**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.

Keywords: behavior, carbon flow, food webs, mangroves, spatial subsidies

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, 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, *Aratus pisonii* (Fig. 1a), is an arboreal crab belonging to the Sesarmidae family (formerly part of the Grapsidae 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 (Wilson, 1989). The crabs migrate up trees at high tide, presumably to escape aquatic predators. Terrestrial predators are also known to prey on *Aratus*; these predators include birds (Bavaro et al., 2007; Olmos et al., 2001), raccoons (Wilson, 1989) and other crabs (Warner, 1967). *Aratus* often jump from trees onto the marsh surface or into the water, presumably to escape predation by terrestrial predators (Bavaro et al., 2007; Warner, 1967); this jumping behavior is highly plastic across the geographic range of this species (CAL, pers. obs.). If the crabs jump into the water, this response may make them more vulnerable to aquatic predators like snapper (Lutjanidae). Once the crabs are in the water, they will either dive to the bottom, crawl back to the marsh edge, or swim along the surface of the water back to the nearest mangrove root (LAY, pers. obv.).

2.2. Study site

Field observations, *Aratus* collections, and tethering experiments were conducted in mangrove habitat adjacent to the campus of Florida International University in northern Biscayne Bay, Florida (North Miami field site, 25.902480° N, 80.142031° W). This system is characterized by largely monospecific stands of red mangrove (Fig. 1b) which flood on high tides. There are also larger mangrove creeks (up to 2 m deep) through the forest where gray

snapper (*Lutjanus griseus* Linnaeus, 1758) and other predatory fishes are common. Potential bird predators were observed at the site, including Great blue heron (*Ardea Herodias* Linnaeus, 1758), Snowy egret (*Egretta thula* Molina, 1782), Green heron (*Butorides virescens* Linnaeus, 1758), and White ibis (*Eudocimus albus* Linnaeus, 1758). Great blue herons and White ibis were noted to actively forage for and consume *Aratus* at the study site.

2.3. Mesocosm experiment

Mesocosm experiments were used to test the effects of simulated avian and fish predators on *Aratus* behavior and microhabitat use. Two round (2 m diameter) fiberglass tanks with a similar set-up were used (Fig. 1c). Each tank had one simulated “marsh” consisting of a plastic pot (57 cm W x 38 cm H) filled with rocks and sand and covered with a 5 cm layer of mangrove mud and detritus collected from adjacent marshes. Three mangrove prop roots and one dead mangrove log (collectively referred to as roots hereafter) were affixed to smaller prop root pieces protruding from the marsh with the roots extending out over and into the water, simulating the lower root structure of a red mangrove tree. Each tank was filled with 25 cm of water 24 h before the beginning of a trial with high salinity (~34) ground water pumped from under the mesocosm facility. A camera was mounted to the edge of each tank so that the behavioral trials could be filmed. *Aratus* were collected from the North Miami field site by hand and snapper were collected from the North Miami field site or Loxahatchee River estuary using hook and line fishing. Crabs and snapper were held in separate holding tanks prior to experimental set-up for periods of 3-7 and 3-20 d, respectively. Crabs were fed green mangroves leaves and aquarium

fish food, and snapper dead Penaeid shrimp and *Aratus*. Trials were conducted from January 25 to April 9, 2013.

Four predator treatments were employed using an additive design: (1) no predators, (2) fish predators only, (3) simulated bird predator only, and (4) fish and simulated bird predators. Six trials were run per treatment for a total of 24 trials with the order randomized. All of the tanks were stocked 24 h before the start of the experiment with 20 experimentally-naïve *Aratus* crabs ranging in carapace width from 7-24 mm. This density of crabs ($\sim 3.2/\text{m}^2$) is within the natural range of *Aratus* densities at the field site (densities as high 40 individuals/tree or $\sim 10/\text{m}^2$ were documented). Mean size of crabs did not differ among treatments or tanks (one-way ANOVA, $P > 0.8$ in both cases). A small cluster of 5-7 green mangrove leaves was placed on the top of the mangrove roots to provide food for the crabs. For tanks with a fish treatment, two gray snapper were added 1 h after the crabs. This density of fish ($0.64/\text{m}^2$) is within the range of natural snapper densities in local sub-tropical mangrove systems (Faunce and Serafy, 2008). By adding crabs first, it allowed them time to acclimate to the tank before snapper were added. Snapper ranged in size from 125 to 170 mm SL. Gray snapper above 100 mm SL are known to eat *Aratus* based on a previous diet study (Yeager and Layman, 2011). Two hours before the start of each trial, cameras were affixed to the mounts on the side of the tanks. All trials were started between 10:00 and 11:00 and ran each for 1 h. For simulated bird predator treatments, a plastic Great blue heron model was used. At 20 min, one researcher (EWS) lowered the plastic heron over the side of the tank on a rod, tapping its beak two times to the top of the mangrove roots to simulate a heron attack. This simulated attack was repeated at 40 min. For the non-bird treatments (no predator and fish only), the researcher made the same movements next to the tank without the plastic bird, but was out of sight of the fish and crabs, to ensure that crab movements

were not induced by human presence. At the end of the trial, the tanks were drained and all crabs were enumerated and measured.

Videos of the trials were analyzed for crab (1) behavior and (2) microhabitat use. Every 10 min, the videos were watched for 1 min ($n = 5$ clips/trial) and all visible crab behaviors were recorded (mean number of crabs visible per 1 min clip $\pm$ SD = 7.7 ± 3.6). Behaviors observed included: resting, feeding (on green leaves, wood, or the marsh surface), crawling (vertical movements up or down the root), jumping, swimming, and shifting position on the root (horizontal movements around the root). Microhabitat use was scored on still frames every 5 min following a 10 min recovery period (to avoid any disturbance associated with starting the camera) during the trial (mean number of crabs visible per still $\pm$ SD = 5.9 ± 2.5). Microhabitats scored included: upper root (>15 cm from the water surface), lower root (<15 cm from the water surface), underwater portions of roots (hereafter roots in water), the top and side of the marsh out of water (marsh), and side of marsh or bottom of the tank in the water (other water). Additionally, all successful and non-successful fish attacks were recorded.

To assess how behavior varied throughout the trials, we divided each into three time periods: (1) before simulated bird strikes (10-11 min), (2) immediately after simulated bird strikes (20-21 and 40-41 min), and (3) post-simulated bird strikes (30-31 and 50-51 min). We a priori divided behaviors into those we considered to potential escape behaviors (i.e., jumping, swimming, and shifting position) and non-escape behaviors (i.e., feeding, crawling, and resting). We then tested whether the probability that crabs would exhibit escape behaviors varied among the three time periods, the predator treatments, or their interaction, with a mixed-effect generalized linear model with a binomial error distribution using the glmer function from the lme4 package (Bates et al., 2015) in R (R Core Team, 2015). Trial day was included as a random

effect to account for any differences in crab behavior associated with the varying conditions on the day of the trial. We used likelihood ratio tests to test the importance of the main effects and the interaction term. Because we found a significant interaction between time period and treatment, we ran post-hoc comparisons to determine which time period-treatment combinations were driving the interaction using the `glht` function in the `multcomp` package (Hothorn et al., 2008). We were also interested in whether the type of escape behavior exhibited varied depending on whether fish were present or not. Because the frequency of escape behaviors was otherwise low, we focused on the time period immediately after simulated bird strikes for the simulated bird and fish + simulated bird treatments for these post-hoc comparisons. We tested whether the number of crabs jumping or shifting position varied between these two treatments using a generalized linear model with a Poisson error distribution with the `glm` function from the `stats` package in R.

To assess how microhabitat use of *Aratus* was affected by simulated bird strikes for the various predator treatments, the proportion of crabs using different microhabitats was compared among three time periods: (1) before simulated bird strikes (10 and 15 min), (2) immediately after simulated bird strikes (21 and 41 minutes), and (3) post-simulated bird strikes (30, 35, 40, 50, and 55 minutes). To deal with issues of non-independence of proportional habitat use observations (i.e., proportions sum to 1 across all habitat types), we $\ln$ -transformed and centered proportions for each microhabitat as suggested by Aebischer et al. (1993). We then used a multivariate, mixed-effects model to test whether proportional habitat use varied among the three time periods, the predator treatments, or their interaction using the `lmer` function from the `lme4` package (Bates et al., 2015) in R. Trial day was again included as a random effect. We used likelihood ratio tests to test the importance of the main effects and the interaction term in the

multivariate model. Because we found an overall differences in microhabitat use among time periods and predator treatments in microhabitat, we ran post-hoc univariate mixed-effects models with similar likelihood ratio tests. In the event of a significant main effect or interaction, we made corresponding post-hoc comparisons using the `glht` function in the `multcomp` package (Hothorn et al., 2008).

2.4. Field observations

In order to determine patterns of microhabitat use and behavior of *Aratus*, field observations were made for two locations at the North Miami field site during diurnal high and low tides for two days at each site during April 2012. These locations were ~40 m apart in similar geophysical settings. During each observation period, one observer (LAY or EWS) noted the microhabitat, height (estimated against a reference pole placed at the site), and behavior of each crab visible on a mangrove tree. The observer began to make observations ~5 m from the tree using binoculars, but gradually neared and rotated around the tree until all crabs had been recorded. The average crab height was ln-transformed to improve homogeneity of variances and compared between tidal levels at the two sites using a two-way ANOVA (`lm` function the `stats` package in R). Additionally, shifts in microhabitat use and behavior observed at each site were summarized (detailed in the Results).

To assess how changes in microhabitat use might lead to differences in predation risk, crabs were tethered at the North Miami field site either below the low tide line or above the high tide line so the crabs were exposed to aquatic or terrestrial predators only. Twenty-five pairs of crabs were tethered at the two heights during April 2013. Each pair was placed >10 m from any

other pair, and pairs were spaced haphazardly along the two mangrove channels at the site where fish were commonly observed. Ten lb test monofilament line was tied around each crab and secured to the carapace with super glue. Crabs were then tied to a mangrove prop root at one of the two heights on a 15 cm tether. To avoid confounding structural complexity with the height comparison, crabs were always tethered within the complex part of the prop root structure (not on the less complex trunk or tree branches). Crabs could still crawl up and down the root, and were positioned so that if the crab jumped, it would be able to reach another root. Crabs were left tethered for 24 h. After 24 h, if the loop was intact and a piece of carapace still attached, it was scored as missing. Four pairs of crabs were excluded because one of the tethers/intact loops could not be found. A Fisher's exact test was used to determine whether the proportion of crabs lost differed between the two tethering heights (low vs. high). To test whether crabs could escape tethers, crabs were tethered in mesocosms to mangrove roots either above or below the water using a similar set-up. All crabs ($n = 5/\text{treatment}$) remained alive and tethered after 24 h in these trials.

2.5 Food web contributions

To assess the relative importance of *Aratus* in estuarine food webs, we used a data set of Gray snapper diets ($n = 398$ snapper) from the Loxahatchee River, Florida, collected using hook-and-line fishing from 2007-2009 (a subset of the data can be found in Yeager et al, 2014). We calculated the average frequency at which snapper consumed *Aratus* at five sites along an estuarine gradient (Table 1). On only one occasion (out of 34 snapper with *Aratus* in their stomach) was a snapper observed to have more than one crab in their stomach, and since snapper

stomach evacuation rates are likely less than 24 h (Starck and Schroeder, 1970), we made the assumption that snapper were eating approximately one crab per day when present in an individual's diet. Next we used the average size of *Aratus* in snapper stomachs (carapace width = 11.5 mm, n = 15 intact individuals that could be measured) along with an empirically-derived size-weight regression (dry weight (g) = $0.0371 \times \text{carapace width (cm)} - 0.268$, $R^2 = 0.72$, n = 14 *Aratus* crabs) to estimate the average daily consumption of *Aratus* biomass across the five sites. We multiplied the per individual consumption of *Aratus* biomass by the average density of snapper found in similar South Florida mainland mangroves (0.36 individuals/m²) (Faunce and Serafy, 2008). From this we estimated areal, annual flux rates of *Aratus* to estuarine food webs in terms of biomass (g DW). We converted biomass flux to carbon flux by multiplying DW by the percent carbon in *Aratus* tissue as calculated from mass spectrometry (mean = 36.4%, n = 7 crabs, L.A. Yeager, unpublished data). Finally, we calculated energy flux using the energy density of *Aratus* (mean = 5.08 kcal/g DW, n = 15 crabs, Yeager et al., 2014).

3. Results

3.1. Mesocosm experiment

Effects of time period on crab behavior varied across the four predator treatments (glmer, likelihood ratio test, time*treatment, d.f. = 7,13, $\chi^2 = 30.4$, $P < 0.0001$, Fig. 2). The interaction between time period and predator treatment was due an increased probability of a crab exhibiting an escape behavior immediately after simulated bird strikes in the simulated bird (predicted probability of escape = 0.57) and fish + simulated bird treatment (0.58) relative to other

treatment and time periods (range in predicted probabilities: $<0.01 - 0.11$, $P < 0.01$ in all post-hoc contrasts). While the probability of a crab exhibiting escape behavior was similar in these two treatments, more crabs were observed shifting position on the root in the fish + simulated bird treatment (mean across trials $\pm$ SD = 3.3 ± 2.2) than in the simulated bird only treatment (1.4 ± 1.4 ; glm, $Z_{1,22} = 2.96$, $P = 0.003$). Conversely, more crabs were observed jumping in the simulated bird (2.0 ± 1.9) than the fish + simulated bird treatment (1.2 ± 1.3), although this difference was not statistically significant (glm, $Z_{1,22} = -1.60$, $P = 0.1$).

Overall microhabitat use of crabs within the mesocosm also differed among treatments, with the effect of treatment on habitat use varying among the time periods (lmer, likelihood ratio test, time*treatment, d.f. = 3,8, $\chi^2 = 15.3$, $P = 0.02$, Fig. 3). Crab use of the upper roots was generally higher in the treatments with fish. The use of upper roots was lower in the simulated bird treatment immediately after bird strikes and in the post bird strike period than in any of other predator treatment-time period combination besides the fish + simulated bird treatment immediately after bird strikes ($P < 0.05$ in post-hoc treatment contrasts from univariate models). Crab use of the lower roots in the bird treatment immediately after bird strikes was higher than in either of the treatments with fish during any time period ($P < 0.05$ in post-hoc contrasts). Use of the roots in the water varied only among predator treatments (lmer, likelihood ratio test, time*treatment, d.f. = 3,6, $\chi^2 = 127.1$, $P < 0.0001$), and was generally highest in the no predator treatment, intermediate in the simulated bird treatment, and lowest in the two treatments with fish ($P < 0.001$ in post-hoc treatment contrasts). Use of the upper roots declined in the simulated bird and fish + simulated bird treatments immediately after bird strikes relative to the pre-strike period, and remained lower in the post-bird strike period ($P < 0.05$ in post-hoc treatment*time contrasts). Use of the lower roots increased following bird strikes for the fish + simulated bird

treatment ($P < 0.05$). Crabs were only observed to use the water (not on roots) immediately after bird strikes and during the post-bird strike period for the simulated bird treatment. Use of the marsh did not vary across the predator treatments, with time period, or their interaction ($P > 0.05$ in all cases).

Snapper were observed striking at *Aratus* when the crabs were in the water during mesocosms trials. Snapper were also commonly observed to strike at crabs above the water surface when the crabs were using the lower portions of the roots. The mean number of snapper strikes was nearly three times greater in the fish + simulated bird treatment (mean $\pm$ SE = 2.0 ± 0.58 strikes/trial) compared to the fish only treatment (0.67 ± 0.33), although this difference was only marginally significant ($t_{1,11} = 2.0$, $P = 0.07$). One crab was observed to be eaten by a snapper while swimming in the water after a bird strike in the fish + bird treatment.

3.2. Field observations

At the two mangrove sites, 181 crabs were observed over four observations periods. Mean crab height varied between tides (lm, $F_{1,175} = 7.5$, $P = 0.007$) and sites ($F_{1,175} = 47.45$, $P < 0.001$), with the effect of tide on crab height being consistent between sites (tide*site, $F_{1,175} = 0.29$, $P = 0.6$). Crab height was on average 0.43 m higher at high tide than at low tide. Differences in crab height between sites were likely the results of differences in tree morphology and elevation, although we did not quantify these. Crabs were observed to crawl as high as 5.5 m above the low tide line. A few crabs ($n = 5$) were observed to crawl down into the water at both tides. Crabs ($n = 8$) were only observed to feed at low tide, where they were feeding on the marsh surface or root epiphytes. Crabs may have consumed mangrove wood and leaves, as well,

but it was difficult to determine from the observation location on the ground. The remaining crabs were either crawling ($n = 50$), resting ($n = 114$), or interacting with other crabs ($n = 4$).

The number of crabs lost varied between the two tethering heights ($n=21$ /treatment, Fisher's Exact Test, $P < 0.001$). The loss rate was over 3 times greater for the crabs tethered in the water (81% missing) as for those tethered above the high tide line (23% missing).

3.3 Food web contributions

In the Loxahatchee, the frequency of snapper with *Aratus* present in their stomachs ranged from 2 to 22% across the five sites examined (Table 2), representing up to 29% of snapper diet by volume. This translated into a biomass contribution of 0.35 to 4.51 g DW m⁻² y⁻¹. Carbon flux due to *Aratus* consumption was calculated to range between 0.13 to 1.64 g C m⁻² y⁻¹. In terms of energy density, *Aratus* contribution to Gray snapper diets ranged from 1.80 to 22.92 kcal m⁻² y⁻¹.

4. Discussion

Prey may respond to a predator in multiple ways, including habitat shifts, seeking alternate refuge, or reducing activity levels. Both hunting mode and habitat domain of predators, relative to that of the prey, provide a useful framework to predict the response of prey (Preisser et al., 2007; Schmitz et al., 2004; Sokol-Hessner and Schmitz, 2002). In this study system, *Aratus* crabs have a relatively broad habitat domain compared to either birds or fishes, which are limited to the terrestrial or aquatic environment, respectively. When the habitat domain of a resident predator is narrow compared to a broad domain for its prey, theory suggests that the

prey should respond with a distinct habitat shift (Schmitz et al., 2004). This likely explains why *Aratus* spend most of their time out of the water, and were less likely to enter the water or use the lower portions of roots when fish were present. In contrast, bird predators are more transient, and prey should respond only to imminent threats. As a result, with a terrestrial predator in close proximity, jumping and shifting to the lower portions of roots to avoid the imminent risk may be the safest option for *Aratus*.

Other biological and physical factors may affect habitat use by *Aratus*. While the terrestrial environment appears safer for these crabs, spending too much time up in the drier mangrove canopy may put *Aratus* at risk of desiccation (Wilson, 1989). In fact, crabs were frequently seen “dipping” the end of their carapace into the water in both the field and mesocosm experiment, which was likely necessary to retain moisture over their gills. Low tide also exposes a diversity of food resources to *Aratus*, including root epibionts and microphytobenthos on the marsh surface. Additionally, *Aratus* must enter the water to spawn, which is known to occur most frequently around full and new moons (Warner, 1967). The experimental results, however, suggest that even in the context of these other potential drivers, predation risk is an important determinant of behavior and microhabitat use.

As with all mesocosm experiments, the set-up for our behavioral trials possibly resulted in some experimental artifacts. *Aratus* were likely over-exposed to fish predators, as they were held together for 24 hours in the mesocosms and most fish are precluded from shallower mangrove areas at low tide in natural systems (i.e., the areas that *Aratus* frequent). This overexposure may have resulted in a stronger behavioral response of *Aratus* to fish than would be expected in natural systems. However, this would have caused us to underestimate the facilitation of snapper predation by birds, and mean strike rates by fish were already nearly three

times greater when bird strikes were simulated than when fish were alone. Similarly, the tethering experiments likely over-exposed crabs to both aquatic and terrestrial predators because the tethers did not allow crabs to escape across the land-water interface. However, their immediate escape tactic in response to a terrestrial predator (i.e., jumping) was likely more limited than that to fish predators (i.e., trying to hide within the prop root matrix). Therefore, the trials likely overestimated the terrestrial relative risk, which was still much lower than in the aquatic habitat.

In snapper diets from South Florida, the relative contributions of *Aratus* varied spatially; however, these data suggest these subsidies could be substantial. For example, estimated daily biomass flux rates ($11\text{--}12\text{ mg DW m}^{-2}\text{ d}^{-1}$) in the mesohaline portions of the Loxahatchee River are similar to the highest rates of aquatic prey flux associated with insect emergence in Nakano and Murakami's (2001) classic study in forest streams in Japan (although less than peak values from terrestrial to aquatic prey flux). In fact, values of biomass flux reported in this study were similar in magnitude to median values ($\sim 2.5\text{ g DW m}^{-2}\text{ yr}^{-1}$) of prey flux from lotic to terrestrial ecosystems reported in a review by Bartels et al. (2012). However, these flux values were less than half of the median value for terrestrial to lotic prey flux ($\sim 14\text{ g DW m}^{-2}\text{ yr}^{-1}$). In addition to the spatial variation in *Aratus* contribution to snapper diets in the present study, other studies have reported temporal variation snapper consumption of *Aratus*; Hammerschalg-Peyer and Layman (2012) found that relative contribution of *Aratus* to Schoolmaster snapper (*Lutjanus apodus*) diets in Bahamian mangrove creeks varied substantially among years (ranging between 9% to 39% of diet by volume). It is important to keep in mind, however, that our estimated flux values were based on a relatively small sample size of observations and do not take into account

variation in snapper density across sites; nevertheless we posit that these values are still helpful in gauging the relative magnitude of these potential subsidy and its variation.

What drives spatial and temporal variation in the magnitude of this trophic pathway is unknown, but, foremost, local population densities of *Aratus* will affect the overall magnitude of subsidy. The importance of this subsidy would then be further modified by the behavioral interaction between multiple predators and their shared prey described herein. While direct manipulation of bird predations (in the field or captivity) is needed to unequivocally link bird predation and *Aratus* behavior, with cascading impacts on snapper diets, our study does indicate that behavioral response to birds is one plausible mechanism affecting this subsidy. Another study similarly found that snapper attack rates on *Aratus* increased following experimentally-produced disturbances that mimic bird predators in mangrove habitat on the Pacific coast of Costa Rica (Bavaro et al., 2007). As such, local community structure and population densities of birds and fishes may mediate the spatial and temporal variation observed. In most South Florida estuaries, wading bird densities are highest in the mesohaline and oligohaline reaches (Cook and Kobza, 2012), possibly explaining the higher contribution of *Aratus* to snapper diets in these areas.

Loss of predators is a primary conservation concern, as predators are known to play a key role in structuring ecological communities (Estes et al., 2011). Furthermore, different predator species are usually not functionally redundant, and maintaining predator diversity is necessary to preserve important ecological functions, like food web stability (Finke and Denno, 2004). Declines in populations of wading birds remain a serious conservation concern for Florida and the greater Caribbean region. Many populations of wading birds were hunted to near extinction by plume hunters by the early 1900's. Since then, populations have partially recovered, but are

still threatened by habitat loss and alteration, specifically by changes in hydrology (Cook and Kobza, 2012). Because wading birds may be important in mediating this aquatic-terrestrial food web subsidy via antipredator behavior in *Aratus* crabs, declines in local populations may have cascading impacts for estuarine systems. Similarly, predatory fish populations have suffered major declines throughout the greater Caribbean due to overharvest (Stallings, 2009) and their loss also could lessen the strength of linkages. More broadly, this system may serve as a model for how predator loss may weaken food web connectivity and the strength of spatial subsidies across habitat boundaries.

Acknowledgements

The authors thank M. Zapata, H. Miller, and L. Pierre for assistance with field work. Funding was provided by a Florida International University (FIU) Dissertation Year Fellowship and the National Socio-Environmental Synthesis Center (SESYNC) under funding received from the National Science Foundation DBI-1052875 to LAY, an Environmental Protection Agency Star Grant to EWS, the FIU Marine Science Department, and the Loxahatchee River District.

References

Aebischer, N.J., Robertson, P.A., Kenward, R.E., 1993. Compositional analysis of habitat use from animal radio-tracking data. *Ecology* 74(5), 1313-1325.

454 Bartels, P., Cucherousset, J., Steger, K., Eklov, P., Tranvik, L.J., Hillebrand, H., 2012.
 455 Reciprocal subsidies between freshwater and terrestrial ecosystems structure consumer
 456 resource dynamics. *Ecology* 93(5), 1173-1182.

457 Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting Linear Mixed-Effects Models
 458 Using lme4. *Journal of Statistical Software* 67(1), 1-48.

459 Bavaro, L.E., Szelistowski, L.M., Szelistowski, W.A., 2007. Grackles foraging may enhance
 460 feeding success of mangrove fishes. *Bull. Mar. Sci.* 80(3), 917-917.

461 Beever, J.W., Simberloff, D., King, L.L., 1979. Herbivory and predation by the mangrove tree
 462 crab *Aratus pisonii*. *Oecologia* 43(3), 317-328.

463 Bouillon, S., Connolly, R.M., Lee, S.Y., 2008. Organic matter exchange and cycling in
 464 mangrove ecosystems: Recent insights from stable isotope studies. *J. Sea Res.* 59(1-2),
 465 44-58.

466 Bouillon, S., Koedam, N., Raman, A.V., Dehairs, F., 2002. Primary producers sustaining macro-
 467 invertebrate communities in intertidal mangrove forests. *Oecologia* 130(3), 441-448.

468 Cook, M.I., Kobza, M., 2012. South Florida wading bird report. South Florida Water
 469 Management District, West Palm Beach, FL, Vol 18.

470 Dreyer, J., Gratton, C., 2014. Habitat linkages in conservation biological control: lessons from
 471 the land–water interface. *Biol. Control* 75, 68-76.

472 Erickson, A.A., Feller, I.C., Paul, V.J., Kwiatkowski, L.M., Lee, W., 2008. Selection of an
 473 omnivorous diet by the mangrove tree crab *Aratus pisonii* in laboratory experiments. *J.*
 474 *Sea Res.* 59(1-2), 59-69.

475 Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R.,
 476 Essington, T.E., Holt, R.D., Jackson, J.B.C., Marquis, R.J., Oksanen, L., Oksanen, T.,

477 Paine, R.T., Pikitch, E.K., Ripple, W.J., Sandin, S.A., Scheffer, M., Schoener, T.W.,
 478 Shurin, J.B., Sinclair, A.R.E., Soule, M.E., Virtanen, R., Wardle, D.A., 2011. Trophic
 479 Downgrading of Planet Earth. *Science* 333(6040), 301-306.

480 Faunce, C.H., Serafy, J.E., 2008. Selective use of mangrove shorelines by snappers, grunts, and
 481 great barracuda. *Mar. Ecol. Prog. Ser.* 356, 153-162.

482 Feller, I.C., Chamberlain, A., 2007. Herbivore responses to nutrient enrichment and landscape
 483 heterogeneity in a mangrove ecosystem. *Oecologia* 153(3), 607-616.

484 Finke, D.L., Denno, R.F., 2004. Predator diversity dampens trophic cascades. *Nature* 429(6990),
 485 407-410.

486 France, R., 1998. Estimating the assimilation of mangrove detritus by fiddler crabs in Laguna
 487 Joyuda, Puerto Rico, using dual stable isotopes. *J. Trop. Ecol.* 14, 413-425.

488 Hothorn, T., Bretz, F., Westfall, P., 2008. Simultaneous Inference in General Parametric Models.
 489 *Biometrical Journal* 50(3), 346-363.

490 Kieckbusch, D.K., Koch, M.S., Serafy, J.E., Anderson, W.T., 2004. Trophic linkages among
 491 primary producers and consumers in fringing mangroves of subtropical lagoons. *Bull.*
 492 *Mar. Sci.* 74(2), 271-285.

493 Lacerda, L.D., Silva, C.A.R., Rezende, C.E., Martinelli, L.A., 1991. Food sources for the
 494 mangrove tree crab, *Aratus pisonii*: A carbon isotopic study. *Rev. Bras. Biol.* 51(3), 685-
 495 687.

496 Layman, C.A., Arrington, D.A., Montana, C.G., Post, D.M., 2007. Can stable isotope ratios
 497 provide for community-wide measures of trophic structure? *Ecology* 88(1), 42-48.

498 Lima, S.L., Dill, L.M., 1990. Behavioral decisions made under the risk of predation: a review
 499 and prospectus. *Can. J. Zool.* 68(4), 619-640.

500 Marcarelli, A.M., Baxter, C.V., Mineau, M.M., Hall Jr, R.O., 2011. Quantity and quality:
 501 unifying food web and ecosystem perspectives on the role of resource subsidies in
 502 freshwaters. *Ecology* 92(6), 1215-1225.

503 Massol, F., Gravel, D., Mouquet, N., Cadotte, M.W., Fukami, T., Leibold, M.A., 2011. Linking
 504 community and ecosystem dynamics through spatial ecology. *Ecol. Lett.* 14(3), 313-323.

505 Nagelkerken, I., Blaber, S.J.M., Bouillon, S., Green, P., Haywood, M., Kirton, L.G., Meynecke,
 506 J.O., Pawlik, J., Penrose, H.M., Sasekumar, A., Somerfield, P.J., 2008. The habitat
 507 function of mangroves for terrestrial and marine fauna: A review. *Aquat. Bot.* 89(2), 155-
 508 185.

509 Odum, W.E., Heald, E.J., 1975. The detritus-based food web of an estuarine mangrove
 510 community. *Estuar. Res.* 1, 265-286.

511 Olmos, F., Silva, R.S.E., Prado, A., 2001. Breeding season diet of Scarlet Ibises and Little Blue
 512 Herons in a Brazilian mangrove swamp. *Waterbirds* 24(1), 50-57.

513 Polis, G.A., Anderson, W.B., Holt, R.D., 1997. Toward an integration of landscape and food web
 514 ecology: the dynamics of spatially subsidized food webs. *Annu. Rev. Ecol. Syst.* 28, 289-
 515 316.

516 Polis, G.A., Power, M.E., Huxel, G.R., 2004. Food webs at the landscape level. University of
 517 Chicago Press, Chicago, USA.

518 Preisser, E.L., Orrock, J.L., Schmitz, O.J., 2007. Predator hunting mode and habitat domain alter
 519 nonconsumptive effects in predator-prey interactions. *Ecology* 88(11), 2744-2751.

520 R Core Team, 2015. R: A language and environment for statistical computing. R Foundation for
 521 Statistical Computing, Vienna, Austria.

522 Schmitz, O.J., 2007. Predator diversity and trophic interactions. *Ecology* 88(10), 2415-2426.

523 Schmitz, O.J., Krivan, V., Ovadia, O., 2004. Trophic cascades: the primacy of trait-mediated
524 indirect interactions. *Ecol. Lett.* 7(2), 153-163.

525 Sih, A., Englund, G., Wooster, D., 1998. Emergent impacts of multiple predators on prey. *Trends*
526 *Ecol. Evol.* 13(9), 350-355.

527 Sokol-Hessner, L., Schmitz, O.J., 2002. Aggregate effects of multiple predator species on a
528 shared prey. *Ecology* 83(9), 2367-2372.

529 Stallings, C.D., 2009. Fishery-Independent Data Reveal Negative Effect of Human Population
530 Density on Caribbean Predatory Fish Communities. *Plos One* 4(5).

531 Starck, W.A., Schroeder, R.E., 1970. Investigations of the Gray Snapper, *Lutjanus griseus*.
532 University of Miami Press, Coral Gables, FL, USA, 224 pp.

533 Vaslet, A., Phillips, D.L., France, C., Feller, I.C., Baldwin, C.C., 2012. The relative importance
534 of mangroves and seagrass beds as feeding areas for resident and transient fishes among
535 different mangrove habitats in Florida and Belize: Evidence from dietary and stable-
536 isotope analyses. *J. Exp. Mar. Biol. Ecol.* 434, 81-93.

537 Warner, G.F., 1967. The life history of the mangrove tree crab, *Aratus pisonii*. *J. Zool.* 153, 321-
538 335.

539 Wilson, K.A., 1989. Ecology of mangrove crabs: predation, physical factors and refuges. *Bull.*
540 *Mar. Sci.* 44(1), 263-273.

541 Yeager, L.A., Layman, C.A., 2011. Energy flow to two abundant consumers in a subtropical
542 oyster reef food web. *Aquat. Ecol.* 45(2), 267-277.

543 Yeager, L.A., Layman, C.A., Hammerschlag-Peyer, C.M., 2014. Diet variation of a generalist
544 fish predator, grey snapper *Lutjanus griseus*, across an estuarine gradient: trade-offs of
545 quantity for quality? *J. Fish Biol.* 85(2), 264-277.

546 Table 1. Flux of biomass, carbon and energy to estuarine food webs due to consumption of *Aratus pisonii* by Gray snapper (*Lutjanus*
547 *griseus*) across five sites the in Loxahatchee River estuary, Florida.

Site	Location	Description	# of snapper examined	Collection years	Proportion of snapper diet comprised of <i>Aratus</i> by volume	Proportion of snapper with <i>Aratus</i> in stomach	Biomass flux (g DW m ⁻² yr ⁻¹)	Carbon flux (g C m ⁻² yr ⁻¹)	Energy flux (kcal m ⁻² yr ⁻¹)
1	26°56'50 N, 80°5'47 W	Polyhaline, fringing mangroves	176	2007-2009	0.02	0.02	0.35	0.13	1.80
2	26°57'20 N, 80°7'15 W	Polyhaline, fringing mangroves	45	2009	0.01	0.02	0.46	0.17	2.34
3	26°58'16 N, 80°7'41 W	Mesohaline, mangrove islands	100	2008-2009	0.29	0.20	4.15	1.51	21.09

4	26°59'7 N, 80°8'35 W	Mesohaline, riverine mangrove	23	2009	0.16	0.22	4.51	1.64	23.06
5	26°59'28 N, 80°9'18 W	Oligohaline, riverine mangrove	52	2007, 2009	0.03	0.11	2.35	0.86	11.92

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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.

Fig. 2. Model predicted probabilities that crabs would exhibit escape behaviors across the four predator treatments over the three time periods: (1) Pre = before simulated bird strikes, (2) Imm = immediately after simulated bird strikes, and (3) Post = at least 10 minutes after simulated bird strikes. Open circles represent the proportion of observed crabs exhibiting escape behaviors in the mesocosm trials. Note each trial had two Imm and Post observation periods.

Online color version:

Fig. 3. Proportion of crabs using available microhabitats across the four predator treatments over the three time periods: (A) before simulated bird strikes, (B) immediately after simulated bird strikes, and (C) at least 10 minutes after simulated bird strikes. Microhabitats are represented by different shading including: Upper root (dark blue), Lower root (yellow), Marsh (green), Root in water (red), and Other water (black).

Printed black and white version:

Fig. 3. Proportion of crabs using available microhabitats across the four predator treatments over the three time periods: (A) before simulated bird strikes, (B) immediately after simulated bird strikes, and (C) at least 10 minutes after simulated bird strikes. Microhabitats are represented by different shading including: Upper root (dark gray), Lower root (light gray), Marsh (diagonal lines), Root in water (medium gray), and Other water (black).

Figure 1

Figure 2

Figure 3