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A terrestrial-aquatic food web subsidy is potentially mediated by multiple predator effects on an arboreal crab

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ABSTRACT

Terrestrial-aquatic food web subsidies are known to affect food web structure, ecosystem productivity, and stability of recipient habitats. This study describes a prey flux across the land–water interface associated with a behavioral response to multiple predators. Specifically, mangrove tree crabs (*Aratus pisonii*, hereafter *Aratus*) are primarily arboreal, but may jump off mangrove trees to escape avian predators, making them vulnerable to fish predation. Mesocosm experiments, field observations, and tethering assays were used to investigate behavioral responses, habitat shifts, and risk for *Aratus* associated with these two predator types. In the field, *Aratus* spent most of their time above the water on mangroves, where risk is lowest. In response to simulated bird strikes in mesocosm trials, crabs jumped off trees to escape imminent risk, and spent more time in and near the water, enhancing risk of fish predation. Fish attacks on crabs were nearly three times greater in treatments with simulated bird attacks. In addition, empirical diet data was used to examine the importance of *Aratus* as a prey item for a fish predator. *Aratus* represented up to 29% of diet by volume for one of the most common mesopredators in the Caribbean (gray snapper *Lutjanus griseus*), with the proportion varying greatly across space. Because *Aratus* consume mangrove-derived carbon, their consumption by aquatic predators represents another pathway by which mangrove production may be incorporated into aquatic food webs. These data suggest how the nexus of behavioral and food web ecology may provide for new perspectives on energy flow between ecosystems.

1. Introduction

Historically food webs were viewed as closed systems, but the importance of exogenous subsidies increasingly has been found to be an important driver of species interactions and local productivity (Polis et al., 2004). In a food web context, spatial subsidies are defined as movement of a donor-controlled resource (e.g., prey, detritus, or nutrients) from one habitat to another with increased productivity (primary or secondary) of the recipient, which in turn alters consumer–resource dynamics (Polis et al., 1997). Recent research on spatial subsidies has shifted away from simply documenting their presence, to a more focused pursuit on identifying the specific mechanisms driving the flow of resources across habitat boundaries (Bartels et al., 2012; Dreyer and Gratton, 2014; Marcarelli et al., 2011; Massol et al., 2011; Polis et al., 1997). Because prey-based subsidies are usually of higher quality than detrital-based subsidies, understanding what drives these fluxes is of particular interest.

Prey respond to predators by changing their behavior or microhabitat use (Lima and Dill, 1990), and the response may depend on the hunting mode and habitat use of the predator (Preisser et al., 2007). When multiple predator species are present, they may elicit varying responses from their shared prey and emergent responses, i.e., those that differ from predicted responses based on the additive effects of both predators in isolation (Sih et al., 1998; Sokol-Hessner and Schmitz, 2002). Likewise, the nature of the prey response to multiple predators may depend on respective foraging mode and overlap in habitat domain of both predators (Schmitz, 2007). For prey species that can move across a land–water interface, behavioral avoidance of a terrestrial predator may enhance risk of predation by an aquatic predator, or vice versa. In this way, behaviorally-plastic movements by prey drive food web connections, with potentially important implications for spatial subsidy dynamics.

Tropical and sub-tropical estuarine food webs were once thought to be supported largely by fluxes of mangrove detritus (Odum and Heald, 1975). However, studies using new advances in food web techniques, such as stable isotope analysis, have questioned the importance of mangrove-derived carbon in supporting associated aquatic food webs,

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and suggest that incorporation of mangrove carbon into marine food webs may be limited to relatively closed systems or resident consumers at a limited spatial scale (sensu Layman, 2007; Bouillon et al., 2008; Nagelkerken et al., 2008). Marine-derived carbon source pools (e.g., seagrass, macroalgae, and/or microphytobenthos) are now thought to be more important in supporting most aquatic consumers, even in mangrove-dominated systems (Bouillon et al., 2002; France, 1998; Kieckbusch et al., 2004; Vaslet et al., 2012). However, a few Grapsid and Sesarimid crabs, like the mangrove tree crab (*Aratus pisonii* H. Milne Edwards 1837, hereafter *Aratus*), are known to feed directly on mangrove-derived carbon (directly on leaves or epiphytic algae closely associated with mangroves) and may represent a link to this carbon pool for marine predators. Although *Aratus* is primarily arboreal, it is capable of crossing the land–water interface, and may therefore serve as an important link between terrestrial and aquatic food web modules.

The objective of the current study was to determine if a behaviorally-plastic response by *Aratus* to multiple predators could factor into a terrestrial-aquatic food web linkage in a mangrove ecosystem. First, mesocosm experiments were used to determine if responses of *Aratus* to aquatic and terrestrial predators may affect their behavior, microhabitat use, and vulnerability to fish predation. We expected to find that *Aratus* would display an emergent antipredator response in the presence of both predators, which could potentially enhance risk from fish predators. Next, *Aratus* were observed in the field to quantify crab behaviors and microhabitat use, and then tethering assays were used to infer whether shifts in microhabitat use across the land–water interface affected predation risk. Because *Aratus* are known to be primarily arboreal, we hypothesized that they would spend most of their time out of the water, and that risk from predation would be higher in the water. Finally, potential contributions of *Aratus* to the diet of a common marine predator were estimated using an empirical diet data set. In the context of other terrestrial-aquatic food web linkages, we expected to find that this flux could be large because it represents a prey-based subsidy. In sum, this study attempts to provide a novel example of how behavioral plasticity may drive spatial food web subsidies, while providing new insights into food web structure in mangrove ecosystems.

2. Material and methods

2.1. Study species

The green mangrove crab, *A. pisonii* (Fig. 1A), is an arboreal crab belonging to the Sesarmidae family (formerly part of the Graspidae family), and is one of the most dominant species inhabiting terrestrial portions of red mangrove (*Rhizophora mangle* L.) forests throughout subtropical and tropical coasts of the Americas and the Caribbean islands. It is the only species belonging to the genus *Aratus*, and will be referred to simply as *Aratus* hereafter. Its diet is known to be omnivorous, consisting of green mangrove leaves, wood, microphytobenthos, mangrove root epiphytes and epibionts, insects, carrion and conspecifics (Beever et al., 1979; Erickson et al., 2008). Isotopic studies have indicated that mangrove carbon may represent 16–42% of the *Aratus*' diet (Lacerda et al., 1991). *Aratus* is the only taxa, apart from insects, that is known to feed on green mangrove leaves in Caribbean mangrove forests (Feller and Chamberlain, 2007).

Aratus spend most of their time on mangrove roots and trunks. However, the crabs make vertical migrations associated with the tide, moving onto the exposed marsh surface and lower roots at low tide

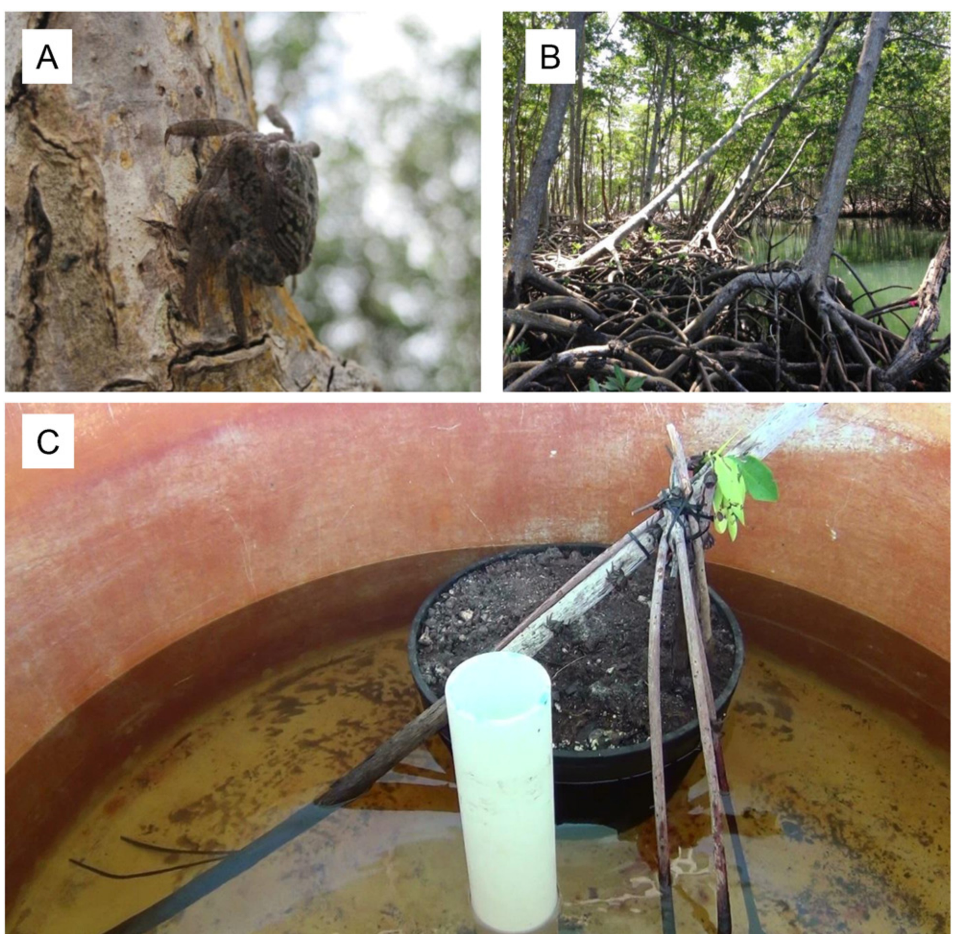

Fig. 1. Pictures of (A) an *Aratus pisonii* on a red mangrove tree, (B) the North Miami field site, and (C) the mesocosm set-up.