

Larder Hoarding Versus Immediate *in situ* Food Consumption in Two Fiddler Crab Species: Is it an Evolutionarily Stable Strategy?

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Larder hoarding behavior in central place foragers has been widely studied in vertebrates, albeit, not as extensively as scatter hoarding. However, scant information is available for the invertebrate taxa, especially aquatic species. We investigated this phenomenon via an *in situ* food supplementation experiment in a community of two sympatric fiddler crabs, *Austruca annulipes* ($n = 80$; 40 males and 40 females) and *Gelasimus vocans* ($n = 60$; 30 males and 30 females), in a Singapore mangrove patch with an intermediate resource level. As the semiterrestrial intertidal crabs can only forage after emergence from their burrows during exposure period, the duration of time available for feeding is finite and constitutes an important constraint in the optimization of food intake. The activity budget (in terms of time spent on feeding activities, all above-ground non-feeding activities, and burrow-sequestration) as well as the occurrence (if any) of larder hoarding behavior in these two species after they first emerged were recorded by hourly intervals (three hours of observation) to determine the effect of time left for foraging on larder hoarding. Regardless of species, *A. annulipes* and *G. vocans* spent most of the time feeding when the tide was out, despite overall significant behavioral heterogeneity (multivariate analyses using ANOSIM) indicating that both species prioritized hunger satiation over other activities. Our results also showed that although the two sympatric crabs live in the same mangrove area with similar food resource levels, only *A. annulipes* larder hoarded. The propensity to larder hoard did not differ significantly between the sexes, nor among the three time periods of the feeding duration. *Gelasimus vocans*, one of the species of crabs known to form feeding droves, did not larder hoard at all. We propose that *A. annulipes* is a species that can deploy larder hoarding as a foraging strategy when it encounters valuable food resources, and such a strategy is highly advantageous for the species as it generally inhabits sandy habitats that are poor in nutrient levels. Hence, larder hoarding can be considered a mixed evolutionarily stable strategy (ESS) adopted by *A. annulipes*. In contrast, *G. vocans* that commonly inhabits muddy sediments—with a high level of food resources—did not larder hoard, even when provided with supplemented food, suggesting perhaps that its mixed ESS is droving behavior.

Key words: Activity budget, *Austruca annulipes*, Central place forager, Food-supplementation experiment, *Gelasimus vocans*.

BACKGROUND

In the animal kingdom, many diverse strategies are

used to maximize fitness, such that the species/individual derives the most benefit for the lowest cost. Among these strategies, the ones involved with the procurement

of food are of primary importance for the continual survival of the species. MacArthur and Pianka (1966) proposed that natural selection should favor animals whose behavioral strategies maximize their net energy intake per unit time spent foraging. They formulated the optimal foraging theory—a behavioral ecology model—that can predict how an animal behaves when searching for food.

When animals forage, they can choose from two options when they encounter food: either to consume the food *in situ* or to transport the food to another place for later consumption (Lima and Valone 1986; Shimada 2001). The removal of food from the original source to store for future consumption is known as food hoarding (Winter et al. 2018). There are two strategies of hoarding: scatter hoarding (also known as food caching) and larder hoarding (also known as central-place foraging). Scatter hoarding involves the sequestration of individual or groups of food items in several different locations—typically unguarded—whereas larder hoarding refers to the storage of food items in a protected central location, *i.e.*, a burrow or a nest, that is actively defended (Vander Wall 1990). Why would a forager hoard when it can feed at the original site of the food resource? Intrinsically, hoarding is related to the estimated time to consume a food item, which, in turn, is linked to physical factors (*e.g.*, morphological characteristics of the forager and the food item which may affect handling time), biotic factors (*e.g.*, predation risks) and environmental factors (*e.g.*, resource level in the habitat, ambient temperature, limited time to forage due to in-coming tides).

Food hoarding behavior has been extensively studied in many vertebrate taxa, especially small mammals and birds, *e.g.*, squirrels (see Lima et al. 1985; Hurlly and Robertson 1987), mice and rats (see Jenkins and Breck 1998; Winter et al. 2018), corvids (see Healy and Krebs 1992; de Kort and Clayton 2006), and parids (see Healy and Krebs 1996; Brodin 2005). For example, Lima et al. (1985) reported that grey squirrels will hoard food items that are large (implying long handling time) and within a certain distance that gives them enough time to escape from predators to minimize risks of predation and maximize energy gain. Wang et al. (2012) categorized the decision-making process of scatter-hoarding rodents into (1) ignore/manipulate; (2) eat *in situ*/remove for storage; (3) near/far hoarding site; and (4) consume/cache for future. The foraging behavior of two field mice (*Apodemus latronum* and *A. chevrieri*) showed that seed size affected all four steps while nutrient and tannin content of the seeds only affected steps (1) and (3). Waite (1992) described how the distance to which gray jays transport food items for storage was affected by the load size and the presence

of other birds. Since many of the birds studied were scatter hoarding species, a number of studies focused on their spatial memory (*e.g.*, Krebs 1990; Brodin 2005; Healy et al. 2005) and cache protection strategies (*e.g.*, Carrascal and Moreno 1993; Martin and Sherry 2021).

Food hoarding behavior is less widespread in invertebrates than in vertebrates, and is mainly observed in terrestrial taxa such as social insects (*e.g.*, bees and ants), primarily for the provision of food for their offspring (see Vander Wall 1990). The hoarding of food items for individual consumption is even rarer, and has mainly been reported on in orb-web spiders, such as *Nephila* spp., that construct durable or permanent webs to wrap up prey for later (see Champion de Crespigny et al. 2001; Griffiths et al. 2003). In decapod crustaceans, there are several brief accounts of food hoarding behavior in fiddler crab, *Gelasimus vocans* (see Salmon 1984), red land crab, *Gecarcoidea natalis* (see O'Dowd and Lake 1989), scopimerid crab, *Dotillopsis brevitarsis* (see Wada 1985), hairy crab, *Pilumnus vespertilio* (see Kyomo 1999), signal crayfish, *Pacifastacus leniusculus*, and yabby, *Cherax destructor* (see Buřič et al. 2016). Salmon (1984) reported that female *Gelasimus vocans* (as *Uca vocans*) individuals, upon emergence, initially fed around their burrows, but as the sediment dried up on the sandy beach, made sallying trips to the low tide region where food was more concentrated. He also observed some individuals carry detritus into their burrows from the more distant areas and assumed that it was hoarding without conducting any further investigations to verify this conclusion. A unique foraging behavior of *Dotillopsis brevitarsis* termed as 'clodding'—the action of bringing a scoop of mud into the burrow—was reported by Wada (1985). He observed the mud clod was carried out about 4 minutes after the crab entered its burrow which led him to conclude that the mud was not used for burrow-filling. Hence, he inferred that the crabs could have fed on the mud clods while inside the burrow, although there were no direct observations of food extraction from the clods provided as evidence in his report. *Pilumnus vespertilio*, a xanthid that lives in the crevices of hard dead coralline substratum, was described by Kyomo (1999) to carry food items such as brittle stars (or parts that were snipped off from the live echinoderm), slugs, gastropods and bivalves into its refuge as the ambient temperature dropped towards the end of its daily feeding cycle.

Kim (2010) was the first to provide quantitative evidence that food hoarding behavior in an intertidal crustacean is influenced by the availability of food resources and semilunar intertidal rhythms. He documented—through a food supplementation field experiment—that female white-clawed fiddler crabs, *Austruca lactea* (as *Uca lactea*), tended to store food-

enriched sediment in their burrows, especially during spring tides when they were most reproductively active. In another population of *A. lactea* from a muddy shore in Korea (see Kim and Choe 2003), these behaviors were not commonly observed, which led Kim (2010) to suggest that food hoarding behavior in this species was related to the scarcity of food in the habitat. Recently, Yong and Lim (2021) compared the food hoarding behavior of two populations of the painted ghost crab, *Ocypode gaudichaudii*, one from Playa Venao (a resource-impooverished sandy flat) and another from Culebra Beach (a resource-rich sandy beach) in Panama, when presented with small and large food pellets at the beginning and end of a daily feeding cycle. Their results indicated that the size of the food items, resource level of the habitat and time when the provision of the supplemented food occurred with respect to the feeding cycle influenced the hoarding behavior of the ghost crabs. Hence, there is evidence that handling time, and environmental factors such as resource-level of the habitat as well as limited time to forage due to incoming tides, affect hoarding behavior in an intertidal semiterrestrial crab.

In mainland Singapore, two sympatric populations of fiddler crabs, *Austruca annulipes* and *Gelasimus vocans*, live in the upper region of a mangrove at Pasir Ris Park. Although it is well-documented that *A. annulipes* usually occurs in sandy habitats and *G. vocans* tends to live in muddier ones (e.g., see Crane 1975; Lim et al. 2005), this mixed community of the two species seem to thrive well in the sandy-muddy part of the mangrove. The resource level of this portion of the mangrove is not considered to be impoverished (cf. sandy sediments) nor extremely rich (cf. muddy sediments); hence, this mixed community provides an opportunity to compare the hoarding behavior (if present) of the two species living in an area of similar resource level.

In this study, we provided supplemented food at the beginning of the feeding cycle and monitored the presence/absence of hoarding of these food particles from the enriched patch at hourly intervals to test the effect that time in the feeding cycle had on hoarding strategy (if any) for both sexes of the two species. It should be noted that *A. annulipes* is regarded as a sister species of *A. lactea* and thus, we predicted that this species was more likely to demonstrate hoarding behavior. In contrast, *G. vocans* has been reported to exhibit droving behavior (see Nakasone 1982), albeit rarely seen on Singapore shores (see Lim and Wong 2010). We, therefore, predicted that *G. vocans* is less likely to store food as hoarding behavior is interrelated to burrow use (see White and Geluso 2012). In addition, if indeed one or both species hoarded food, we would

expect the behavior to be more prevalent towards the end of the feeding cycle as the incoming tide would curtail all further foraging activities.

MATERIALS AND METHODS

Study site and habitat resource level

This study was conducted at Pasir Ris Park (1°22'53.8"N, 103°57'16.5"E) on mainland Singapore island between August 2019 and March 2021 when tidal heights were below 2.0 m, whereby the regions of the shore where the fiddler crabs live were adequately exposed, inclusive of both spring and neap tides. It is pertinent to note that the study was interrupted by park closure due to the pandemic lockdown in 2020. At this field site, two species of fiddler crabs, *Austruca annulipes* and *Gelasimus vocans*, form a mixed community whereby individuals of each species live near one another at the same sandy-muddy habitat among mangrove roots. This area of the mangrove is considered an 'intermediate-resource' habitat as the mean chlorophyll a content (a proxy for organic carbon content) in the sediment was significantly higher than that of an adjacent sand patch where no crabs lived ($t = 7.70$, $d.f. = 9$, $p < 0.05$; $16.87 \pm 1.73 \mu\text{g g}^{-1} > 3.29 \pm 0.36 \mu\text{g g}^{-1}$; mean $\pm$ S.E., respectively) (unpublished data for study period).

Activity budgets of *A. annulipes* and *G. vocans*

Eight males and eight females of each species were randomly selected and their activities were video-recorded using a hand-held video camera (Sony Handycam HDR-PJ675) for three hours from the time of first emergence. A duration of three hours was chosen as the fiddler crabs are usually active for about three hours after the tide recedes. No field observations were carried out on rainy days as the crabs did not emerge from their burrows. From the video recordings, the percentage time spent by each crab engaged in feeding activities, non-feeding related surface activities (e.g., walking, running, and social interactions such as waving, fighting, etc.) and burrow-sequestering activities were determined to construct the time activity budget within the first, second and third hour after emergence from their respective burrows.

We compared the overall activity budgets of the two species by constructing a Bray-Curtis similarity/dissimilarity matrix, followed by a similarity percentage (SIMPER) procedure to examine the contribution of each behavior to the similarity within each species and average dissimilarity between the species (see Baladrón

et al. 2016). Non-metric multidimensional scaling based on the Bray-Curtis similarity matrix was then applied to visualize the ordination distribution between *A. annulipes* and *G. vocans*. 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 species. The ordination plot was superimposed with the results of the cluster analysis at 80% similarity to determine trends of heterogeneity in crab behavior. A one-way analysis of similarities (ANOSIM) was performed to verify the behavioral heterogeneity between the species. All multivariate statistical analyses were carried out using the PRIMER software (PRIMER-E Ltd., Version 6.1.2, 2005; see Clarke and Gorley 2001).

The mean percentages of time spent on feeding were arcsine transformed, checked for equal variances using Bartlett's test, before two-way ANOVAs were used to test for effects of the factors—'sex' and 'time to end of feeding cycle'—within each species. If there was no significant interaction between the two main factors, additional ANOVA tests were used to test for significant differences between means for each main factor. Tukey's tests were conducted for multiple comparisons within a main factor that is significant.

Food supplementation experiment

The carapace width (CW) and corresponding burrow diameter (BD) of 20 males and 20 females of each crab species were measured, during two field sessions, using a pair of digital vernier calipers (Mitutoyo) to establish standard relationships between the two variables. Regression analyses were conducted separately for the two sexes as their respective CW range within the same species were different. The size of the fiddler crab occupant could be estimated without having to excavate the burrow to capture the inhabitant—which will disturb the population—thereby

affecting the food supplementation experiments. Strong relationships between CW and BD were demonstrated as the r^2 of the four linear regressions were ≈ 0.9 (Table 1); henceforth, the CW of the experimental crabs were extrapolated using these equations.

Food supplementation experiments were conducted on 80 *A. annulipes* and 60 *G. vocans* individuals. The diameter of each crab's burrow was measured using a pair of digital vernier calipers (Mitutoyo) to determine the size of its occupant (using the regressions in Table 1) before approximately 3.00 ± 0.02 g of crushed commercial crab food (Crab Cuisine, Hikari Tropical, Kyorin Co Ltd) was randomly seeded 5 cm from each crab's burrow. The observed crabs were: 40 male (CW_{range} = 8.80–15.83 mm) and 40 female (CW_{range} = 6.99–13.91 mm) individuals of *A. annulipes* and 30 male (CW_{range} = 12.43–22.85 mm) and 30 female (CW_{range} = 10.06–18.41 mm) individuals of *G. vocans*.

Different seeding areas were chosen each day, with each area demarcated based on landmarks such as large rocks and pneumatophores. Care was taken so that crabs of both species were tested on each experimental day, which thus removed the confounding factor of 'day'. All crabs were observed for three hours. During each observation, we recorded the number of fiddler crabs that transported the supplemented food into their burrows within each hour, the time of emergence and burrow-plugging time of each individual crab. The tidal conditions (*i.e.*, spring/neap tide) of the days during which food hoarding behavior was observed were noted, and a Chi-squared test was used to determine association between tidal conditions and the occurrence of food hoarding behavior. A Chi-squared contingency table was used to determine if the number of *A. annulipes* that food hoarded within the different hours of the feeding cycle was independent of the sex of the crabs. Another two Chi-squared tests for goodness-of-fit were conducted to test for difference in the frequency of hoarding behavior (1) between male and female *A. annulipes* and (2) among the three hours of the feeding duration. All ANOVA and Chi-squared statistical

Table 1. Regression equations for burrow diameter (BD) against carapace width (CW) of male and female crabs: a) *Austruca annulipes*; b) *Gelasimus vocans*

Species	<i>n</i>	Regression equation	r^2
a) <i>Austruca annulipes</i>			
Male	20	BD = 0.86CW + 0.79	0.938
Female	20	BD = 0.92CW + 0.04	0.967
b) <i>Gelasimus vocans</i>			
Male	20	BD = 1.07CW - 1.33	0.973
Female	20	BD = 1.03CW - 0.86	0.975

analyses were conducted using MINITAB (MINITAB 18, Inc., Release 2017).

RESULTS

Activity budgets of *A. annulipes* and *G. vocans*

The results of SIMPER indicated that there was minimal overlap in the overall activity budget of *A. annulipes* and *G. vocans* (Table 2, Fig. 1). Among the three behaviors, feeding contributed the most (48.60%) and sequestration in burrow the least (22.66%) to the difference in activity budgets of the two species. The nMDS plot superimposed with the Bray-Curtis cluster analysis using 80% similarity showed two distinct clusters for the activity budgets of all 32 crabs. The cluster on the left is comprised almost entirely of *G. vocans* (except for the presence of one individual of *A. annulipes*) while the one on the right has mainly

A. annulipes (15 cf. six *G. vocans* individuals) (Fig. 1). The results of the one-way ANOSIM showed a significant difference between the activity budgets of the two species (Global R = 0.36, $p < 0.05$), indicating behavioral heterogeneity between *A. annulipes* and *G. vocans* individuals. After this analysis was conducted, all analyses for behavior were conducted separately for each species.

Regardless of species, *A. annulipes* and *G. vocans* spent most of the time feeding when the tide was out with a small decrease, hour to hour, during the three-hour observation period (Fig. 2a and 2d). Non-feeding surface activities generally constituted approximately 20% of the activity budget, with a slight increase in activity with each passing hour. The time spent sequestered in the burrow did not vary considerably for *A. annulipes* individuals ($< 10\%$) whereas *G. vocans* spent an increasing duration of time (from $< 10\%$ in the first hour to ca. 20% in the third hour) in the burrow as time progressed. Male and female crabs of both

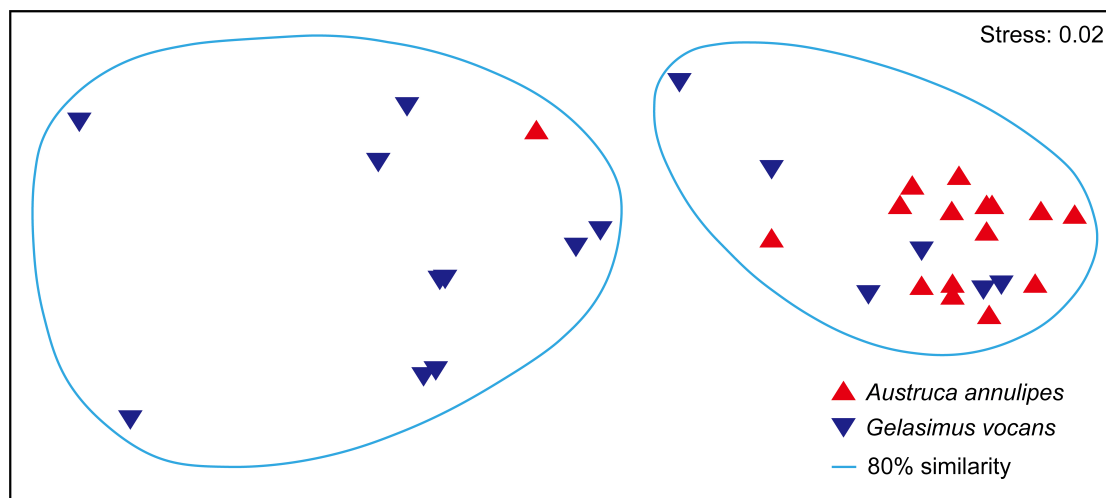


Fig. 1. Non-metric multidimensional scaling plot of the overall activity budget of *Austruca annulipes* and *Gelasimus vocans* superimposed with Bray-Curtis cluster analysis using 80% similarity. 2D stress = 0.02.

Table 2. Contribution of each behavior to the dissimilarities between the activity budgets of *Austruca annulipes* and *Gelasimus vocans*, according to SIMPER analysis. Behaviors were arranged in decreasing order according to their contribution to the average dissimilarity

Behavior	% Similarity (Average $\pm$ SD)		% Dissimilarity <i>A. annulipes</i> vs <i>G. vocans</i>	
	<i>A. annulipes</i>	<i>G. vocans</i>	Contribution	Cumulative
Feeding	77.39 $\pm$ 11.69	55.76 $\pm$ 5.51	48.60	48.60
Non-feeding surface activities	11.87 $\pm$ 5.87	18.55 $\pm$ 2.94	28.74	77.34
In burrow	4.03 $\pm$ 2.15	9.08 $\pm$ 1.99	22.66	100.00
Average similarity	93.29	83.38		
Average dissimilarity			18.73	

species exhibited the same pattern of feeding activities, *i.e.*, spending less time feeding from hour to hour. Instead, more time was spent on non-feeding surface activities (Fig. 2b and 2c; Fig. 2e and 2f). The time spent sequestered in the burrow remained constant for *A. annulipes* regardless of sex but increased in proportion from hour to hour for male and female *G. vocans*.

For both *A. annulipes* and *G. vocans*, the results of Bartlett's Tests indicated that variances were homogeneous after arcsine transformation of the percentage of time spent feeding (Test statistic = 3.96, $p > 0.05$; Test statistic = 0.61, $p > 0.05$, respectively). The interaction term of 'Sex $\times$ Observation period' was not significant in the results of the two-way ANOVA for the percentage of time spent feeding in both species of fiddler crabs (Table 3, a(i) and b(i)). Analyses of the main factors showed that, for both species, males and females did not differ significantly in the time devoted to feeding activities (Table 3, a (ii), a(iii), b(ii) and b(iii)). However, different trends were seen in *A. annulipes* and *G. vocans* for the duration of feeding time across the three hours of observation. In *A. annulipes*, the time

spent in the first hour was significantly greater than the second and third hours, with no difference between the latter two observation periods (Table 3, a(iii)). In contrast, the difference was only observed in *G. vocans* between the first and third hour, with no significant decrease between the first and second hour, nor between the second and the third (Table 3, b(iii)).

Food supplementation experiment

Food hoarding behavior was observed during all sessions whereby supplemented food was provided, and the behavior was independent of tidal conditions for 11 days ($\chi^2_{0.05,1} = 0.818$, $p > 0.05$). None of the *G. vocans* crabs exhibited food hoarding behavior throughout the three hours after emergence from their burrow (Fig. 3). In contrast, 42.5% of *A. annulipes* larger hoarded (Fig. 3). We observed that *A. annulipes* may exhibit food hoarding behavior more than once within each hour, *e.g.*, during one field session, one female carried the supplemented food six times from the same patch of crushed food pellets within the first hour before

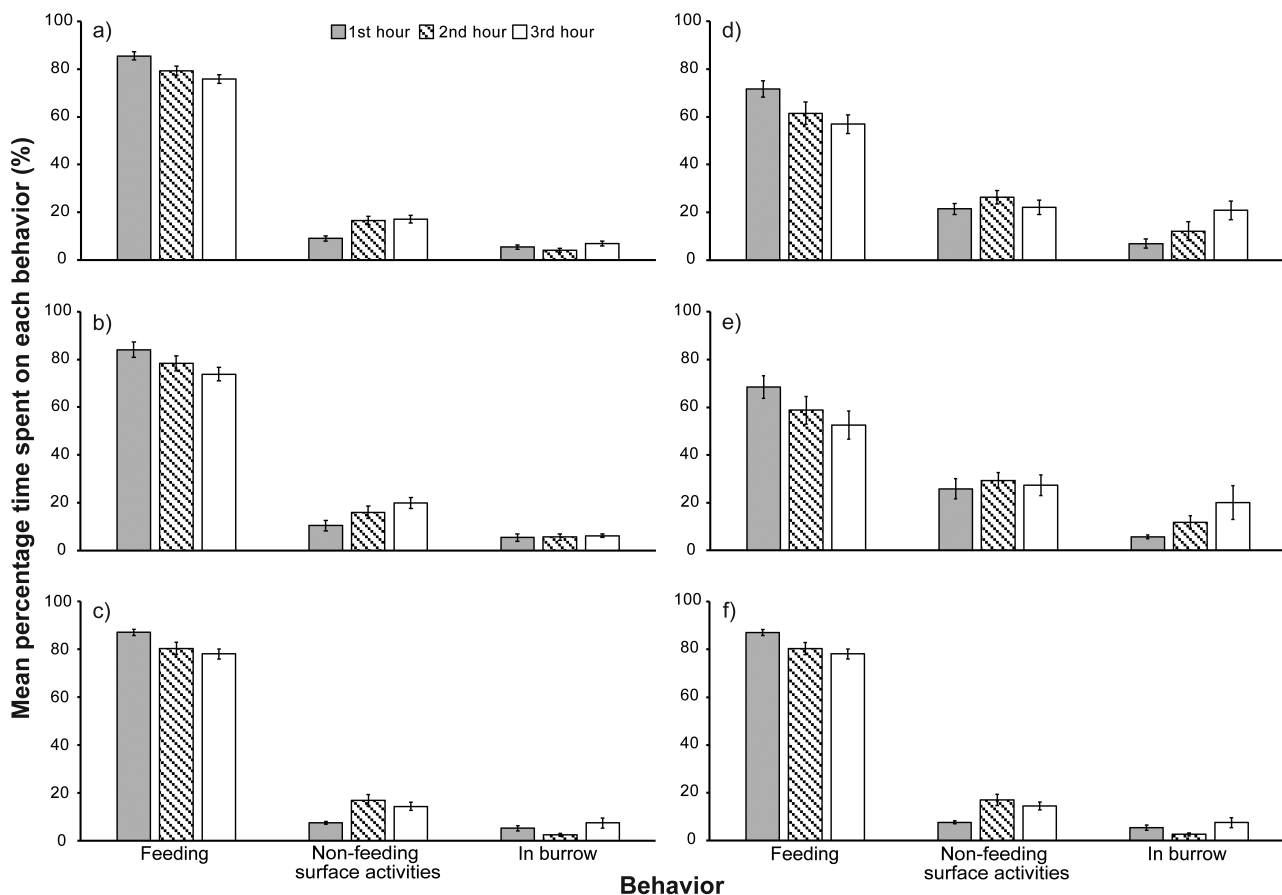


Fig. 2. Mean percentage time ($\pm$ S.E.) that *Austruca annulipes* (a–c) and *Gelasimus vocans* (d–f) were engaged in three behaviors after burrow emergence a, d: both sexes combined ($n = 16$ for each species); b, e: male crabs only; c, f: female crabs only.

plugging its burrow at the second hour. This female individual subsequently did not emerge from its burrow for the rest of the ebb tide duration. In one instance, the entire patch of supplemented food was carried by the crab, all at once, into the burrow (see Video S1).

Results from the Chi-squared contingency table analysis showed that frequencies of food hoarding in the three hours were independent of sex ($\chi^2_{0.05,2} = 0.035$, $p > 0.05$). The propensity to larder hoard did not differ significantly between the sexes ($\chi^2_{0.05,1} = 0.470$, $p > 0.05$), nor among the three time periods of the feeding duration

$$(\chi^2_{0.05,2} = 2.529, p > 0.05).$$

DISCUSSION

Although similar behaviors—feeding, non-feeding surface activities and sequestration in the burrow—were observed, the overall activity budgets differed between *A. annulipes* and *G. vocans* as evidenced by the two distinct clusters in the nMDS plot (Fig. 1), indicating that the proportion of time spent on each behavior

Table 3. Results of ANOVA analyses for arcsine transformed percentage time spent on feeding by a) *Austruca annulipes*, and b) *Gelasimus vocans*, factored across sex and time to end of foraging period (Obs period): i) full model; ii) reduced model; iii) main effects. sig.: significant; n.s.: not significant

a) <i>Austruca annulipes</i>						
Source of variation		df ₁ , df ₂	F	p	Tukey's test	
i)	Full model					
	Sex	1, 42	2.08	0.156		
	Obs period	2, 42	7.42	0.001		
	Sex × Obs period	2, 42	0.07	0.930	n.s.	
ii)	Reduced model					
	Sex	1, 44	2.18	0.147	n.s.	
	Obs period	2, 44	8.80	0.001	sig.	
iii)	Main effects					
	Sex	1, 46	1.62	0.209	n.s.	<u>Male ≈ Female</u> <u>67.06 ± 1.37 ≈ 69.14 ± 0.67%</u>
	Obs period	2, 45	8.57	0.001	sig.	<u>1st > 2nd ≈ 3rd</u> <u>68.10 ± 1.30 > 63.26 ± 1.28 ≈</u> <u>60.86 ± 1.19%</u>
b) <i>Gelasimus vocans</i>						
Source of variation		df ₁ , df ₂	F	p	Tukey's test	
i)	Full model					
	Sex	1, 42	3.02	0.090		
	Obs period	2, 42	4.61	0.016		
	Sex × Obs period	2, 42	0.06	0.944	n.s.	
ii)	Reduced model					
	Sex	1, 44	3.15	0.083	n.s.	
	Obs period	2, 44	4.82	0.013	sig.	
iii)	Main effects					
	Sex	1, 46	2.70	0.107	n.s.	<u>Male ≈ Female</u> <u>56.29 ± 1.74 ≈ 60.37 ± 1.51%</u>
	Obs period	2, 45	8.57	0.001	sig.	<u>1st ≈ 2nd ≈ 3rd</u> <u>58.32 ± 2.00 ≈ 51.97 ± 2.10 ≈</u> <u>49.25 ± 2.40%</u>

differed. As central place foragers that reside in burrows at the intertidal shore—with limited time during which to feed—it is not surprising that both species of fiddler crabs indulged in feeding activities for most of the ebb tide period, as compared to the other two behaviors (Fig. 2). Regardless of sex, crabs of both species generally spent less time on foraging, and more time engaged in non-feeding related activities at the sediment surface from hour to hour. This gradual change in routine is expected because when crabs become satiated after their initial feeding binge upon emergence, the time allocated for social activities will increase. The main difference in the activity pattern was contributed by the increase in time spent in the burrow by *G. vocans*, which is a more reclusive species (SSLL, DM personal observation) than *A. annulipes*. In a study on four species of fiddler crabs in Sulawesi, Indonesia, Weis and Weis (2004) reported similar decreases and increases in the proportion of time devoted to feeding activities and time in burrow respectively, in male and female *G. vocans* (as *U. vocans*) during ebb and flood tides, albeit their observations were based on 5-minute durations of focal sampling (cf. 3 hours in our study).

Our results from the food supplementation experiment showed that although both fiddler crab

species live sympatrically in the same mangrove area with similar levels of food resources, only *A. annulipes* larder hoarded. This suggests that the larder hoarding behavior in fiddler crabs is probably genetically governed and less likely to be influenced largely by environmental factors. Andersson and Krebs (1978) commented that for food hoarding behavior to be evolutionarily stable in group-living-populations whereby there may be high possibility of ‘cheaters’ consuming the food stored by others, the hoarder should have a higher probability of recovering its own cached items—this situation applies mainly to scatter hoarders. In the case of larder hoarders, since all the food is in one location, which is usually well-defended, the threat to successful retrieval of cached food is, thus, a moot point (see Pravosudov and Smulders 2010). Burrows of fiddler crabs are actively defended, hence, the chances of pilfering are low unless the burrow owner is evicted by another crab. It should be noted that *A. annulipes* lives in sandy habitats where resources are generally lower than that of the muddy habitats where *G. vocans* typically occur (see Crane 1975; Lim et al. 2005). Smulders (1998) stated that the food hoarding genotype would spread because, in times of food scarcity, hoarders would fare better than the average non-hoarder

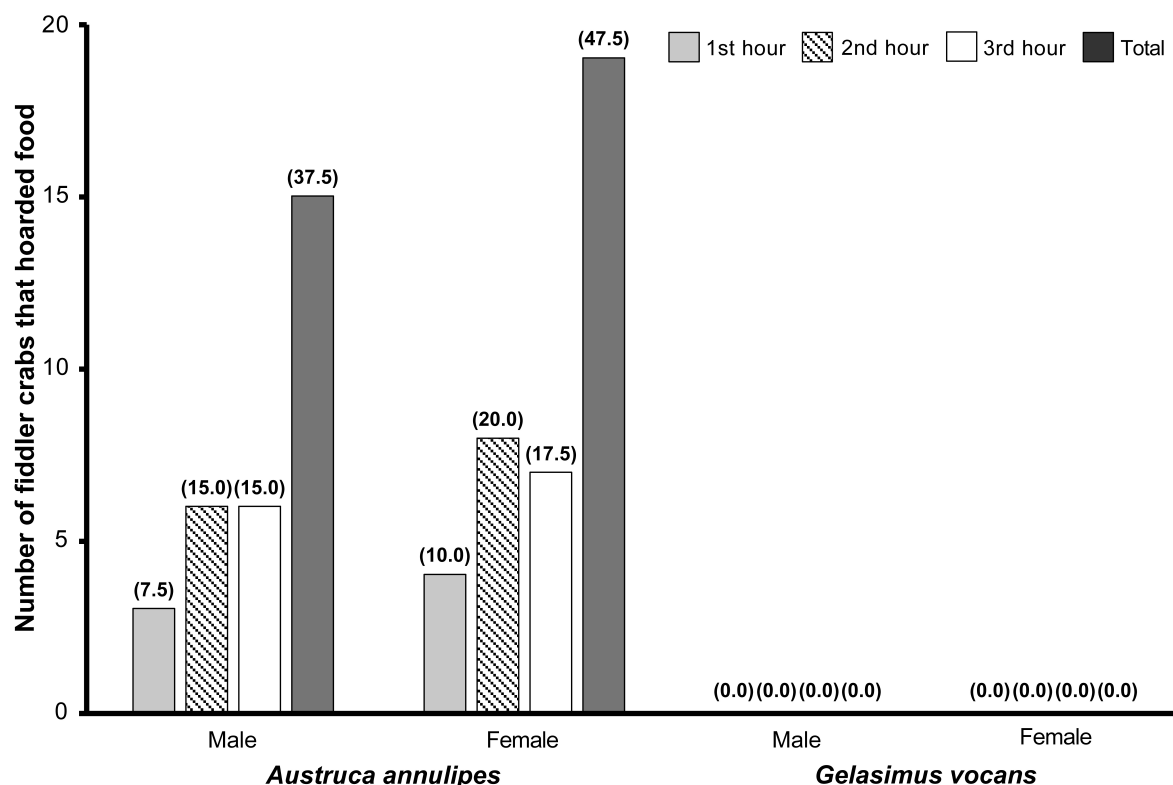


Fig. 3. Number of *Austruca annulipes* and *Gelasimus vocans* individuals that hoarded supplemented food during different periods of the feeding cycle (3 hours). For *A. annulipes*, $n = 80$ (40 males and 40 females) and *G. vocans*, $n = 60$ (30 males and 30 females). Percentages of crabs (out of the respective numbers of male, female crabs, and both sexes combined) are provided within parentheses above the respective bars.

in the population. Perhaps *A. annulipes* has been hardwired to store food to tide itself over during periods whereby food is less abundant. Thus, the establishment of a mixed evolutionarily stable strategy (ESS) for larder hoarding in *A. annulipes* is highly feasible.

While Kim (2010) reported that females' hoarding behavior varied with the semilunar tidal rhythms, and correlated this with the crabs' reproductive activity cycle, we did not detect any influence of spring/neap tides on the occurrence of larder hoarding during our experiment. In Singapore, recruitment of crabs can be observed during the entire year (SSLL, DM and CKWT personal observation) suggesting that there is no discrete reproductive season. Furthermore, our results showed that both male and female *A. annulipes* individuals larder hoard, with no preponderance of females exhibiting the behavior (Fig. 3).

It is pertinent to note that Kim's (2010) account of food hoarding in *A. lactea* was based mainly on observations of carrion feeding and storage of sediments that were repeatedly enriched with a solution of sardine flakes in water every other day. In our study, our criterion for larder hoarding was the carrying of the crushed food particulates from the discrete patches of supplemented food into the burrows (see Video S1). While occasional occurrences of surface sediment transportation were observed in both species, this behavior was not recorded as food storage because we wanted to determine if the crabs would hoard a richer energy source (supplemented food) despite living in a micro-habitat that is not resource impoverished. In other ocypodids, there are also some anecdotal accounts of opportunistic carrion transportation into burrows, e.g., *O. quadrata* and *O. kuhlii* (see Cowles 1908; Evans et al. 1976). However, the only other study that has documented hoarding of discrete food items (in the form of small and large food pellets) in a food supplementation experiment is Yong and Lim's (2021) work on the painted ghost crab, *Ocypode gaudichaudii*, at a resource-impoveryed beach (Playa Venao, PV) in Panama.

Yong and Lim (2021) tested the effects of the size of the food item and the point in time in the feeding cycle when the supplemented food was offered. Their results showed that regardless of when the small and large food pellets were offered, no hoarding behavior was seen at another sandy beach that was resource rich (Culebra Beach, CB) in Panama. In contrast, at PV, *O. gaudichaudii* hoarded large pellets at the beginning of the feeding cycle and hoarded both small and large pellets towards the end of the feeding cycle, indicating a distinct size selection in the hoarding strategy. In our study, *A. annulipes* individuals began hoarding the food particulates from the first hour of observation.

However, although the frequency of hoarding in the second and third hour of observation increased, it was not statistically significant to conclude that more hoarding was carried out at the end of the feeding cycle. Perhaps the probability of food scarcity in the mangrove habitat in which the fiddler crab lives is lower than that of the sandy shores where the ghost crab lives, such that the necessity to 'save for a rainy day' is not so dire. Nonetheless, larder hoarding is likely to be evolutionarily stable in this species as it stored food when a rich food resource was encountered even when there was no imminent threat of food shortage.

For *G. vocans*, it seemed that the mixed ESS adopted to overcome the possibility of shortage of food is to feed at the water's edge in droves. Hence, despite being presented with supplemented food, it did not switch to larder hoarding. We have observed that a small sub-population of this species living further down the shore—at a bare sandy patch that is not their typical habitat—drove on occasions of lowered food concentration in the sediment (CKWT, SSLL unpublished data). However, in our current study, individuals of this mangrove sub-population did not form droves to move down to the water's edge to feed at all during the study period, possibly due to the presence of sufficient resources at this microhabitat. Yong and Lim (2021) carried out a transplantation experiment to determine if the droving behavior of *O. gaudichaudii* was habitat dependent. When the crabs from the resource impoverished beach (i.e., PV) were transplanted to the new environment with high food resource levels (CB), instead of droving, they deposited around their burrows like their CB conspecifics. Perhaps, the sub-population of *G. vocans* at the mangrove region behaves like the *O. gaudichaudii* population that was transplanted to CB.

Quispe et al. (2009) conducted an inter-population study on the foraging behavior of degus, *Octodon degus*, from two geographically separated populations in Chile: high- versus low-altitude populations. Variations were observed between populations, with individuals from the low-altitude habitat exhibiting scatter hoarding exclusively whereas the high-altitude conspecifics conducted both larder hoarding and scatter hoarding. They concluded that larder hoarding is favored under harsher environmental conditions. Furthermore, the inter-population differences in larder hoarding were maintained despite six months of acclimation to a common environment, leading them to conclude that larder hoarding might be the result of local adaptation or an ontogenetically acquired irreversible behavior. Although the two sub-populations of *G. vocans* at Pasir Ris Park are not geographically distant, they, nonetheless represent two distinct congregations of the

species in ‘micro-habitats’ that differ in food resource availability. It would be interesting to conduct a similar food supplementation study at the sandy region where the droving *G. vocans* live to shed further light on the seemingly rigid feeding strategy adopted by this species in the mangrove area.

When ocypodid crabs such as fiddler crabs and ghost crabs drove, they abandon their burrows to move *en masse* to feed at the water’s edge (see Nakasone 1982; Murai et al. 1983; Yong and Lim 2021). After their feeding bouts at the resource-rich areas, they generally return upshore but do not actively seek their original burrows to ride out the period of high water. White and Geluso (2012) surmised that food hoarding and burrow use are interrelated based on the reason that if animals were to store their resources inside a burrow, then it behooves them to use that burrow consistently. The burrow fidelity of a droving species is expected to be shorter than that of a non-droving species. In fact, Lim and Wong (2010) provided evidence from both field and *ex situ* studies that *G. vocans* (as *U. vocans*) abandoned burrows more frequently than *A. annulipes* (as *U. annulipes*), albeit not daily. Hence, the trait for larder hoarding is probably not favored in natural selection in the droving species, coupled with more ephemeral burrows.

CONCLUSIONS

It is evident that larder hoarding is species specific in fiddler crabs, although these aquatic invertebrates are central place foragers, that can benefit greatly from adopting this strategy. Almost half of the *A. annulipes* individuals in the food supplementation experiment larder hoarded when they encountered a rich food resource, even though the habitat in which they lived was not impoverished. This suggests that the propensity to hoard could be a mixed ESS. In contrast, not even a single *G. vocans* hoarded when presented with the opportunity to hoard a rich food resource. Perhaps this could be linked to its inherent tendency to form droves to feed at the water’s edge when food resources are low, implying that droving behavior, rather than larder hoarding, is this species’ mixed ESS.

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DM; and wrote the paper. DM and CKWT collected the field data, conducted the laboratory/video analyses as well as the some of the data analyses. All authors read and approved the final manuscript.

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Supplementary materials

Video S1. (download)