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Vagility of Aquatic Salamanders: Implications for Wetland Connectivity

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ABSTRACT.—Research on landscape connectivity for amphibians that use isolated wetlands has focused on terrestrial and semiterrestrial species. Although aquatic species are commonly encountered in isolated wetlands, their dispersal capability and mode of dispersal has yet to be conclusively determined. For these salamander species, temporary waterways formed during heavy rains may provide transient dispersal opportunities among otherwise terrestrially isolated wetland patches and large contiguous sources (e.g., river swamps, lake systems). We assessed the vagility of two aquatic salamanders, the Greater Siren (*Siren lacertina*) and Two-Toed Amphiuma (*Amphiuma means*), under three simulated environmental conditions: terrestrial (damp but no standing water); shallow standing water (1 cm of water); and complete submergence (approximately 5 cm of water). Salamanders were placed inside a modified Living Stream container and stimulated into moving through each treatment. Both species demonstrated a trend toward exhaustion for all treatments and failed to move more than 8 m in the terrestrial or shallow water treatments. As expected, animals in the fully submerged treatment were able to disperse the farthest. Physical characteristics of salamanders did not affect vagility. To disperse, these species likely rely on the formation of aquatic corridors during flooding events. Therefore, successful dispersal among isolated wetlands depends on the ability of the surrounding landscape either to be periodically inundated with water or to form temporary waterways during heavy rains. Human activities that alter flooding events and watershed connectivity, such as flood control regimes and roads, may have important implications for wetland connectivity and, thus, metapopulation viability of aquatic salamanders.

The influence landscape configuration has on movement patterns of amphibians is poorly understood (Gibbs, 2000). The vagility of amphibians with similar life histories can vary, and even natural landscape features (e.g., edges within forests) affect the movement of amphibians differently (Gibbs, 1998). Therefore, a species-specific examination of landscape influences on movement patterns (e.g., immigration, emigration) must be conducted to design conservation strategies. Although the movement ecology of amphibians with adult or juvenile terrestrial stages has been the subject of study previously (Berven and Grudzien, 1990; Gibbs, 1998; Funk and Dunlap, 1999; Lehtinen and Galatowitsch, 2001), the movement of aquatic species that inhabit isolated wetlands has received little attention.

Some aquatic salamanders (e.g., Sirenidae and Amphiumidae) do not have a terrestrial life stage but are commonly found in isolated

wetlands (Snodgrass et al., 1999). The Greater Siren (*Siren lacertina*) and Two-Toed Amphiuma (*Amphiuma means*) are two such species commonly found in a variety of isolated semipermanent to permanent wetlands in the southeastern United States. *Siren* and *Amphiuma* are considered poor overland dispersers (Fauth et al., 1990; Snodgrass et al., 1999). Although there have been no direct tests of the terrestrial dispersal ability of *Siren* or *Amphiuma*, there are limited records of both being found on land. *Siren lacertina* were observed retreating onto the terrestrial margins of a creek following the application of rotenone (Gibbons and Semlitsch, 1991). An *A. means* was captured in a pitfall trap on a rainy night approximately 5 m from water (Gibbons and Semlitsch, 1991), whereas another individual was found surrounding a clutch of eggs 36 m from the nearest source of water (Johnson and Owen, 2005).

Siren lacertina and *A. means* can occupy wetlands as far as 0.7 km and 0.6 km, respectively, from other bodies of water, which is suggestive of considerable dispersal capability (Snodgrass et al., 1999). Temporary waterways, channels that connect wetlands during heavy rains, have been proposed as the method of dispersal for *Siren* and *Amphiuma* (Snodgrass et al., 1999). Although Lesser Siren (*Siren inter-*

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media) were found in a temporary waterway connecting two isolated wetlands (J. W. Snodgrass, pers. comm.), this has not been observed for *S. lacertina* or *A. means*.

Anecdotal observations indicate limited terrestrial activity and use of temporary waterways but do not provide conclusive evidence on the dispersal ability and method of dispersal for aquatic salamanders. Because such events are very difficult to observe in the field, we simulated dispersal events for these species in a laboratory experiment. We tested five hypotheses to determine dispersal abilities of *S. lacertina* and *A. means* under these simulated environmental conditions: (1) Does the vagility of *S. lacertina* and *A. means* vary with water depth? (2) Does water depth affect recovery time for *S. lacertina* and *A. means*? (3) Does vagility differ between *S. lacertina* and *A. means*? (4) Do physical characteristics (snout-vent length, mass, and body condition) affect vagility? (5) Do physical characteristics (snout-vent length, mass, and body condition) affect recovery?

MATERIALS AND METHODS

Siren lacertina and *A. means* were trapped with unbaited minnow traps, hoop nets, and trash-can traps (Luhring and Jennison, 2008) at Peat Bay and Steel Creek Bay, two semipermanent shallow water ponds on the United States Department of Energy's Savannah River Site (SRS) in Aiken, South Carolina (Davis and Janecek, 1997). Additional *A. means* were provided from an unrelated trapping effort at Dry Bay, a Carolina Bay, on the SRS (Luhring, 2008).

Snout-vent length (SVL) to the nearest 1.0 mm, and body mass (BM) to the nearest 0.1 g were recorded on the day of capture for all animals. Body condition index, BCI, (Romero and Wikelski, 2003) was then calculated as:

$$[(\text{BM in grams})/(\text{SVL in millimeters})^3] \times 10^6$$

Salamanders were individually housed in plastic bins (55 × 23 × 8.5 cm if salamanders were under 400 mm in total length or 78 × 50 × 20 cm if salamanders were over 400 mm in total length), which were then placed inside a temperature-controlled room kept at 19.2 ± 1.4°C and acclimated for 24 h prior to being used for the experiment. All animals were run from 12 June to 26 July 2007 between 1000 and 1700 h.

Salamanders over or under 400 mm in total length were run on a 2.0 × 0.2 m or a 2.0 × 0.1 m track, respectively. Widths of the track were adjusted to prevent longer individuals from pushing off the sides of the track. Wooden boards (230 × 9 × 5 cm and 224 × 4 × 2 cm)

were moved laterally inside of the tank to adjust track width. Metal meter sticks were placed on top of the wood guides to measure distance moved during each trial. An artificial grass mat was used as a substrate for all treatments. The entire track was set up inside a Living Stream® container (Frigid Unit, Toledo, OH) measuring 273.5 × 61 × 59 cm. Well water was then added to or drained from the track according to treatment and allowed to reach room temperature before the trial began.

Vagility was assessed under three simulated environmental conditions: terrestrial dispersal on a damp substrate (0 cm of water), dispersal through shallow standing water (1 cm of water), and dispersal under complete submergence (approximately 5 cm of water). Individuals were randomly assigned to treatments. Salamanders were run twice through the assigned treatment with one hour to recover between each trial. A total of 16 *A. means* was run through the terrestrial ($N = 5$), 1-cm ($N = 7$), and the submerged treatments ($N = 4$). A total of 39 *S. lacertina* was run through the terrestrial ($N = 14$), 1-cm ($N = 14$), and the submerged treatments ($N = 11$). Animals were run in random order with amphiumas and sirens being interspersed in time.

Each salamander was run on a track for 15 min or until exhaustion (Shine et al., 2003; Winne and Hopkins, 2006). Salamanders were stimulated to traverse the track by lightly tapping a blunt object (e.g., pen shaft) on the side of the tail posterior to the cloaca. A single tap was administered whenever the salamander remained motionless for >5 sec. Individuals were considered to be exhausted when they received five successive taps and did not move. All trials were videotaped using a Panasonic Progressive Photoshot camcorder (model number: PV-DV73D). During film review, the total distance traveled and the time to exhaustion were recorded.

After data collection, and prior to building ANCOVA models, we analyzed correlations between our three proposed physical metrics (SVL, BM, and BCI) with Pearson correlation coefficients. Body mass was highly correlated with SVL for *S. lacertina* ($r = 0.938$, $P < 0.0001$) and *A. means* ($r = 0.922$, $P < 0.0001$) and was removed from further analyses. Body condition index was weakly correlated with SVL for *S. lacertina* ($r = 0.346$, $P = 0.031$) but not for *A. means* ($r = 0.125$, $P = 0.644$) and was retained in the analyses. We tested the effects of treatment, SVL, BCI, and species on the distance traveled during each run and on the percentage decrease in distance traveled from the first run to the second run using analysis of covariance (ANCOVA; PROC GLM). A ratio (percentage

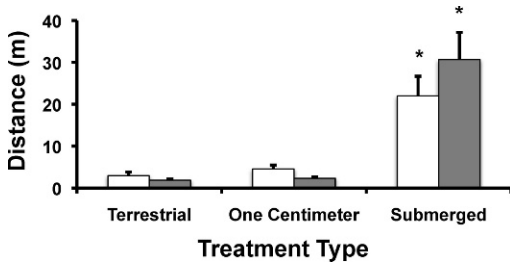


FIG. 1. Average distance traveled (± 1 SE) on first run with standard error bars for *Amphiuma means* (white) and *Siren lacertina* (grey) in the terrestrial, 1-cm, and submerged treatments. An asterisk denotes a significant difference in distance traveled between treatments.

decrease), instead of a net difference, was used to assess recovery between the first and second trials to account for the differences in total distances traveled in each treatment (i.e., animals in the submerged treatment traveled several-fold times farther than those in the other two treatments). An intercept only model was run to see whether the percentage decrease was equal to zero (i.e., to test whether animals were recovering between trials). All possible interactions between variables were included in preliminary ANCOVA models. Interactions between variables were tested for significance and then removed to create the most parsimonious model. Tukey's pairwise comparison test was used to test for differences of treatment effects. Both species were included in the final analyses so that they could be directly compared. We plotted residuals against predicted values of each model to assess homogeneity of variances. Distance traveled was log-transformed to meet the assumptions of homoscedasticity. All analyses were performed using SAS[®] version 9 (SAS Institute Inc., Cary, NC, 2000).

RESULTS

The ANCOVA model for the distance traveled in the first run (log-transformed) included species, treatment, SVL, BCI, and an interaction term for species and treatment. The model had strong support for explaining distance traveled ($F_{8,47} = 381.11, P < 0.0001$). Only treatment type ($F_{2,47} = 29.82, P < 0.0001$) proved significant. Removal of the interaction term had no effect on overall significance and was retained to test whether there was an interaction between species and treatments. A Tukey's studentized range test indicated that aquatic salamanders moved farther in the submerged treatment than either the 1-cm or terrestrial treatment.

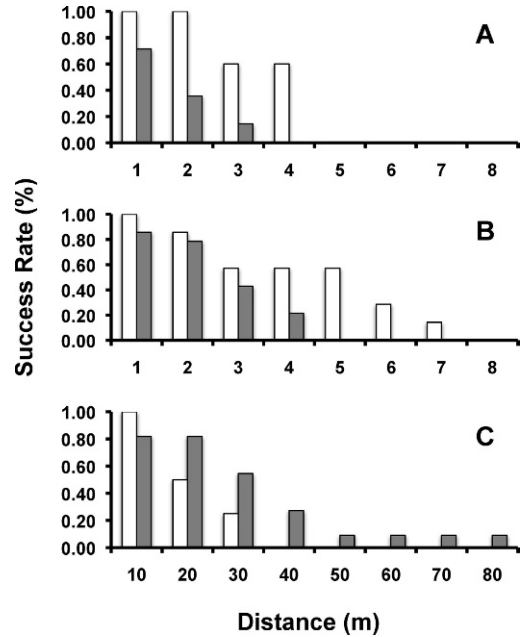


FIG. 2. Success rate (% of animals reaching distance x) by distance traveled for *Amphiuma means* (white) and *Siren lacertina* (grey) in (A) terrestrial, (B) 1-cm, and (C) submerged treatments.

When submerged, *A. means*, on average, traveled more than 6 \times and 4.5 \times farther than those in the terrestrial and 1-cm treatments, respectively (Fig. 1). *Siren lacertina* in the submerged treatment, on average, traveled more than 15 \times and 11 \times farther than those in the terrestrial and 1-cm treatment, respectively (Fig. 1). Distance traveled did not differ significantly between the terrestrial and 1-cm treatments although animals generally moved farther in 1-cm of water.

Species did not affect distance traveled in the first run ($F_{1,47} = 1.89, P = 0.175$). Although a significant difference was not detected between species for distance traveled, the high degree of variability between animals and the low number of *A. means* used in each treatment may have reduced power to detect differences between species. For this reason, and because of the lack of any such data in the literature, we include a brief description of movements (Fig. 2). The farthest distances traveled in the terrestrial treatment for *A. means* and *S. lacertina* were 4.6 m and 3.8 m, respectively. In the 1-cm treatment, the maximum distances traveled by *A. means* and *S. lacertina* were 7.9 m and 4.3 m, respectively. Approximately 21% of sirens traveled a minimum of 4 m in the 1-cm treatment (farther than any traveled in the terrestrial treatment). Although no *A. means*

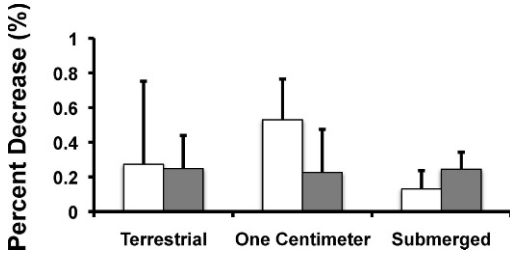


FIG. 3. Average percentage decrease (± 1 SE) in distance traveled from first run to second run for *Amphiuma means* (white) and *Siren lacertina* (grey).

traveled farther than 5 m in the terrestrial treatment, more than 57% traveled a minimum of 5 m in the 1-cm treatment. The maximum distances traveled in the submerged treatment for *A. means* and *S. lacertina* were 33.0 m and 80.1 m, respectively. Although no *A. means* traveled more than 40 m in the submerged treatment, 27% of *S. lacertina* moved farther than 40 m. Most salamanders moved for the entire 15-min period in the submerged treatment.

The ANCOVA model for percentage decrease from the first run to the second run included species, treatment, SVL, and BCI and did not explain a significant amount of the variance ($F_{6,42} = 1.55$, $P = 0.19$) nor did simpler models. Overall, animals did not travel as far in their second trial ($F_{1,47} = 8.62$, $P = 0.0051$), indicating that they did not recover fully during the one-hour rest period. On average, animals demonstrated a decrease of 27.8% in distance traveled from their first run to second run (Fig. 3). One major outlier (an *A. means* in the terrestrial treatment that barely moved on the first run and then moved 5.3 times as far in its second run) was removed from analyses of percentage decrease. Interaction terms for this model were not significant. Analyses of ratios are considered questionable (see Atchley and Anderson, 1978). To account for this, we also ran a logistic regression (Proc Logistic) with recovery as a binomial but did not get a different result than the ANCOVA model.

DISCUSSION

Distance traveled for *S. lacertina* and *A. means* in the terrestrial and 1-cm treatments were limited compared to the submerged treatment. Generally, distance traveled increased for both species with increasing water depth with full submergence resulting in the greatest observed distances. These results support the idea that temporary waterways are the likely conditions that enable animals to disperse to and from otherwise terrestrially isolated wetlands. The

methods used to encourage salamanders to traverse the track may not have been optimum for *A. means* because they appeared to respond to tapping by remaining motionless. Conversely, *S. lacertina* responded immediately to tapping by traversing the track until they became exhausted. Because of this perceived difference in response, we believe that the dispersal distances we observed for *A. means* are conservative and possibly underestimated. However, simulated dispersal distances for *S. lacertina* with limited or no water are likely more indicative of their maximum short-term dispersal capabilities as they consistently demonstrated signs of exhaustion (e.g., indifference to human touch, limp body when transferred to holding bin) at the end of their terrestrial and shallow water trials. Both species appeared to move across the terrestrial treatment in short bursts, tiring shortly after the trial began. Neither species recovered fully after an hour of rest in complete submergence, which would presumably be more optimal than terrestrial recovery. In the wild, individuals would be forced to recover on land between these periodic movements. Although both species are well suited to surviving droughts in organic sediments at the bottom of wetlands, it is unclear whether either species can find and use suitable terrestrial refugia between dispersal events.

Multiple accounts report finding *Amphiuma* on land, especially on rainy nights (Carr, 1940; Gibbons and Semlitsch, 1991), which may be attributable to egg deposition (Gunzburger, 2003). *Amphiuma* nests have been found in the terrestrial environment but are often close to a body of water (Gunzburger, 2003). Their moderate ability to traverse terrain with little to no standing water may be an important adaptation for terrestrial egg deposition within a few meters of water. However, it is still likely that *A. means* require temporary waterways to move among terrestrially isolated wetlands hundreds of meters apart. In contrast, *S. lacertina* lay their eggs in water (Goin, 1947), and the absence of reproductive necessity to venture onto land may have precluded physiological or morphological adaptations for terrestrial movement.

Although physical features were not correlated with dispersal distance or recovery in any of the treatments, all animals used in the trials were greater than 100 mm or 18 g. The dispersal ability of smaller aquatic salamanders may be important for interwetland connectivity because they may be able to disperse greater distances in less water than larger animals. Although small sirens (e.g., young of year) can survive short-term droughts in the field (TML, unpubl. data), laboratory-simulated conditions indicate that

increased body size increases the ability to survive prolonged periods of drought (Martof, 1969; Etheridge, 1990a,b). Thus, there may be a trade-off between dispersal ability and drought survival as body size increases.

The spatial arrangement of wetlands with respect to elevation gradients and degree of isolation affects the distribution of *Siren* and *Amphiuma* within a landscape (Snodgrass et al., 1999). Furthermore, these results suggest that aquatic salamanders require terrain between wetlands to be inundated with water during flooding events, leading to the creation of aquatic corridors that allow for their dispersal. Maintaining a landscape that permits aquatic corridors to form enhances wetland connectivity and can ameliorate the loss of local populations of these species to periodic severe drought or other stochastic extirpation events. Landscape alterations that change the dynamics of natural processes such as flood control regimes may likely prevent dispersal of *Siren* and *Amphiuma* among terrestrially isolated wetlands. Roads also fragment landscapes (Gibbs, 1998) and may act as a barrier for the formation of temporary waterways between wetlands, effectively isolating populations. However, roadside ditches may increase the accessibility of otherwise isolated wetlands to aquatic salamanders and predatory fishes.

The degree with which populations of aquatic salamanders in isolated wetlands and large permanent bodies of water interact as discrete populations (e.g., mainland-island metapopulations; Harrison, 1994) is unknown. In a hydrologically controlled area (e.g., wet units in a management area), a large scale cohort marking of sirens (see Luhring, in press) prior to predictable flooding events would provide insight into behavioral responses to floods and dispersal abilities in the field. In natural systems, molecular techniques may provide the most efficient method of determining movements among wetlands of varying sizes, hydroperiods, and degrees of isolation.

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