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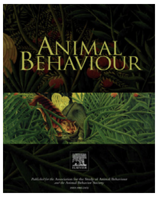

Changes in spatial behaviour patterns by mangrove tree crabs following climate-induced range shift into novel habitat

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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.

As the global climate continues to change, species are expanding or shifting their rages 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

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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 et al., 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 eco-evolutionary novel habitat of the salt marshes of the southern Atlantic coast of the United States (Riley, Johnston, Feller, & Griffen, 2014). *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 lepsozoma*, 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).