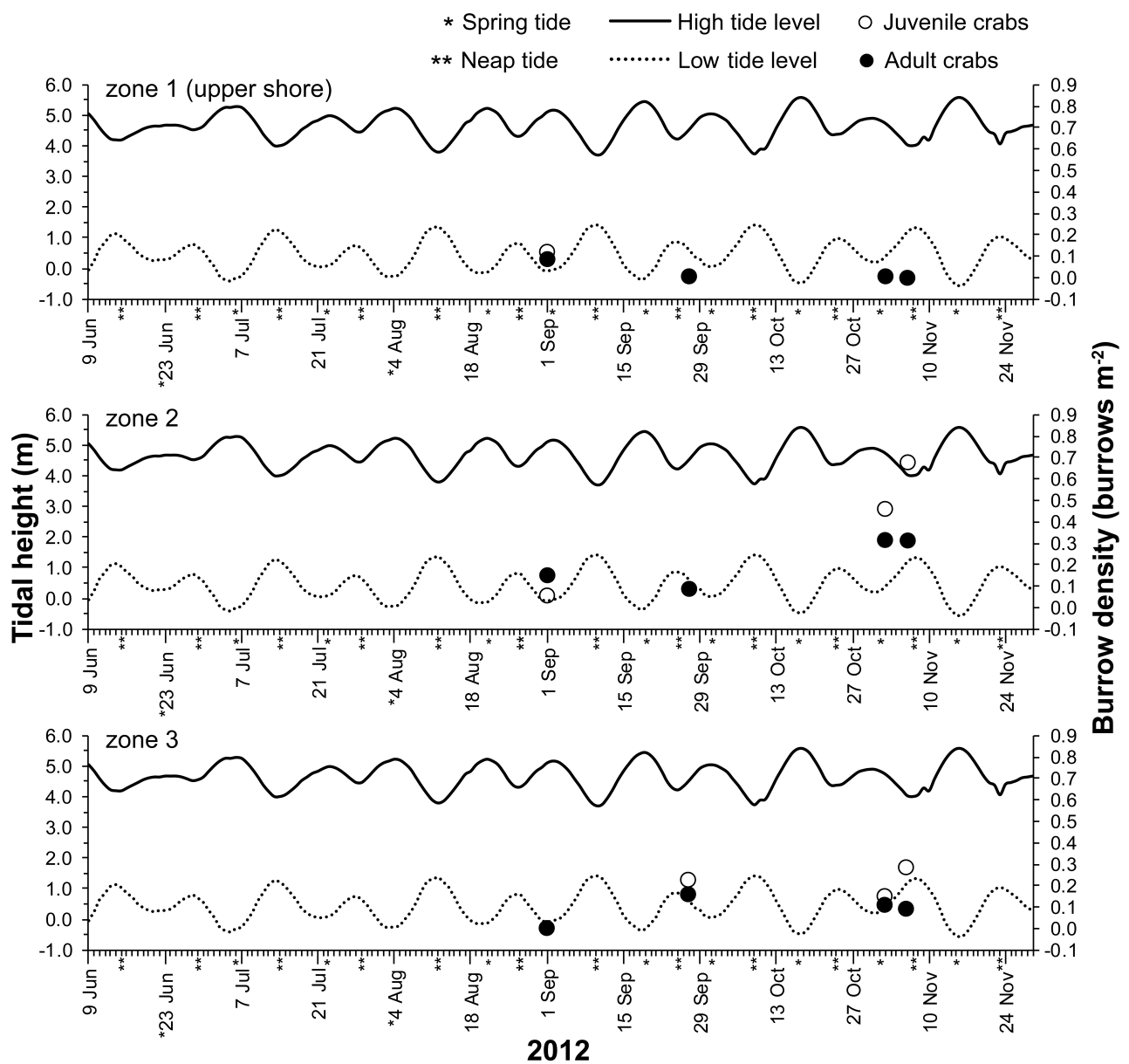


Fig. 5. Burrow densities of the juvenile and adult *Ocypode gaudichaudii* in zones 1 to 3 of Culebra Beach during the night with respect to the high and low tide levels from 9 June to 29 November, 2012.

adults engaged in the seven behaviors after burrow emergence ($t = 4.75$, $d.f. = 39$, $p < 0.05$; 146 ± 12 min $< 216 \pm 9$ min; mean $\pm$ S.E., respectively).

All 46 crabs spent the highest mean proportion of time on foraging-related activities upon emergence. Out of the three feeding-related behaviors (*i.e.*, deposit-feeding, scavenging/predation, and probing), the adult crabs spent the most time deposit-feeding (Fig. 6). Scavenging/predation was not observed in the adults during the day, and the juveniles spent more time on probing than the adults. Both stages of crabs spent a similar amount of time on burrow maintenance (Fig. 6). Adult crabs spent similar amount of time in the burrows as the juveniles, but the juveniles spent more time resting at the burrow entrance than the adults (Fig. 6).

Results of SIMPER indicated that there was limited overlap in the activity budget of the juvenile and adult crabs (Table 2). Among the six behaviors, deposit-feeding contributed the most and walking contributed the least to the difference in activity budgets of the

two life stages. The nMDS plot superimposed with the Bray-Curtis cluster analysis using 60% similarity showed five clusters for the activity budgets of all 46 crabs: three clusters comprising solely juvenile crabs on the left, a cluster of only adult crabs on the right, and one cluster of mixed juveniles (9 individuals) and adults (13 individuals) in the middle of the plot (Fig. 7). When 80% similarity was used to differentiate the activity budgets of this middle cluster, only one of the nine groups had mixed life stages. Results of the one-way ANOSIM showed a significant difference between the activity budgets of the juveniles and adults (Global $R = 0.45$, $p < 0.05$). The evidence indicated behavioral heterogeneity between the juvenile and adults.

DISCUSSION

Schober and Christy (1993) studied the abundance and distribution of *O. gaudichaudii* at Culebra Beach.

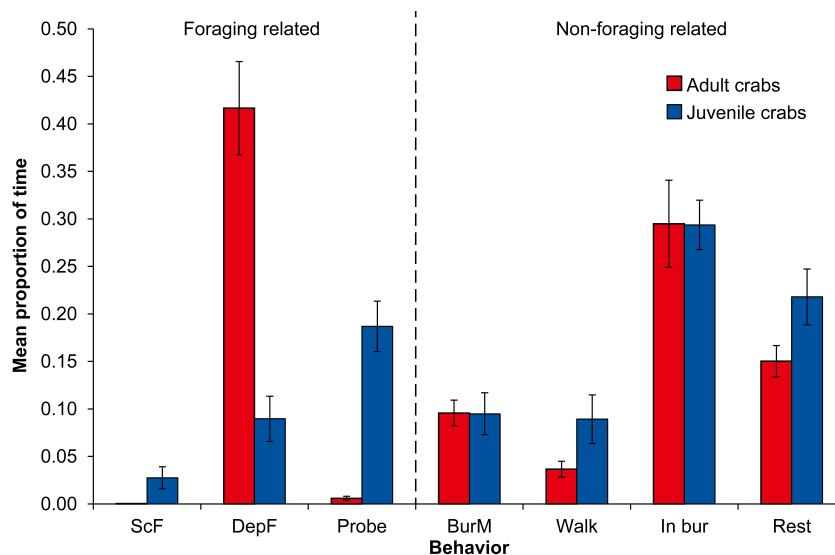


Fig. 6. Mean proportion of time ($\pm$ S.E.) that *Ocypode gaudichaudii* from Culebra Beach were engaged in seven behaviors after burrow emergence. ScF, scavenging; DepF, deposit-feeding; Probe, probing for food; BurM, burrow maintenance; Walk, walking; In bur, staying within the burrow; Rest, resting at the burrow entrance.

Table 1. Ethogram for *Ocypode gaudichaudii* based on field observations

Behavior	Definition
Deposit-feeding	Scooping up portions of surficial sediment into the buccal cavity with chela and producing pseudofecal pellets
Probing	Inserting chela into the substrate repeatedly
Scavenging/predation	Picking up living or dead plant or animal matter from the substrate and placing food into the buccal cavity
Burrow maintenance	Excavation and cleaning of burrows and moving of sand away from the burrows
Walking	Lateral movements across the substrate surface
Resting	Standing motionless
In burrow	Staying in the burrow

The highest mean burrow density that they observed was higher than the mean diurnal burrow density in the current study ($0.78 \text{ burrows m}^{-2} > 0.18 \pm 0.01 \text{ burrows m}^{-2}$). In addition, Schober and Christy (1993) reported that the burrow densities varied with the tidal regime and lunar cycle; the height of the high tide immediately before the sampling period was significantly positively correlated with the burrow density within one to five days later. In comparison, the tidal cycles, did not affect the burrow densities of the crabs in the current study.

Although the size range of *O. gaudichaudii* reported by Schober and Christy (1993) is different from that of the current study (the largest mean CW: $37.3 \pm 0.78 \text{ mm}$ cf. 35.6 mm , respectively), the zonation patterns of *O. gaudichaudii* of both studies are comparable with the highest burrow densities at zone 1 to zone 3 (Fig. 4).

Burrow densities and zonation patterns of the juvenile and adult crabs varied throughout the study, but the burrow densities of adult crabs were generally higher. Although the adult crabs had a wider distribution

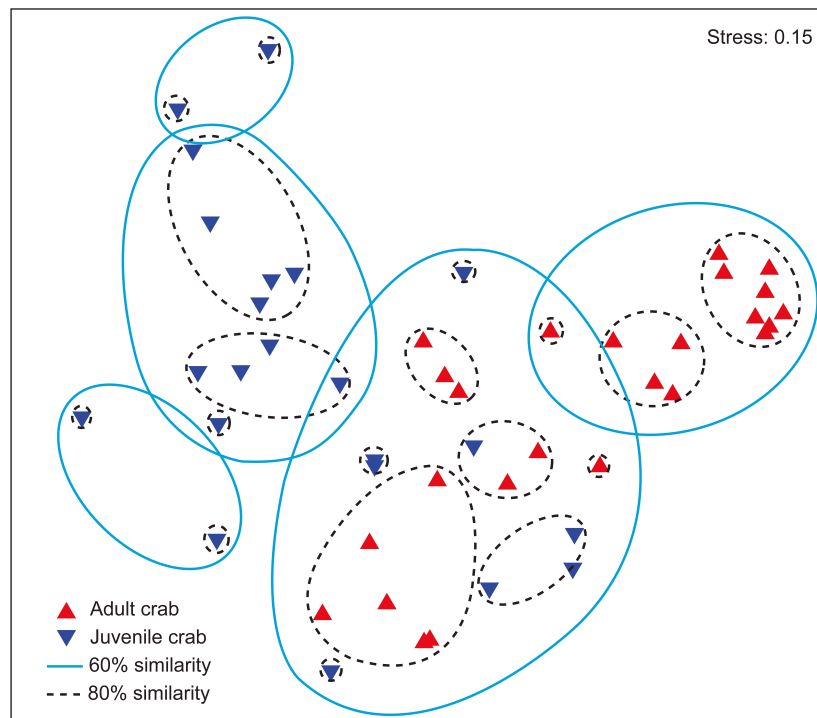


Fig. 7. Non-metric Multidimensional Scaling plot of the activity budget of the juvenile and adult *Ocypode gaudichaudii* from Culebra Beach superimposed with Bray-Curtis cluster analysis using 60% and 80% similarity. 2D stress = 0.15.

Table 2. Contribution of each behavior to the dissimilarities between the activity budgets of adult and juvenile *Ocypode gaudichaudii*, according to SIMPER analysis. Behaviors were arranged in decreasing order according to their contribution to the average dissimilarity

Behavior	% Similarity (Average $\pm$ SD)		% Dissimilarity adult vs juvenile	
	Adult	Juvenile	Contribution	Cumulative
Deposit-feeding	27.72 ± 1.45	2.93 ± 0.49	32.06	32.06
In burrow	16.72 ± 1.17	22.48 ± 2.05	18.94	51.00
Probing	0	11.40 ± 1.18	16.75	67.75
Resting	10.50 ± 2.04	13.64 ± 1.33	12.66	80.40
Burrow maintenance	6.01 ± 1.71	3.96 ± 0.72	8.53	88.94
Walking	0	0	8.52	97.46
Average similarity	62.58	57.54		
Average dissimilarity			54.42	

than juveniles, most of the juvenile and adult crabs excavated their burrows in the upper and middle intertidal zones, respectively (Figs. 4, 5), indicative of spatial segregation despite uniform sediment characteristics across the zones. However, the density of food at the upper shore was lower than that of the lower shore (see Yong and Lim 2021), which implies that the juveniles living at the upper shore would have to spend more time searching for food. The increase in food searching time was evident from the higher proportion of time that the juveniles spent on probing the substrate and scavenging than the adults (Fig. 6). The difference between the zonation patterns during the day and at night could be due to the absence of diatoms at night since diatoms are phototactic and migrate below the sand surface after dark (see Mitbavkar and Anil 2002). As the adults are not able to deposit-feed at night, those that emerged at night would have to prey on invertebrates such as amphipods, which are prevalent on the sand surface at upper littoral zone at night (personal observation AYPY).

Since adult crabs had access to more food (see Yong and Lim 2021), they spent more time in their burrows than the juveniles, suggesting that they needed to seek refuge more often than the juveniles. Being bright red in color, *i.e.*, more conspicuous than the cryptic juveniles (sand colored; see Crane 1941), adult crabs are more prone to predation by birds than the juveniles (AYPY personal observation). Similar to Crane's (1941) observations, smaller crabs that burrowed too near to larger conspecifics' burrows were evicted from their burrows by their larger neighbors, followed by the filling-in of the unoccupied burrows of the evictees by the larger crab (AYPY personal observation). This aggressive displacement of juveniles by adults could play a large role in habitat segregation (see Hughes 1966). Also, the aggression from adult conspecifics during the day could have driven the juvenile crabs to be nocturnally active. With a lower risk of encountering adult conspecifics, juveniles were able to feed on the sand surface for longer periods. These juvenile crabs also wandered further away from their burrows to hunt for prey at night (AYPY personal observation). In addition, the prevalence of shallow pits around their burrows (see Yong and Lim 2019) suggests that juvenile crabs spend more time digging for prey after low tide at night.

The proportion of time that adult crabs spent on deposit-feeding was about four times longer than that in juvenile crabs and was consistent with previous reports that described adult *O. gaudichaudii* as deposit-feeders and the juvenile as scavengers and predators (Crane 1941; Koepcke and Koepcke 1953; Lim et al. 2016). Adult *O. gaudichaudii* primarily deposit-feed on

diatoms and detritus, although they can prey on small invertebrates of higher protein content (see Crane 1941; Lim et al. 2016). This could be because less effort is needed to deposit-feed as diatoms and detritus are in abundance as compared to predation whereby the prey needs to be captured and subdued. Therefore, the choice of feeding mode could be the result of the balance of trade-offs between foraging effort and energy gain from the type of food. Although the pointed claw tips of juveniles do not restrict them from deposit-feeding as previously described (see Crane 1941; Lim et al. 2016), deposit-feeding was still more prevalent in the adult crabs, probably because it was less cost-effective for the adult crabs to capture and eat small, highly-mobile prey.

The results from this study suggest that the feeding habits and habitat use patterns of *O. gaudichaudii* were influenced by multiple factors. *Ocypode gaudichaudii* seem to be able to adjust their feeding and aggression-avoidance behaviors to the different levels of food abundance and predation risks at various tidal levels. The optimal behaviors would require each crab to assess and balance the benefits of aggression avoidance and the cost of reduced feeding time to stay alive and meet its energetic demands (see Werner and Gilliam 1984; Lima and Dill 1990; Jennions et al. 2003) before the rising tide inundates the burrows.

In his classic paper on resource partitioning in communities, Schoener (1974a) stated that temporal segregation is relatively rare and will only occur when the ability to process food is limited relative to the risk of being eaten during foraging. Yet, in some ecological communities, temporal partitioning is a significant mechanism of coexistence between competitors and between predators and their prey (Kronfeld-Schor and Dayan 2003). They further iterated that relatively few animal species would invert their activity patterns as a result of interspecific or intraspecific interactions in the opposite activity phase as the overall reduction in activity time is costly to the animals. Kronfeld-Schor and Dayan (2003) concluded their review on temporal partitioning by posing many thought-provoking questions: "Is temporal partitioning a last-resource mechanism of coexistence where other mechanisms fail?"; "Do some taxa have greater evolutionary plasticity than others?"; "Are some environments (*e.g.*, aquatic habitats) more conducive to shift in activity patterns than others?" and "How does phenotypic plasticity in the response of species to ecological interactions translate into phase shifts and the evolution of different activity patterns?"

Our study organism, *O. gaudichaudii*, a semi-terrestrial macroinvertebrate, may provide some partial answers to these questions. At Culebra Beach, there is distinct spatial segregation (albeit with a small overlap

in distribution), which implies that this strategy of partitioning did play a role in reducing competition. However, diel temporal partitioning seems to play the larger role in reducing competition between the two life stages and allow the juvenile crabs to avoid the adults without being costly to the juveniles as there are many amphipods at night to compensate for the shift in feeding activity phase (see Yong and Lim 2019). In contrast, these strategies of partitioning are not present to the same extent in another population of *O. gaudichaudii* at Playa Venao, Panama (personal observation by AYPY). The high population density there, coupled with limited areas whereby the sand is deep enough to excavate burrows at the high surf beach constraint the spatial distribution of juvenile and adult burrows, such that spatial partitioning is not possible. Moreover, both juvenile and adult crabs are only active during the day—with no diel temporal partitioning of the two life stages observed (Yong and Lim 2021). A plausible reason for the lack of diel temporal partitioning of the population at Playa Venao could be the presence of a nocturnal predator, a larger species of ghost crab, *Hoplocypode occidentalis*. Since there is a larger predator prowling the beach during the night, it does not benefit the juveniles to invert their activities to become nocturnal to avoid being eaten by their conspecific adult crabs. Although both life stages emerge during daylight hours, juveniles actively avoided the adults by emerging earlier to feed after the tide receded—still considered as a form of temporal partitioning, albeit not as drastic as an inversion of activities to the extent of diel segregation. A future experiment to determine whether displacement (or avoidance) of the adult crabs by the juveniles is a major factor in niche segregation could be conducted: viz. adult crabs from a section of the beach could either be removed or prevented from emerging from their burrow to determine if the juvenile crabs move lower on the beach away from the zone with abundant amphipods and cease being nocturnally active.

In a meta-analysis of competition in field experiments, large differences among trophic levels in competitive effects were observed: carnivores tend to experience effects from both interspecific and intraspecific competition regardless of terrestrial or aquatic habitats, while herbivores generally experience more intraspecific effects than interspecific effects (see Gurevitch et al. 1992). *Ocypode gaudichaudii* is omnivorous and the juveniles at Culebra Beach are more carnivorous, feeding on amphipods and rove beetles (see Yong and Lim 2019), while adults are primarily herbivorous and opportunistic carnivores; hence, it ‘straddles’ both trophic levels at this study site. At Playa Venao, however, both juvenile and adult *O.*

gaudichaudii are primarily herbivores. Stable isotope analyses of these two life stages could potentially shed more light on their trophic level in their respective food-web structures at the two beaches (see Morrow et al. 2014).

It is evident that the strategies for intraspecific niche partitioning in populations of *O. gaudichaudii* at Culebra Beach differ from those at Playa Venao, suggesting that the strategies adopted are highly dependent on the specific environmental conditions at each site. Hence, there is a need for researchers to recognize that, while niche partitioning is a multifaceted ecological process that is essential to ensure survival of species as well as individuals within a species, a strong understanding of the local conditions of the habitat in which the community or the species occurs is crucial.

CONCLUSIONS

The two life stages of *Ocypode gaudichaudii* showed intra-specific niche partitioning in two axes of a species niche hyper-volume, space, and time, both of which are essential niche dimensions for coexistence. While spatial partitioning is a relatively common phenomenon for reduction of interactions between species, and between size and age-classes within a species, temporal segregation implies a cost in the overall reduction in activity time. Furthermore, most studies suggest that competition- or predation-induced segregation of activity patterns deal with temporal shifts within the normal nocturnal or diurnal activity time, e.g., emergence at a slightly later time within the night or daytime (see Kronfeld-Schor and Dayan 2003). However, at Culebra Beach, coupled with spatial partitioning (albeit, with some overlaps in distribution), juvenile *O. gaudichaudii* resort to the drastic measure of temporal partitioning to the extent of inverting their activity phase to avoid the territorial adults for survival. This intra-specific temporal-spatial niche partitioning, thus, alleviates competition, and reduces predation, which may ultimately increase the carrying capacity of the population with implications for ecology, evolution, and conservation.

Acknowledgments: We thank Dr. John Christy, the Smithsonian Tropical Research Institute, and the Culebra Nature Centre for access to CB and the facilities at Naos Marine Laboratories. The authors would also like to thank Autoridad de los Recursos Acuáticos de Panamá (ARAP) for permission to conduct research at the study sites under the ARAP Collection Permit. This study was funded by a grant (RI 8/10 SL) from the

National Institute of Education, Nanyang Technological University, to the second author. The first author would like to thank Nanyang Technological University for the Nanyang Research Scholarship during her PhD candidature. Review comments from Dr. John Christy and another anonymous reviewer are appreciated and helped to improve the clarity and depth of discussion of this paper.

Authors' contributions: AYPY conceived, designed, and performed the observations as well as analyzed the data. Both authors participated in drafting and revising the manuscript. Both authors read and approved the final manuscript.

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.

Ethics approval consent to participate: ARAP Collection Permit.

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