Summer microhabitat use of the Greater Siren (*Siren lacertina*) and Two-toed Amphiuma (*Amphiuma means*) in an isolated wetland

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Abstract. Although the habitats of the Greater Siren (*Siren lacertina*) and Two-toed Amphiuma (*Amphiuma means*) have been described on a coarse scale; the microhabitat(s) of these species has not been examined. We trapped from 12 June 2008 to 1 July 2008 in an isolated wetland on the Savannah River Site in South Carolina where these two salamander species occur in sympatry. Traps were set in three different microhabitats; the water's surface and benthic zone in deep water, and in a littoral zone. *Siren lacertina* captures were highest in the benthic zone, while *A. means* were captured more in the littoral zone. This differentiation in microhabitat usage may reflect a difference in prey availability or habitat structure; alternatively, it may be a response to interspecific interactions between species.

Keywords: Amphibian, aquatic habitat, aquatic salamanders, Caudata, depth, distribution.

Introduction

Understanding why an animal utilizes a certain habitat is a key component to understanding its ecology; microhabitat use reflects a trade-off between maximizing access to food resources, while minimizing exposure to predation and competition (Warkentin, 1992). In microhabitat studies of animals inhabiting lentic aquatic habitats, water depth adds a third dimension that also needs to be considered (Dodd and Smith, 2003). Larval *Ambystoma* have been observed using this third dimension by making nocturnal vertical migrations up the water column in response to reduced light intensity and increased prey movement (Anderson and Graham, 1967; Anderson and Williamson, 1974; Branch and Altig, 1981). In studies of the aquatic phase of *Triturus* newts, diet analyses of *Triturus* species (Joly and Giacoma, 1992) and *Triturus* morphs (i.e., paedomorphs and metamorphs; Denoël and Joly, 2001; Denoël and

Schabetsberger, 2003) revealed that differences in diet reflected differences in microhabitat use. While this previous work establishes a precedent for other aquatic salamanders to partition aquatic habitats on a finer scale, little information exists for sirenids and amphiumids.

The Greater Siren (*Siren lacertina*) and Two-toed Amphiuma (*Amphiuma means*) are two species of aquatic salamanders that commonly co-occur in wetlands throughout the southeastern United States (Martof, 1973; Salthe, 1973). Despite being large and often abundant, little is known about their general ecology because their cryptic nature makes them difficult to study (Hendricks, 2005; Johnson and Owens, 2005). However, *S. lacertina* and *A. means* can contribute a substantial amount of biomass (233 g/m^2 and 44 g/m^2, respectively; Sorenson, 2004) to the bodies of water in which they inhabit and are thought to play an important role in aquatic food webs. They are mid-level predators (Hamilton, 1950; Hanlin, 1978) that are themselves food sources for a variety of other animals (reviewed for siren in Luhring, 2008). Thus, understanding their microhabitat use may provide a better understanding of their roles within their local system.

Although Lesser Siren (*Siren intermedia*) exhibited differing population densities among

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microhabitats within a beaver pond (Gehlbach and Kennedy, 1978), only Duellman and Schwartz's (1958) note that larger *S. lacertina* occur in deeper water and provides any indication of differentiation in intra-wetland microhabitat use. We investigated whether relative abundance of *S. lacertina* and *A. means* were associated with water depth. Additionally, we measured the relative abundance of potential prey and microhabitat variables to help explain any difference in the distribution of these salamanders.

Materials and methods

Trapping was conducted at Peat Bay, a 14.3-ha semi-permanent isolated wetland located on the U.S. Department of Energy's Savannah River Site (SRS) in Barnwell County, South Carolina, USA (33°09′21″N, 81°38′23″W). A ring of dead trees, predominately Swamp Tulepo (*Nyssa biflora*), divides the wetland into an inner circle and outer ring. The inner circle is dominated by Water Lily (*Nymphaea* sp.), Jointed Spikesedge (*Eleocharis equisetoides*), and Panic Grass (*Panicum* sp.), whereas the outer ring has higher plant diversity and *Nymphaea* sp., Watershield (*Brasenia schreberi*), and various sedges are more common.

Trashcan traps (Luhring, in press) were employed to assess depth-specific distribution in three microhabitats; the water's surface in deep water, the deep benthic zone, and the littoral zone. Trashcan traps consist of 120-L heavy-duty household trashcans fitted with four steel funnels situated around the outside of the trashcan. The traps either had funnels situated at the top of the trashcan, effectively sampling the upper 30 cm of the water column, or at the bottom of the trashcan, effectively sampling the lower 30 cm of the water column. Trashcan traps were used as they can trap aquatic animals at depths of up to 70 cm without drowning obligate air breathers and have proven effective at capturing both sirens and amphiumas in nearby wetlands (Luhring and Jennison, 2008). A wooden dowel was used to standardize the openings of all the funnels on the traps to a width of 4 cm because differences in funnel openings can affect the capture rates and retention of aquatic herpetofauna (Willson et al., 2008). The type of traps used in this study may have biased the size of animals captured; the smallest size class of *Siren* sp. and *A. means* are usually not captured in passive funnel traps, while the limited funnel width in the traps used may also have precluded capture of larger *S. lacertina* (Luhring, unpubl. data). However, these traps are effective in sampling the widest breadth of size classes of both *Siren* sp. (88-434 mm SVL for *S. lacertina*; Luhring, unpubl. data) and *Amphiuma means* at variable water depths in comparison to other traps (e.g., hoop nets, minnow traps; Luhring, unpubl. data) and, thus, would be most effective in sampling the largest subset of the population.

Sampling efforts were divided into two arrays: a deep water array (in the inner circle; depth ranging from 42-70 cm) and a littoral zone array (in the outer ring; depths ranging from 20-42 cm). The deep water array consisted of a pair of transects with alternating trap types that were spaced 5 m apart from one another. A total of 15 surface-sampling trashcan traps and 15 bottom-sampling trashcan traps were set in the deep water array. The littoral zone array contained one transect of 15 bottom-sampling trashcan traps which were set 5 m apart from one another. Traps were set within areas of vegetation in each array. Trap funnels were cleared of vegetation when they were set to limit the amount of vegetation entering the traps. All traps were opened for 20 consecutive nights from 12 June to 1 July 2008 with each microhabitat sampled across 300 trap-nights. Traps were checked daily between 0600 hrs and 1000 hrs (E.S.T.). All captures of vertebrates and invertebrates were recorded. Salamanders were removed from the field for the duration of the study and housed under conditions previously determined to be effective for maintaining both species (Schalk and Luhring, 2010). Salamanders were measured using a wooden meter stick. All bycatch was immediately identified (invertebrates were identified to order, while fish were identified to family) and immediately released. To accurately assess the distribution of potential prey, traps containing a salamander were considered predated and, thus, were not included in statistical analyses.

Microhabitat characteristics were measured with a 1 m^2 quadrat at randomly chosen points in both arrays. To estimate vegetation cover in the quadrat, a modified version of the Daubenmire cover scale was used for floating vegetation, emergent vegetation, trees/shrubs, vegetation growing logs (e.g., sedges), and submersed vegetation, and open water (Daubenmire, 1968; Sharitz, pers. com.). Each array was considered sufficiently sampled when quadrats contained no new plant species (deep array: $n = 5$, littoral zone array: $n = 12$). The deep water array was fairly uniform in its vegetation composition and primarily consisted of floating and emergent vegetation (e.g., *Nymphaea* sp., and *E. equisetoides*, respectively), which accounted for 91% of the vegetation cover (fig. 1). The littoral zone array, however, was
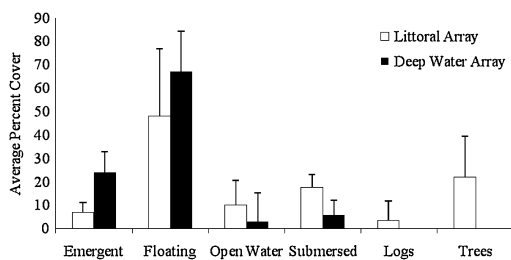

Figure 1. Estimated average percent cover (+1 SD) of vegetation/microhabitat type in the littoral array (white bars) and deep water array (which includes both the surface zone and deep benthic zone; black bars) in Peat Bay on the Savannah River Site, Barnwell County, South Carolina, USA based on a modified version of the Daubenmire (1968) cover scale.

more heterogeneous and structurally complex; floating vegetation was the most common vegetation type followed by submersed vegetation (e.g., Bladderwort [*Utricularia* sp.]), and logs/vegetation growing on logs, accounting for nearly 81% of the vegetation cover (fig. 1).

For statistical analyses, *S. lacertina*, *A. means*, and crayfish were each analyzed independently, whereas aquatic insects and fish were lumped into general taxonomic categories. Because the data were not normally distributed for all groups, a non-parametric ANOVA (Kruskal-Wallis; $\alpha = 0.05$) was used to assess differences between daily captures of salamanders captured amongst the three microhabitats. Statistical analyses were run in Statgraphics (Centurion XV Version 15.2.06).

Results

Fifty-seven *S. lacertina* were caught during the trapping period. Thirty-seven individuals were captured in the benthic zone (capture per unit effort [CPUE]; the number of individuals captured across total trap nights in each microhabitat = 0.123) while captures totaled 8 salamanders (CPUE = 0.027) and 13 salamanders (CPUE = 0.043) for the surface of the water and littoral zone, respectively (fig. 2). *Siren lacertina* capture rates were significantly higher in the deep benthic zone than the other microhabitats ($H = 20.5905$, df = 19, $P < 0.01$, fig. 2). The snout-vent length (SVL) of the *S. lacertina* captured averaged 162 mm (range

Figure 2. Average daily capture rates (+1 SD) with for Greater Siren, Two-toed Amphiuma, crayfish, fish, and aquatic insects from 12 June to 1 July 2008 in Peat Bay, on the Savannah River Site, Barnwell County, South Carolina, USA amongst the three microhabitats; the water's surface (black bars), deep benthic zone (grey bars), and littoral zone (white bars). A significant difference in capture rate among the habitats is indicated by an asterisk (∗).

92-398 mm), while total length (TL) averaged 252 mm (range 149-561 mm). *Siren lacertina* did not appear to become locally depleted as there were more captures in the last 5 days ($n = 20$) than there were for days 1-5 ($n = 12$), 6-10 ($n = 12$), and 11-15 ($n = 14$).

A total of 15 *A. means* were captured during the trapping period. Captures for *A. means* were lower than *S. lacertina* across all three habitat types; the highest number of captures occurred in the littoral zone with 12 salamanders (CPUE = 0.040), decreased to 3 individuals in the deep benthic zone (CPUE = 0.010), and none at the water's surface (fig. 2). *Amphiuma means* were captured significantly more in the littoral zone than the other microhabitats ($H = 9.36681$, df = 19, $P < 0.01$, fig. 2). Average SVL for *A. means* was 480 mm (range 346-647 mm) and 650 mm for TL (range 418-836 mm). Unlike *S. lacertina*, *A. means* may have become locally depleted during the last quarter of the study with no captures occurring during the last 5 days (there were 5, 6 and 4 captures in the first, second, and third 5-day periods, respectively).

A total of 155 aquatic insects were captured and included members of the orders Hemiptera, Coleoptera, and Odonata. Aquatic insects were captured significantly more in the deep water array than the littoral zone array ($H = 21.4507$, df = 19, $P < 0.01$, fig. 2). There was no difference in daily capture rate of aquatic insects between surface and the benthic zone of the deep water array (fig. 2). Forty-four crayfish were captured during the trapping period. Crayfish captures were significantly higher in the littoral zone than in either of the other two microhabitats ($H = 30.2815$, df = 19, $P < 0.01$, fig. 2). A total of 203 fish were captured and included six species from five families; including Amiidae, Centrarchidae, Esocidae, Poecillidae, and Umbridae. Fish were captured significantly less in the benthic zone as compared to water's surface and the littoral zone ($H = 33.4253$, df = 19, $P < 0.01$, fig. 2).
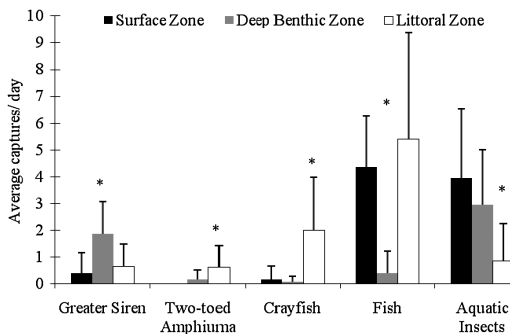
Discussion

Siren lacertina were predominately found in the deep benthic zone (where aquatic insects were most abundant and vegetation was predominately of floating and emergent types) while *A. means* occurred more frequently in the littoral zone (where fish and crayfish were most abundant and vegetation was predominantly floating, on logs, or submersed). Additionally, *S. lacertina* appeared to use the entire water column, as they were caught in both the bottom and top-sampling trashcan traps, while *A. means* were only caught in the bottom-sampling trashcan traps.

Breeding for *S. lacertina* commences in early spring (Ultsch, 1973; Hanlin and Mount, 1978), and lasts through April in South Carolina (Luhring, unpubl. data). In Florida, Ultsch (1973) noted that *S. lacertina* form breeding congregations in shallow waters and streams; thus the high occurrence of *S. lacertina* in the benthic zone may reflect a post-breeding season movement back into deeper waters. Information on the breeding biology of *A. means* is lacking; in the western portion of their range, breeding occurs in late winter (Rose, 1967) but the timing of egg deposition is unknown (Gunzburger, 2003). While it is known that the Three-toed Amphiuma (*A. tridactylum*) deposits its eggs in June (Fontenot, 1999), nests of *A. means* have been found across all seasons (Brimley, 1910; Weber, 1944; Seyle, 1985); thus, no conclusions can be drawn correlating the occurrence of *A. means* in the littoral zone to its reproductive cycle.

Amphiuma means have been described as an "opportunistic carnivore", capable of consuming aquatic insects, mollusks, and crayfish, fish, frogs, and even snakes (Carr, 1940; Hamilton, 1950; Duellman and Schwartz, 1958). However, diet analyses of *A. means* have revealed that crayfish comprise the largest part of their diet (Mount, 1975; Dundee and Rossman, 1989; Whitaker and Ruckdeschel, 2009). *Siren lacertina* have a smaller gape; while this gape limitation restricts their vertebrate prey to occasional small minnows (Hanlin, 1978) and paedomorphic Mole Salamanders (*Ambystoma talpoideum*; Luhring, 2007), they generally consume a wide variety of invertebrates with aquatic insects and mollusks comprising the largest part of their diet (Duellman and Schwartz, 1958; Hanlin, 1978; Moler, 1994).

The vegetation type differed between arrays; the deep water array primarily consisted of floating and emergent vegetation while the littoral zone array contained a higher diversity of vegetation types (with floating vegetation, logs/vegetation growing on logs, and submersed vegetation being the most common), creating a more structurally complex habitat (fig. 1). *Amphiuma means* employ both active foraging (Dundee and Rossman, 1989) and sit-and-wait (Conant and Collins, 1998) feeding strategies; they occupy crayfish burrows and other hiding places and emerge to ambush any prey passing by the entrance. While they do forage for prey, *A. means* tend to have small home range sizes and are generally more sedentary (Luhring, unpubl. data). *Siren lacertina* actively forage and have larger home ranges as compared to *A. means* (Luhring, unpubl. data). The movement ecologies of each species is reflected in our captures rates over time; no *A. means* were captured the last five days of the study while *S. lacertina* capture rates were not negatively impacted by removal over time. The high occurrence of crayfish and fish in the littoral zone array in combination with the structurally complex habitat may have been utilized by the *A. means* as suitable ambush sites. Because *S. lacertina* generally move over larger areas, the deep water array, with its higher number of aquatic insects in a more homogeneous habitat, may allow *S. lacertina* to actively forage more easily.

Previous studies have suggested possible negative interactions influencing the distribution of these two species on landscape (Snodgrass et al., 1999) and local (Luhring and Jennison, 2008) scales. Future studies should investigate spatial-temporal changes in habitat usage for *A. means* and *S. lacertina* over a longer time pe-

riod to capture changes in habitat usage associated with life history events such as reproduction and drought survival. While *A. means* have been known to consume *S. lacertina* (Schalk et al., 2009), and both species will bite each other when in an enclosed space (pers. obs.), the dynamics of any interspecific interactions existing between the two species remains unclear. These potential mechanisms could be tested through the use of manipulative field experiments in the future.

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