Changes in spatial behaviour patterns by mangrove tree crabs following climate-induced range shift into novel habitat

Zachary J. Cannizzo ^{a, *}, Blaine D. Griffen ^{a, b}

^a *Marine Science Program, University of South Carolina, Columbia, SC, U.S.A.*

^b *Department of Biological Sciences, University of South Carolina, Columbia, SC, U.S.A.*

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* Correspondence: Z. J. Cannizzo, Marine Science Program, University of South Carolina, Columbia, SC 29208, U.S.A.

E-mail address: cannizzz@email.sc.edu

Climate-mediated range shifts into eco-evolutionary novel habitats have the potential to alter the ecology and behaviour of range-expanding species. Of particular concern are behaviours that have a strong impact on the ecology and life history of expanding species. Behaviours that control the spatial patterns of habitat use may be particularly important. We examined site fidelity and foraging foray behaviour of the mangrove tree crab, *Aratus pisonii*, in its historic mangrove habitat and the recently colonized eco-evolutionary novel salt marsh. In the mangrove, *A. pisonii* showed both strong site fidelity to individual trees and a foraging pattern wherein they made foraging forays that decreased in frequency as their distance from the home tree increased; but they displayed neither behaviour in the salt marsh.”. Chemical cues from faeces appear to be the mechanism behind site fidelity in the mangrove and may suggest the mechanism for the loss of this behaviour in the salt marsh where substrate is regularly submerged, potentially preventing establishment of such cues. The loss of site fidelity may affect the foraging behaviour and predation risk of *A. pisonii* in the salt marsh, leading to a shift in its ecology and bioenergetics. As more species are forced to shift ranges into eco-evolutionary novel habitats, it is important to understand how this shift may affect their life history, behaviour and ecology in indirect ways.

Keywords:

Aratus pisonii

climate change

novel ecosystem

philopatry

range shift

site fidelity

As the global climate continues to change, species are expanding or shifting their ranges in response, which is often associated with an accompanying shift in ecosystem foundation species (Walther, 2010). However, differences in temporal and spatial responses to climate change can lead to a species outpacing its foundation species and entering an eco-evolutionary novel ecosystem (Schweiger, Settle, & Kudrna, 2008; Walther, 2010). Eco-evolutionary novel ecosystems often differ greatly in structure and in foundation species from the historic habitat of a range-shifting species. This results in the exposure of range-shifting species to biological and environmental interactions that differ from their historic ecosystem (i.e. novel interactions). These novel interactions have the potential to alter the ecology of both the shifting species and the ecosystem that it has colonized. Similar alterations of ecology have been demonstrated in biological invasions (Gallardo, Clavero, Sánchez, & Vilá, 2016), which parallel climate-induced range shifts in the production of novel interactions. However, the invasion literature focuses mainly on the effects of the invasion on the ecosystem being invaded. This focus is a result of invading species being seen as unnatural because they are often introduced through human intervention. In contrast, in a climate-induced range shift the colonizing species is entering a novel ecosystem without direct human aid. Unlike in the invasion literature, these species are often native species forced or encouraged to shift ranges due to climate change. Thus, the effects of the move into a novel ecosystem upon the range-expanding species itself is of concern. Climate-induced colonization of novel habitats is expected to increase as climate change continues (Lenoir & Svenning, 2015) and is likely to alter the ecology of both the shifting species and the colonized ecosystem.

A shift by a species into a novel ecosystem may alter its behaviour. Aspects of behaviour such as foraging, behavioural syndromes and niche construction can alter both the fitness of a species and the ecosystem that it inhabits (Jones, Lawton, & Shachak, 1994; Naiman, 1988; Sih, Cote, Evans, Fogarty, & Pruitt, 2012). Behaviours that affect how a species interacts with its

environment may be especially important to range-shifting species as they colonize novel ecosystems. There are often several interacting behaviours that determine how species interact spatially with their environment, including site fidelity and exploratory/foraging behaviour (Evans & Williams, 1991). Thus, it is important to understand how these behaviours change in novel ecosystems. Site fidelity is of particular importance as it may govern how a species interacts spatially with its environment by providing an area where an individual spends a large portion of its time and returns after exploratory/foraging forays.

Site fidelity, or philopatry, is the behaviour of staying at or repeatedly returning to the same area. It is seen as fidelity to breeding sites (Bollinger & Gavin, 1989; Pomeroy Anderson, Twiss, & McConnell, 1994; Refsnider, Daugherty, Keall, & Nelson, 2009) and natal sites to breed (Berven & Grudzien, 1990) and to foraging areas (Cannicci, Ruwa, Ritossa, & Vannini, 1996; Driggers et al., 2014) and home areas such as dens (Sebastian, Steffani, & Branch, 2002; Yoshimura & Yamakawa, 1988). In addition, site fidelity influences how an organism interacts with its environment through alterations of other behaviours such as foraging (Evans & Williams, 1991). Site fidelity is observed in a wide diversity of animal taxa including insects (Ackerman, Beckers, Deneubourg, & Pasteels, 1982; Fresneau, 1985), molluscs (Sebastian et al., 2002), crustaceans (Cannicci et al., 1996; Stone & O'Clair, 2002; Yoshimura & Yamakawa, 1988), amphibians (Bell, 1977; Berven & Grudzien, 1990), reptiles (Refsnider, Daugherty, Keall, & Nelson, 2009; Refsnider, Strickland, & Janzen 2012), fishes (Driggers et al., 2014; Marnane, 2000), birds (Sedgwick, 2004; Warkentin & Hernández, 1996) and mammals (Hillen, Kiefer, & Veith, 2009; Lowther, Harcourt, Goldsworthy, & Stow, 2012). Colonization of a novel habitat has the potential to alter site fidelity. If a species' site fidelity is associated with particular structures, then its site fidelity is especially likely to be affected by colonizing a habitat that differs from its historic habitat in structural make-up and foundation species. Site fidelity is often associated with important ecological and life history events, such as breeding and foraging

(Bollinger & Gavin, 1989; Cannicci et al., 1996; Driggers et al., 2014; Pomeroy et al., 1994).

Thus, disturbances or changes in site fidelity behaviour may have unexpected consequences for a population or species.

Here, we examined site fidelity in the arboreal mangrove tree crab, *Aratus pisonii* (Decapoda: Sesarmidae), following its shift into a novel ecosystem in response to climate change. Historically *A. pisonii* was a Neotropical mangrove-associated species (Beever, Simberloff, & King, 1979; Rathbun, 1918; Warner, 1967). However, the climate-driven northward range expansion of *A. pisonii* has recently outpaced that of its historic foundation species, the red mangrove, *Rhizophora mangle*, resulting in an expansion into the evolutionary novel habitat of the salt marshes of the southern Atlantic coast of the United States (Riley, Johnston, Feller, & Griffen, 2014a). *Aratus pisonii* is the dominant herbivore of the red mangrove (Feller & Chamberlain, 2007) and its ecology and behaviour are closely tied to these trees (Beever et al., 1979; Warner, 1967), which are absent in the salt marsh. A sesarmid mangrove crab with a similar ecology to *A. pisonii*, the African mangrove tree crab, *Sesarma leprozoma*, has been shown to display site fidelity to foraging trees (Cannicci et al., 1996). Given the similarities between these two species, we anticipated that *A. pisonii* would also show site fidelity to individual trees in its historic mangrove habitat. However, as these trees are absent in the salt marsh, we anticipated that any site fidelity shown by *A. pisonii* in the mangrove might break down in the salt marsh.

To fully understand how climate change and range shifts affect site fidelity, it is necessary to examine the mechanisms behind this behaviour. The mechanisms behind site fidelity often vary widely among species and include visual (Fresneau, 1985) and chemical or olfactory cues (Døving, Stabell, Östlund-Nilsson, & Fischer, 2006). Chemical cues are often implicated and have been hypothesized to be important in the site fidelity and homing behaviours

of many aquatic species including sea turtles (Grassman, Owens, McVey, & Marquez, 1984), reef fishes (Døving et al., 2006) and spiny lobsters (Ratchford & Eggleston, 1998). Chemical cues have also been implicated in the communication and site fidelity of many terrestrial arthropod species, most notably ants (Greene & Gordon, 2007; Salo & Rosengren, 2001). Based on observations that faeces are abundant on the branches, trunks and prop roots of mangrove trees in areas where *A. pisonii* is found, it is possible that if *A. pisonii* shows site fidelity, it may use chemical cues from its faeces to distinguish one area from another.

Site fidelity often interacts with exploratory/foraging behaviour to affect foraging distribution (Evans & Williams, 1991). The foraging distribution of an important herbivore such as *A. pisonii* is likely to have implications for the ecosystem that it inhabits. Species that display site fidelity are likely to forage more efficiently within a habitat than are coincident species that do not display philopatry (Benhamou, 1989). This may occur if an individual has information about the distribution of food near its home site or in its home range (Benhamou, 1989). Individuals can decrease foraging time by showing site fidelity to areas near high-quality foraging sites. Yet, this still may not eliminate the periodic need for long forays to explore for higher-quality foraging areas. Thus, we might expect to see forays from the home site of varying distances, with long forays being less likely than short forays (Adams, Takekawa, & Carter, 2004; Aguilera & Navarrete, 2011; Coleman, Richmond, Rudstam, & Mattison, 2005). Such a species would also be expected to return to its place of origin, its home site, after each foray.

Despite the possibility of fidelity to individual mangrove trees in its historic habitat, individual *A. pisonii* in the salt marsh find themselves in a habitat devoid of mangroves. The salt marsh is instead dominated by the grass *Spartina alterniflora*, which differs greatly in structure from the red mangrove. Differences between the habitats also may negate or confuse any chemical cues used to identify “home sites”. We therefore anticipated that even if *A. pisonii*

shows site fidelity in the mangrove habitat, it might show no site fidelity in the salt marsh habitat (i.e. be incapable of doing so), or it might alter its site fidelity behaviour in the salt marsh. A change in site fidelity behaviour would necessarily alter how *A. pisonii* interacts with its environment and result in differing ecological patterns and interactions from its historic habitat. Thus, in this study, we sought to explore site fidelity behaviour of *A. pisonii*, and its mechanisms, in both the historic mangrove and the novel salt marsh ecosystems. We predicted that *A. pisonii* would show site fidelity to individual mangrove trees in mangrove habitat, use its own faeces as a cue to maintain site fidelity and make fewer long-distance foraging trips away from home sites. We further predicted that *A. pisonii* would not show site fidelity in salt marsh habitat.

METHODS

Ethical Note

This research met all animal care guidelines of the supporting institutions and conformed to the legal requirements of the United States of America and the state of Florida. Permits and licenses for this study were granted by the Florida Department of Environmental Protection, the Florida Fish and Wildlife Conservation Commission and the Guana Tolomato Matanzas National Estuarine Research Reserve (GTM).

Site Description

Aratus pisonii were observed at five mangrove forest sites in and around Fort Pierce, Florida, and two salt marsh sites in and around St Augustine, Florida, between May and August of 2015 (Table 1). The mangrove sites represent habitat within the historic range of *A. pisonii* while the salt marsh sites represent recently colonized novel habitats (Riley et al., 2014a).

Collection

At each mangrove site, we haphazardly captured five *A. pisonii* by hand and marked the tree from which they were captured with flagging tape. We measured (to the nearest 0.1 mm) and determined sex of all individuals and painted the dorsal carapace of each crab with one of five colours of nail polish to aid in identification. Following a short period of observation to ensure normal behaviour, we released all five crabs onto one tree within 10 m of all collection trees but different from any of the trees on which they had been captured. We did this to avoid biasing the interpretation of an individual's site fidelity as it was impossible to know whether an individual was captured on the tree to which it showed fidelity or while on a foraging foray. We collected 35 individual *A. pisonii* from the mangrove and observed their behaviour over seven observational periods (Table 1).

We used the same methodology for capture of crabs in the salt marsh with some slight modifications due to the difference in habitat. We collected five individual *A. pisonii* and marked the *S. alterniflora* stalk nearest to the collection site with flagging tape. We recorded the sex and size of each crab and painted the dorsal carapace of each crab with one of five colours of nail

polish. After a short observational period, we released the crabs onto separate *S. alterniflora* stalks within 10 m of the collection area. This was done during a rising tide, so that crabs had no access to the sediment, and thus, could not immediately retreat into holes. Due to differences in the behaviour of crabs in the salt marsh as compared to the mangrove, this collection and release was repeated each day with different crabs in order to increase observation sample size. During one observational day at Anastasia State Park, nine crabs were captured because of the rapid loss of many of the original five. Additionally, on one of the days at GTM, only three crabs were captured because of the difficulty in locating individuals before the tide rose. Due to these anomalous days, we collected a total of 67 individual *A. pisonii* from the salt marsh (Table 1).

Site Fidelity

Each site was observed for a minimum of 3 days (Table 1). Each day, crabs were observed from the time they no longer had access to the sediment until the receding tide once again allowed access to the sediment (~6 h depending on site and day). The timing of this observation assured that crabs were not simply hiding in holes or burrows in the sediment as *A. pisonii* climbs out of the water onto nearby structures to avoid aquatic predators. We recorded the location of each crab each day. A crab that was seen to spend the majority of its time on a given tree or area of salt marsh over two or more consecutive days was considered to display fidelity to that tree or area. These were referred to as the “home tree” and “home area” of the crab, respectively. In the salt marsh, the home area was a 1 m radius area around the *S. alterniflora* stalk where the individual was observed to spend the majority of its time. This represents an area roughly equal to the basal prop root area of a red mangrove. We also recorded the number of consecutive days an individual was observed to spend the majority of its time on

its home tree/area. No crab was seen to display fidelity to more than one tree or area over the duration of the study.

Most sites were visited numerous times with intervening periods of no observation. When an individual continued to show fidelity to its previously established home tree/area after such an intervening period, that crab was considered to have displayed fidelity to that tree/area during the intervening time. This period of time was recorded as the number of days a crab used a home tree/area as opposed to the number of days observed. These distinctions were treated as separate variables in analysis. The number of days that each crab was seen on its home tree/area (response variable) was compared to the number of days each crab was sought (time spent at the site of that crab, predictor variable) using a generalized linear model with a negative binomial error distribution. Separate models were run for each habitat. The use of a negative binomial error distribution corrected for overdispersion. While there was still slight overdispersion in the mangrove model (residual deviation = 44.2, $df = 33$), this error distribution minimized overdispersion. In this analysis, we explored whether any difference in site fidelity between habitats or sites was a statistical artefact resulting from differential effort (days sought).

We explored site fidelity of *A. pisonii* in each habitat type by constructing Kaplan–Meyer survivorship curves using days on the home tree/area instead of survival. The measure of site fidelity is analogous to survival as crabs lose fidelity to their home tree/area at different times over the course of the study much like individuals in a sample population die at different times throughout a survivorship study. Crabs that had not ceased fidelity by the end of the observational period were right-censored in the analysis (Harrington, 2005; Klein & Moeschberger, 2005). This corrected for the fact that crabs may have continued to show fidelity after the observational period ended. Owing to the use of right censoring, we compared site

fidelity from the mangrove and salt marsh habitats using a log-rank test (Mantel, 1966) (often referred to as a Mantel–Cox or Mantel–Haenszel test) (Harrington, 2005).

Exploration of the Site Fidelity Mechanism

To test the ability of *A. pisonii* to detect its own faeces as a mechanism facilitating site fidelity, we collected 10 individual *A. pisonii* from the representative mangrove site Round Island (Table 1). These individuals were kept for 1 week in individual plastic aquaria ($22.8 \times 15.2 \times 16.5$ cm, l $\times$ w $\times$ h) containing a finger bowl of unfiltered sea water. During this time, crabs were given fresh *R. mangle* leaves and had their water changed every other day. At the end of the week, we collected the faeces from each crab.

On the seventh day of the experiment, we collected terminal mangrove branches (~50 cm long, ~1 cm in diameter), with little or no *A. pisonii* faeces, from a representative mangrove site (Pepper Park, Table 1) that differed from site where the crabs were collected, thus ensuring that none of the experimental crabs had prior association with the branches used for experimentation. The branches were always cut below the first leaf, then cleaned of all faeces with salt water and allowed to dry.

We then placed each crab in a 5-gallon (18.9-litre) bucket with two mangrove branches of similar length and diameter. One branch was kept clean and the bottom 10 cm of the other was covered in the faeces of that crab. To avoid contamination, we always handled faeces with entomological forceps and cleaned the forceps after each use with 95% ethyl alcohol. The two branches were placed crossing and leaning on the inside of the bucket (Fig. 1). The crab was then placed in the bottom of the bucket between the two branches. We recorded which branch each

crab chose to climb and then returned the crab to its aquarium. If the crab had not chosen a branch after 15 min, we added a small amount of unfiltered salt water to the bucket to encourage the crab to choose. We then haphazardly changed the position of the branches in the bucket to control for biases in crab choice due to external factors, and we repeated the experiment with the same crab. We performed three trials on each of the 10 crabs in this way. In all but one trial the crab quickly chose a branch when water was added. The trial in which the crab did not choose either branch was dropped from the analysis. In between each crab, we rinsed and dried the bucket to avoid cross-contamination.

To examine the effect of the faeces of another *A. pisonii* on the site fidelity mechanism of individuals, we again collected 10 additional *A. pisonii* from Round Island. We used the same methodology as above except that instead of a clean branch, the crab had the choice between a branch with the faeces of another individual or their own faeces. As before, three trials were run for each individual. Two individuals did not choose a branch during one of their trials and these trials were dropped from the analysis.

We used a generalized linear random effects model with a binomial error distribution to test whether the crabs' choice of branch (with own faeces versus clean, and with own faeces versus other crab's faeces) differed significantly from random (Agresti, 2002). We ran separate models for each experiment. For both experiments, the model was run with choice as the response variable and individual crab as the random effect to account for repeated measures. We then used a linear probability model to determine the likelihood of an individual choosing the branch with faeces as opposed to a clean branch. We did this by applying an antilogit function ($\frac{1}{1+e^{-\text{intercept}}}$) to the intercept of the model, which acts to backtransform the intercept and gives the probability of one outcome occurring instead of the other (Agresti, 2002). Thus, this methodology allows for the determination of the likelihood that a crab will choose one branch

over the other. We also ran this linear probability model for the second experiment to determine the likelihood of an individual choosing the branch with its own faeces as opposed to a branch with faeces of another individual.

Foraging Forays

If an individual from the site fidelity study described above displayed site fidelity, we noted forays away from the home tree or area. We recorded the regularity of forays and measured the distance from the home tree or area. The distance of a foray was determined with a measuring tape in a direct line from the trunk of the home tree to the end location of the foray. While crabs must travel along roots and branches and thus do not travel in a straight line, this was done to normalize methodology as the exact path of crabs that travelled through the canopy was either not known or unreachable. This methodology results in the measured distance being shorter than the distance a crab actually travelled. Therefore, the foray distances presented reflect conservative estimates. The proportion of days that an individual was observed to undertake a foray was then compared to the distance of that foray. Visual observation of the data suggested that the number of forays decreased exponentially with distance from the home site. Thus, we fitted the relationship to an exponential decay using a nonlinear least squares regression.

RESULTS

Site Fidelity

Aratus pisonii displayed greater site fidelity in the historic mangrove habitat (77.14% of individuals) than in the novel salt marsh habitat (8.95% of individuals) (log-rank test: $\chi^2_1 = 20.8$, $P < 0.001$; Fig. 2). This low fidelity in the salt marsh led to the necessity of collecting five new crabs each day of observation, as outlined in the Methods. In addition, many individuals in the mangrove showed fidelity throughout the observational period, with one crab displaying fidelity on at least 88 days. In contrast, most individuals in the salt marsh were unlikely to be seen again, either in the designated area where the crab was released, or in the surrounding marsh more broadly. Those individuals that showed fidelity throughout the observational period were right-censored in the analysis (Fig. 2b, d).

The longer a crab was sought in the mangrove, the longer it was likely to be seen on its home tree (GLM: $z_{33} = 0.03743$, $P < 0.001$; Fig. 2b). In the salt marsh, individuals were unlikely to be seen again regardless of search effort (GLM: $z_{65} = 0.837$, $P = 0.427$; Fig. 2d). This suggests that the difference in site fidelity behaviour between the mangrove and salt marsh was not simply a statistical artefact due to differences in the observational periods and sample sizes of the two habitats. In fact, the sample size in the salt marsh was almost twice that in the mangrove and the 1 m radius of the home area of the salt marsh was larger than the basal area of many mangroves chosen as home trees; both of these factors would make it more likely to find site fidelity in the salt marsh.

Site Fidelity Mechanism

When given the choice between a clean branch and a branch with their own faeces, individual *A. pisonii* showed an 88.96% likelihood of choosing the branch with their own faeces (GLMM: $z_{28} = 2.202$, $P = 0.0277$). Comparatively, when given the choice between a branch with their own faeces and one with faeces from another individual, individual *A. pisonii* showed an 80.53% likelihood of choosing the branch with their own faeces (GLMM: $z_{26} = 1.901$, $P = 0.0573$).

Foraging Forays

Given the overall lack of site fidelity behaviour in the salt marsh, we only explored foraging forays in the mangrove. Two of the 28 individuals that were observed to show site fidelity behaviour were dropped from the foraging foray analysis because of uncertainty in the distance travelled during forays, leaving 26 individuals with known foray distance. Despite spending the majority of their time on their home tree, 80.7% of individuals went on forays at some point during the observational period and 73.1% went on forays daily (Fig. 3a).

The regularity of a foray (proportion of days undertaken) was related to foray distance via the exponential decay equation

$$\text{Proportion} = Ce^{-k \times \text{distance}}$$

where $C = 1.020 \pm 0.051$ (nonlinear least squares regression: $t_{27} = 19.864$, $P < 0.001$) and $k = 0.053 \pm 0.188$ (nonlinear least squares regression: $t_{27} = 2.833$, $P < 0.01$) (Fig. 3a). In addition, as

foray distance increased, the number of crabs observed taking such forays decreased (Fig. 3b). Note, our measure of foray distance does not reflect the total distance travelled by each crab (because we measured straight-line distances as opposed to actual paths taken by the crabs; see Methods). In addition, crabs are more likely to travel nonlinearly as foray distance increases. Therefore, the distance measured, using our methodology, was biased towards being progressively shorter than the actual distance travelled as foray distance increased. The removal of this bias would progressively increase the distance of the longest forays (longer distances become even longer), making the reported results a conservative estimate. Together, these results support the conclusion that individual *A. pisonii* usually make short-distance foraging forays and seldom make long-distance foraging forays away from their home trees within mangrove habitat.

DISCUSSION

We have shown that in its native mangrove habitat, *A. pisonii* displays both site fidelity to a home tree and a foraging pattern that may be expected from a philopatric species. However, site fidelity behaviour of *A. pisonii* does not appear to be retained in the novel salt marsh habitat. As site fidelity is often associated with important ecological and life history events such as breeding (Bollinger & Gavin, 1989; Pomeroy et al., 1994) and foraging (Cannicci et al., 1996; Driggers et al., 2014), the loss of this behaviour represents a potential shift in the ecology of *A. pisonii*.

Cues from faeces appear to play some role in the site fidelity behaviour of *A. pisonii* in the mangrove. This result may also suggest the mechanism behind the loss of this behaviour in the salt marsh. Despite the large amount of time *A. pisonii* spent on marsh grasses, little faeces were observed on marsh grass stalks. This could be due to submergence of grass stalks at each

high tide. Submergence likely cleans any faeces from the grasses, preventing cues used by *A. pisonii* from developing. In contrast, in the mangrove, many trees are connected by prop roots and branches, parts of which always remain out of the water, and could thus maintain a cue or cue trail throughout the tidal cycle. As the observation period took place during inundation, the observed foraging pathways were maintained on areas of branches and prop roots that remained unsubmerged. Such out-of-water connectivity is drastically reduced in the salt marsh. Individual *A. pisonii* often entered the water to travel between grass stalks. This lack of connectivity during inundation likely prevents the development of any cue trails in the salt marsh. Thus, it is possible that the loss of site fidelity in the salt marsh is a result of an inability for individuals to establish the cues that aid in this behaviour.

The same chemical cues that facilitate site fidelity may also lead to the observed fidelity in daily foraging paths. Chemical cues would allow the establishment of trails to known high-quality food sources as seen in a number of ant species (Aaron, Beckers, Deneuborg, & Pasteels, 1993; Greene & Gordon, 2007) and may suggest route-based navigation, where information on location is generated while in route (Etienne, 1987). The potential display of route-based navigation is additionally supported by the result that 18 of the 19 individuals that went on daily forays were observed to always travel to the same place and almost always followed the same path. The 19th individual also travelled to the same area daily but, in addition to its normal foray, it undertook the longest foray recorded (23 m) on one of the days it was observed. This suggests that individual *A. pisonii* show fidelity to foraging areas and to the paths they take to these foraging areas.

The observed forays also showed a distinct decline in frequency as distance from the home tree increased (i.e. crabs made short forays more often than long forays; Fig. 3). Fidelity to a particular tree with nearby high-quality resources would be beneficial and likely result in such

a foraging pattern. This conclusion is further supported by the observation that some individuals that made forays fed at the end of the foray. One individual in particular took the same path daily to visit a wooden board trapped in the roots of a mangrove neighbouring its home tree. The board was submerged during high tide, but as the tide receded, this individual would leave its home tree and travel to the board where, along with a number of other *A. pisonii*, it would feed. As evidenced by the common use of fouling plates to study mangrove epibenthic communities (Bingham, 1992; Bingham & Young, 1995; Sutherland, 1980), organisms grow on any hard substrate in the mangrove habitat. These substrates support a diverse fouling community of flora and fauna, including sponges, bivalves, bryozoans, ascidians and arthropods (Bingham, 1992; Bingham & Young, 1995; Kathiresan & Bingham, 2001). *Aratus pisonii* is known to feed on such fouling organisms (Díaz & Conde, 1988), and the wooden board to which one of our marked *A. pisonii* travelled daily had a number of these organisms upon it. Additionally, animal protein is an important dietary supplement for *A. pisonii* (Riley, Vogel, & Griffen, 2014b) and, when given a choice, *A. pisonii* preferentially feeds on animal material (Erickson, Feller, Paul, Kwiatowski, & Lee, 2008). Thus, the wooden board likely provided easy access to a high-quality food source. Maintaining fidelity to a tree near such a high-quality foraging area would be energetically beneficial, allowing the individual to spend less time and energy finding food (i.e. reducing the need to explore for potentially more favourable foraging areas via long forays).

While crabs in mangrove habitat clearly made few long-distance foraging forays away from their home tree, this pattern of foraging could reflect a number of exploratory patterns. A decrease in the regularity of steps as distance increases is a characteristic of many random walk models including biased random walks, correlated random walks, Brownian random walks and Lévy walks, among others (Benhamou, 2005). In addition, our results suggest that *A. pisonii* foraging movements are driven by faecal cues, which may result in a foraging pattern resembling scent-marking orientation shown to explain mammal movements (Benhamou, 1989). However,

the purpose of our study was not to identify the precise mathematical form of the foraging patterns displayed by *A. pisonii* but simply to show that they display a foraging pattern that is likely to be closely tied to and affected by site fidelity behaviour.

Regardless of the cause, the loss of site fidelity in the salt marsh could have important implications for the ecology and life history of *A. pisonii* in this novel ecosystem. If *A. pisonii* employs site fidelity to maintain favourable foraging sites like other ecologically similar species (Cannicci et al., 1996) and as suggested by the observed foray behaviour, loss of this behaviour in the salt marsh could lead to loss of favourable foraging sites and increased search time during foraging. Increased search time is energetically detrimental as individuals spend energy attempting to find food as opposed to eating. Additionally, increases in searching and exploration may lead to increased predation risk. While it is unknown whether *A. pisonii* shows site fidelity to predation refuges, many species do (Branch, 1978; Sebastian et al., 2002; Shields, 1984). If the loss of site fidelity leads to a loss of fidelity to predation refuges, this would further increase predation risk. It is therefore possible that the loss of site fidelity in the salt marsh could represent a significant alteration to both the behaviour and ecology of *A. pisonii*.

It is also possible that the loss of site fidelity behaviour represents an adaptation to the novel salt marsh ecosystem rather than a consequence of the inability to establish cues in the marsh. Previous work has found that *A. pisonii* displays smaller size at maturity, lower larval quality and lower fecundity in the salt marsh (Riley & Griffen, 2016). This would suggest that the salt marsh is a suboptimal habitat for *A. pisonii*. Thus, it is possible that the loss of site fidelity is an adaptation in response to these negative impacts. Yet, it is difficult to see how abandoning site fidelity would improve these life history characteristics. Addressing these shifts in life history would probably require *A. pisonii* to improve its bioenergetics. However, as argued above, site fidelity is likely to facilitate access to bioenergetically favourable habitat and thus a

loss of site fidelity would be more likely to contribute to the observed life history shifts than to counteract them. It is more probable that the loss of site fidelity is a result of novel conditions interfering with this behaviour (such as elimination of odour cues). Thus, the loss of site fidelity is more likely to be a mechanism contributing to the suboptimal nature of the salt marsh than an adaptation of *A. pisonii* to counteract negative novel conditions.

As more species are forced to shift ranges into eco-evolutionary novel habitats, it is important to understand how these shifts may affect their life history, behaviour and ecology in indirect ways. The change in site fidelity behaviour that we have shown in *A. pisonii* demonstrates that the successful response of species to climate change depends on more than just their ability to shift their ranges fast enough to keep up with rapidly changing environmental conditions. Rather, this work suggests that successful responses to climate change also hinge on the ability of behaviours and other adaptations that have evolved in historic conditions to provide suitable strategies under the novel conditions that arise following range shifts into eco-evolutionary novel habitats. Thus, as climate-mediated range shifts become more common, it will be important to explore changes in the ecology and behaviour of the species involved to determine whether behaviours that facilitate success in historical habitats are still viable under the novel conditions that these species now face.

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Table 1 Observation sites, days observed and total number of *A. pisonii* observed at each site

Site	Habitat	Coordinates	Observational periods	Total days observed	Crabs observed
Round Island Park	Mangrove	27°33'33"N 80°19'53"W	9–19, 23 May; 4 Aug	11	5
Pepper Park	Mangrove	27°29'42"N 80°18'12"W	25 May–4 Jun; 13–16 Jul	10	10
Oslo Park	Mangrove	27°35'14"N 80°21'55"W	28–30 Jul	3	5
North Causeway Park	Mangrove	27°28'28"N 80°19'12"W	23–30 Jun; 5–7, 10 Aug	9	10
Bear Point	Mangrove	27°25'48"N 80°17'10"W	1–3, 12 Jul		
GTM NERR	Salt marsh	30°0'49"N 81°20'42"W	20–22 May; 16–21 Jun; 7–9 Jul	12	48
Anastasia State Park	Salt marsh	29°52'40"N 81°16'32"W	21–23 Jul	3	19

GTM NERR: Guana Tolomato Matanzas National Estuarine Research Reserve.

Figure 1. Set-up of two-choice experiments examining faeces as a mechanism of site fidelity in *A. pisonii*. Two mangrove branches were placed in crosswise fashion in a bucket and an individual *A. pisonii* was placed between them. In one experiment, one branch was treated with the crab's own faeces and the other branch was left untreated (clean). In a second experiment, one branch was treated with the crab's own faeces and the other branch was treated with another crab's faeces. The branch onto which the crab climbed was recorded as its choice.

Figure 2. Site fidelity in *A. pisonii*. Days observed on home tree/area versus days from first to last seen on home tree/area in the (a) mangrove and (c) salt marsh habitats; numbers within each circle represent the number of data points at that location. The number of days individual crabs were sought and observed in the (b) mangrove and (d) salt marsh are also represented; crabs that were right-censored are represented as squares, with data points jittered to facilitate observation of density.

Figure 3. Foraging foray behaviour of crabs from the mangrove habitat. (a) Proportion of days that the observed crab travelled a certain distance. The solid line shows the exponential decay from the equation given in the main text (see Results, Foraging Forays). (b) Number of crabs that made forays of particular distances.

Figure 1

Figure 2

Figure 3