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Responses of Semi-aquatic Snakes to Drought

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by

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ABSTRACT

Aquatic ecosystems and their associated wildlife are threatened by alteration in the frequency and intensity of precipitation events predicted to affect many regions as a consequence of global climate change. Semi-aquatic snakes serve important roles as predators and prey within aquatic ecosystems, yet little is known about the effects of drought on these species due to their secretive behavior. Long-term studies at an isolated wetland in South Carolina found that drought caused populations of banded watersnakes (*Nerodia fasciata*) and Florida green watersnakes (*Nerodia floridana*) to crash. Alternatively, black swamp snakes (*Seminatrix pygaea*) fared well, exhibiting a resistance strategy by aestivating within the wetland. This thesis presents two studies that build on our understanding of these observed patterns. The first chapter evaluates the generality of these interspecific differences in drought susceptibility by conducting a landscape scale analysis of semi-aquatic snake responses to drought using an occupancy modeling approach. We compared changes in occupancy and detectability from 20 isolated wetlands in South Carolina before drought to after drought. Our results confirm that interspecific patterns of drought sensitivity observed previously at one wetland are paralleled at the landscape scale. Specifically, site occupancy decreased dramatically for *N. fasciata* (0.95 to 0.69) and *N. floridana* (0.32 to 0.05) but was relatively unchanged for *S. pygaea* (0.41 to 0.45), *Farancia abacura* (0.49 to 0.49) and *Regina rigida* (0.10 to 0.28). Our results confirm that supra-seasonal drought can have negative effects on some, but not all, semi-aquatic snake species. The second chapter investigates interspecific variation in two traits that may mediate species' responses to drought: evaporative mass loss (EML; the rate of water and product lost through respiratory, cutaneous and ocular pathways) and locomotor endurance (total distance, total time, and speed traveled before exhaustion in aquatic habitats and in hydrated and dehydrated state in terrestrial habitats). We find that for EML, species group into three categories that do not follow taxonomic relationships, with *N. floridana* exhibiting unexpectedly high and *Regina rigida* (glossy crayfish snake) exhibiting unexpectedly low rates of EML. Species also vary in their ability and willingness to move over land, suggesting that some species may be more willing or able to make terrestrial overland movements in response to drought than others. Our results identify important mechanisms that may drive variable responses of semi-aquatic snakes to environmental variation. In particular, the apparent sensitivity of *N. floridana* to drought may be driven in part by its high rate of EML and reluctance to move terrestrially. Taken together, this thesis builds our understanding of patterns of interspecific variation in sensitivity to drought and traits that may underpin this variation. This information is a critical component of understanding, predicting, and mitigating populations threated by climate change and other anthropogenic alterations to the environment.

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I. INTRODUCTION

Unlike any other celestial body known to man, planet Earth provides bountiful and essential resources necessary to support and sustain life. Many of these resources and their renewable qualities are deteriorating due to rapidly increasing human populations (United Nations, 1999) engaged in gross over-consumption. This phenomenon has brought Earth to the brink of an ecological catastrophe, as the pace of human activity outpaces compensatory ecosystem processes. These rapid changes have altered many of Earth's natural processes, producing or accelerating many phenomena such as shifts in mean global temperature, loss of sea ice, sea level rise, and ocean acidification (Meehl et al., 2007). Synergistically, these factors contribute to changes in global climate that include dramatic changes in precipitation patterns and increases in extreme weather events (Trenberth et al., 2007).

In coincidence with altered precipitation extremes, the frequency and intensity of drought has increased globally (Trenberth et al., 2007). Arguably, droughts are formed by sunspots (Tannehill, 1949), solar forcing (Hodell et al., 2001), or fluctuations in large scale sea-surface temperatures that stall dry, high pressure, air systems (Lake, 2011). Although, there are many ways to define drought and no universal definition (Bond et al., 2008), two types fit into the context of freshwater systems addressed in this thesis: 1) periodic and predictable seasonal droughts, and, that which is the focus of thesis, 2) longer and unpredictable supraseasonal droughts characterized by a decline in precipitation and available water (Lake, 2003). Droughts alter the structure and function of ecological systems (Lake, 2003; Dahm et al., 2003) and associated wildlife (e.g., Rhind & Bradley, 2002; Sperry & Weatherhead, 2008).

Previous research regarding effects of drought on wildlife populations is limited compared to some other types of stochastic events (e.g., flooding; Ratcliffe et al., 2005) due to droughts' unpredictability, long temporal extent, and the lack of a standardized system for characterizing drought severity (Lake et al., 2007). Nevertheless, drought-associated population declines have been documented in focal studies of a diverse array of species, including primates (e.g., Gould et al., 1999), marsupials (e.g., Fisher et al., 2001; Gordon et al., 1988), fish (e.g., Matthews & Marsh-Matthews, 2003; Hakala & Hartman, 2004), insects (e.g., Rouault et al., 2006; Mattson & Haack, 1987), reptiles (e.g., Sperry & Weatherhead, 2008; Lillywhite & Tu, 2011), amphibians (e.g., Dodd, 1994), and birds (e.g., Robertson, 1987; Brenner, 1966). Although these focal studies build a foundation for understanding species' responses and population trends, they have intrinsic limitations since they often represent trends over small spatial scales. Few studies have tested how universal these patterns are across the landscape (e.g., Walls et al., 2013; Price et al., 2012).

Regardless of the information available about trends of a particular population of interest, identification of organismal traits that are important in mediating drought responses is often difficult (Williams et al., 2008). Species vulnerability to climatic change such as drought, depends on the species exposure, sensitivity, resilience, and potential to adapt to these changes (Huey et al., 2012). Particularly, physiological traits often determine a species sensitivity to environmental extremes (Huey et al., 2012), and have been of particular focus in predicting extinction risk (Sinervo et al., 2010), and range-shifts (Humphries et al., 2002), due to climatic changes. For example changes in sea surface temperature were found to result in behavioral limitations and reproductive failure related to the physiology of intertidal species like barnacles and polychaetes, resulting in significant range shifts over the last century (Wethey & Woodin, 2008; Mangum & Cox, 1981). However, to our knowledge, few studies have investigated physiological mechanisms that might explain observed population responses to drought. Identification and understanding of these mechanisms will help forecast the impacts of climate change to assist researchers, resource managers and policy makers (Helmuth, 2009). However, the current information gap impedes our ability to generalize trends from focal studies to other scales, populations, or species.

Species with physiological adaptations to drought are said to have ‘resistant’ and/or ‘resilient’ traits (Bond et al., 2008). Those species termed ‘resistant’ avoid mortality through desiccation resistance or by selecting habitat less affected by drought. Alternatively, resilient species have high capacities for dispersal and/or recruitment that allow them to recover rapidly from drought-induced declines (Bond et al., 2008). Two physiological mechanisms that may be important in mediating drought effects are evaporative mass loss and locomotor performance. Since water is scarce during drought and is likely a limiting factor for survival, minimizing evaporative water loss via respiratory, cutaneous, and ocular pathways, (Mautz, 1982) may be an essential adaptation for resistant species. For resilient species, overall capacity to disperse, quantified by metrics like maximum dispersal distance and speed, is likely a critical attribute influencing drought survival and recovery.

Snakes are one group of organisms that may possess resistance or resilience traits to cope with drought. As ectotherms, many snakes can persist for long durations without eating, separating themselves from the often cyclical abundance patterns of their prey (McCue, 2007). For semi-aquatic snakes, explosive prey-densities, limited competition, and high feeding frequency allows snakes to reach unprecedented abundances in some ecosystems. For example, dog-faced watersnakes (*Cerberus schnederii*) can reach densities of 102 snakes per hectare in mangrove tidal swamps in Singapore (Chim & Doiong, 2013) and black swamp snakes (*Seminatrix pygaea*) and banded watersnakes (*Nerodia fasciata*) were estimated to reach densities of 171 snakes per hectare and consume over 37 kg per hectare of amphibian prey annually in isolated wetlands of South Carolina, USA. Therefore, since snakes can reach high abundances and consume large quantities of prey in aquatic systems, they are considered important predators to aquatic systems like isolated wetlands (Willson & Winne, 2016).

Long-term research on semi-aquatic snake population dynamics within one wetland in the Southeastern United States has yielded substantial information on the effects of drought on semi-aquatic snake communities. Ellenton Bay is a 10 hectare, semi-permanent, isolated wetland rich in reptile and amphibian diversity. Since 1975, this wetland has experienced multiple short-term periodic droughts and three multi-year supraseasonal droughts that resulted in periods of sustained and complete drying. Seigel et al. (1995), Winne (2008) and Willson et al. (2006) sampled snakes at Ellenton Bay using diverse methods before and after supraseasonal drought events, piecing together drought responses and population trends for a number of semi-aquatic snake species. The highly aquatic black swamp snake (*Seminatrix pygaea*) was least effected by drought, exhibiting a resistance strategy by aestivating within the wetland, and exhibiting little change in relative abundance over multi-year droughts (Winne, 2008). Conversely, the banded watersnake (*Nerodia fasciata*) suffered a drastic reduction in relative abundance during droughts, but quickly recovered post-drought through rapid reproduction and recruitment as a resilience strategy. Exhibiting neither a resistance nor resilience strategy, the Florida green watersnake (*Nerodia floridana*) was locally extirpated by drought, took years to reestablish, and never regained its pre-drought relative abundance (Willson et al., 2006; Seigel et al., 1995). Thus, dramatic interspecific variation in both behavioral and population responses to drought was observed. This thesis addresses two main objectives: 1) to determine if these population-level patterns in drought sensitivity among semi-aquatic snakes translate to landscape-scale changes in occupancy and abundance; 2) to identify important physiological mechanisms that might drive interspecific variation in drought responses.

In my first chapter, I used an occupancy modeling framework to investigate the effect of a supra-seasonal drought on the distribution and abundance of a semi-aquatic snake community in the Southeastern Coastal Plain of the Southeastern United States. I collected presence/absence data using repeated systematic trapping of snakes within 20 isolated wetlands in South Carolina. I then compared our results with similar data collected in 2006, prior to the drought to assess changes in occupancy and abundance during drought. I also investigated wetland and landscape covariates that might relate to species occupancy or detectability. I hypothesized that historical species patterns documented at one wetland would translate for all species across the landscape. For example, I predicted that both occupancy and detectability of *S. pygaea* would remain constant and that both *N. fasciata* and *N. floridana* would experience significant reductions in both parameters.

In my second chapter, I investigate mechanisms that might explain observed interspecific variation in snake responses to drought. I hypothesize that EML and locomotor performance are key traits that might heavily influence a species' ability to respond to drought. I measured interspecific differences in EML for five semi-aquatic snake species by mass lost by individuals held for six hours in an environmental chamber at 27°C and 50% relative humidity. I hypothesized that species would vary in their rates of water loss and locomotor ability, and that these physiological capabilities might relate to documented population and community dynamics related to periodic extreme droughts. For example, I predicted that severe declines in *N.*

floridana might be partially explained by high rates of EML. I also constructed two circular tracks (aquatic and terrestrial) to evaluate interspecific variation in locomotor performance of 50 individual snakes of four species. Each snake performed three trial types: fully aquatic, hydrated terrestrial, and dehydrated terrestrial and performance of each species was quantified using metrics such as total distance to exhaustion, total time to exhaustion, and speed traveled before exhaustion. We predicted that hydrated snakes would travel farther terrestrially than dehydrated snakes, and that large species known to disperse long distances (e.g., *N. fasciata* and *F. abacura*) would travel farther terrestrially than smaller species that are rarely encountered out of water (e.g., *S. pygaea*).

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II. LANDSCAPE-SCALE CHANGES IN OCCUPANCY AND DETECTABILITY OF SEMI-AQUATIC SNAKES DURING A SUPRASEASONAL DROUGHT

A. Abstract

Climate change is predicted to result in increased average temperatures and alteration in the frequency and intensity of precipitation events, placing stress on aquatic ecosystems and their associated wildlife. Semi-aquatic snakes serve important roles as predators and prey within aquatic ecosystems and several species are threatened. Yet, little is known about the effects of drought on semi-aquatic snakes due to their secretive behavior. Long-term studies at an isolated wetland in South Carolina found that drought caused populations of banded watersnakes (*Nerodia fasciata*) and Florida green watersnakes (*Nerodia floridana*) to crash. Alternatively, black swamp snakes (*Seminatrix pygaea*) fared well, exhibiting a resistance strategy by aestivating within the wetland. However, the generality of these interspecific differences in drought susceptibility remains unknown. We collected presence/absence data using repeated systematic trapping of snakes within 20 isolated wetlands in South Carolina before the onset of a multi-year supraseasonal drought in 2006. After the drought ended in 2013, we resampled those same 20 wetlands and used occupancy modeling to determine drought-induced shifts in occupancy and detection for five semi-aquatic snake species. We also collected wetland and landscape covariates that may influence species occupancy, detectability, and drought susceptibility. Site occupancy decreased dramatically for *N. fasciata* (0.95 to 0.69) and *N. floridana* (0.32 to 0.05) but was relatively unchanged for *S. pygaea*, *Farancia abacura* (mudsnake), and *Regina rigida* (glossy crayfish snake). Our results confirm that supra-seasonal drought can have varying effects on distribution and abundance of semi-aquatic snake species**.**

Species that lack adaptations that make them resistant or resilient to drought may become locally extirpated.

B. Introduction

Earth is currently experiencing a sixth mass extinction (Barnosky et al., 2011). Various anthropogenic impacts contribute to rapid environmental changes that have altered ecosystems and eliminated species across the globe (Allen, 2010). In combination with other drivers of change, such as invasive species introductions and habitat destruction, global climate change produces a synergistic effect on biodiversity loss and ecological responses (Walther, 2010; Tilman, 1994; Przeslawski et al., 2005; Dukes & Mooney, 1999). For example, at least one vertebrate extinction is attributed to climate change (Pounds et al., 1999), and minimal climate warming scenarios estimate approximately 18% of species are committed to extinction by 2050 (Thomas et al., 2004). Two important consequences of global climate change are increased warming and alteration of precipitation regimes that may affect community composition and species distributions (Trenberth, 2011; Brown et al., 1997; Walther et al., 2002). For example, both the frequency of heavy precipitation events and drought have increased in many regions (Trenberth et al., 2007), resulting in shifts in habitat suitability for many species. Thus, species distributions may rapidly shift in elevation or latitude (Chen et al., 2011). As shifts occur, well established species interactions may change or unravel (Walther et al., 2002; Yang & Rudolf, 2010). This reorganization of community composition may result in trophic cascades and changes in processes essential to ecosystem integrity (Dukes & Mooney, 1999).

One undesirable consequence of alterations in precipitation due to global climate change is supra-seasonal drought. Climate change models predict that drought frequency, intensity, and duration will increase in many regions (Meehl et al., 2007). Defined as long, irregular, and unpredictable periods of below average rainfall (Lake, 2003), supra-seasonal drought can strongly influence the magnitude of other stochastic disturbance events. For example, prolonged drought desiccates dead and decaying organic materials, increasing their flammability and fire risk (Knight, 1987; Bigler et al., 2005). Drought can also reduce the available water, food, and habitat resources within an ecosystem, thereby influencing survival, growth, and reproduction of wildlife. For example, brush-tailed phascogales (*Phascogale tapoatafa*) suffered 15-25% reductions in body size and a one-third reduction in species detection probability during drought (Rhind & Bradley, 2002). Depending on the severity, drought may result in simple negative effects on the health of individual organisms or large reductions in populations (Seabrook et al., 2011). Metapopulation dynamics can also be altered, as drought influences home range sizes, dispersal, and colonization. For example, during a drought year, desert tortoises (*Gopherus agassizii*) occupied smaller home ranges, fewer burrows, and were less active than in non-drought years (Duda et al., 1999). Finally, as the available surface water across a landscape is limited, wildlife is forced to concentrate, increasing the severity of competition and probability of disease (Kock, 2005).

Drought inflicts considerable stress on a variety of organisms, especially those that are closely tied to aquatic systems. Traditionally, species regularly confronted with drought exhibit either resistance or resilience traits (strategies) that allow them to either survive or recolonize and repopulate after drought-induced declines, respectively (Bond et al., 2008). However, projected increases in drought intensity may be too extreme for even “drought-tolerant” species to withstand (Bond et al., 2008). Of the organisms vulnerable to climatic changes in aquatic environments, semi-aquatic snakes fall into a peculiar category in regards to their ability to confront change. Semi-aquatic snakes that rely on aquatic habitats for shelter and food and can withstand long periods of starvation due to low metabolic demands (Pough, 1980), but exhibit limited vagility due to physiological characteristics such as high rates of evaporative water loss and small body size (Winne et al., 2001 & 2006). However, due to their secretive behavior, little is known about what strategies semi-aquatic snake species employ to deal with drought or the consequences of these strategies for long term dynamics of populations and communities that experience periodic supra-seasonal drought events.

Decades of intense herpetological research at Ellenton Bay, a ten hectare isolated semi-permanent wetland in the Coastal Plain of the Southeastern United States, has yielded insight into the influence of drought on semi-aquatic snake population and community dynamics. Since 1974, Ellenton bay experience multiple periodic droughts including three multi-year supraseasonal droughts (Fig 1.) The highly aquatic black swamp snake (*Seminatrix pygaea*) was least effected by drought, exhibiting a resistance strategy by aestivating within the wetland and exhibiting little change in relative abundance over multi-year droughts that left the wetland dry and devoid of larval amphibian prey for months (Willson et al., 2006). Conversely, the banded watersnake (*Nerodia fasciata*) severely, but quickly recovered post-drought through rapid reproduction and recruitment as a resilience strategy. In fact, *N. fasciata* represented nearly half of captures pre-drought, was nearly undetectable for at least a year following drought, but recovered to and exceeded pre-drought abundances within three years (Winne, 2008; Willson et al., 2006). Exhibiting neither a resistance nor resilience strategy, the Florida green watersnake (*Nerodia floridana*) was locally extirpated, took three years to reestablish, and never regained its pre-drought relative abundance (Willson et al., 2006; Seigel et al., 1995). Thus, dramatic interspecific variation in both behavioral and population responses to drought was observed.

However, additional investigation is needed to determine if these patterns are location-specific, or if they occur broadly across the landscape.

In this study, we investigated variation in landscape scale-effects of drought on distribution and abundance of five sympatric semi-aquatic snake species –*Nerodia fasciata, N. floridana, Seminatrix pygaea*, mud snake (*Faranacia abacura*), and glossy crayfish snake (*Regina rigida*). We capitalized on an intense supraseasonal drought occurring from 2007- 2012 to systematically sample for semi-aquatic snakes before and after drought. We estimated pre- and post-drought species-specific detectability (p) and occupancy (psi) across twenty wetlands using an occupancy modeling framework (MacKenzie, 2006). We investigated landscape and wetland characteristics that may influence shifts in abundance and distribution associated with drought. Our study represents the first landscape-scale analysis of drought effects on snake communities, and highlights the importance of understanding species' responses to environmental variation that may be exacerbated by climate change.

C. Methods

Study Sites

Twenty freshwater wetlands located on the US Department of Energy's Savannah River Site (SRS) representing a diverse hydrological gradient from semi-permanent to permanent were surveyed in 2006 (pre-drought; Fig. 1) and 2013 (post-drought) for semi-aquatic snakes. From 2007-2012 the SRS experienced the most severe drought in at least the past three decades, leaving most isolated wetlands dry for months at a time (Fig. 1). The SRS encompasses nearly 932 km^2 within the Upper Coast Plain of South Carolina (Aiken and Barnwell Counties), USA, and includes a variety of habitats such as bald cypress swamp, long leaf pine forest, black water creeks, and Carolina bays, and other freshwater wetlands. The Savannah River forms the western boundary of the site, with an extensive floodplain composed of semi-permanent water and lowland forest. The SRS encourages management (fire), conservation (set aside areas), and research, while limiting anthropogenic impacts, resulting in relatively pristine and unfragmented habitats in comparison to surrounding landscape.

The 20 wetlands selected for sampling were between 5 and 150 ha in size and were chosen to meet the following criteria: 1) open canopy, 2) surface water/precipitation dominated, 3) <1 mile from access (road), 4) non-polluted, and 5) within SRS boundaries. The selected wetlands included most of those available that met the aforementioned selection criteria and were selected to be representative of the entire population (e.g., Thompson & Seber, 1996; Mackenzie, 2005).

Field Methods

All wetlands were sampled during May and June in 2006 (pre-drought; Durso et al., 2011) and 2013 (post-drought). Snakes were captured using plastic minnow traps (model 700, Gator Buckets, Ladoga, IN) which are effective for capturing semi-aquatic snakes (Willson et al., 2008). In both years, one array of 60 traps was set each night for five consecutive nights (300 trap-nights) per wetland; thus one array-night (60 trap-nights) represented one sampling unit. In 2006, five wetlands had dried sufficiently that they could not accommodate the full array of 60 traps. Thus, these five wetlands were trapped with half of the standard effort: 30 traps for 5 nights (150 trap-nights). To account for this heterogeneity in effort, a sampling covariate for effort was incorporated into model selection in 2006. Effort was categorized by “1” for the 5 wetlands that were trapped with 30 traps and “2” for the remaining 15 wetlands that were trapped with 60 traps. Traps were placed 2-3 m apart in shallow water at the vegetated periphery of each wetland, leaving (~1”) of trap above water to provide air for captured animals. Traps were checked daily and captured snakes were measured (sex, snout-vent length [mm], body mass [nearest 0.01 g on a digital balance]), and released at the capture location within 10 m of the trap array, immediately (2013) or within 24 h (2006). Traps were self-baited due to the capture and accumulation of prey such as amphibians, fish, and crayfish. Predatory invertebrates (large diving beetles, giant water bugs, and large crayfish) that could potentially harm captured snakes were removed each day.

Covariates

We measured seven site covariates based on perceived importance and previous research (Durso et al., 2011). Distance to the Savannah River floodplain was measured from the center of the wetland of interest to the nearest boundary of the floodplain, using ArcGIS. Wetland permanence was assigned either quantitatively, depending on the number of days each wetland contained standing water during drought, based on historical hydrological data for some wetlands, or qualitatively, based on observations of wetland hydrology by the authors between 1998 and 2013, a time frame that included at least two supraseasonal droughts (Fig. 1). Wetlands were ranked as follows: 1 (never dries), 0.80 (only dries during supra-seasonal droughts), 0.60 (only dries periodically), 0.40 (dries annually but stays filled in wet years), 0.20 (dries annually).

Four site covariates representing wetland prey communities were generated based on relative abundance in minnow traps: (mole salamander larvae [*Ambystoma talpodium*] relative abundance, fish relative abundance, crayfish relative abundance, giant salamander relative abundance [*Siren* and *Amphiuma*]) were recorded before and after drought. A fifth habit covariate was created by subtracting pre-drought fish abundances from post-drought fish relative abundances, producing the change in fish abundance associated with drought for each wetland. Minnow traps were allowed to accumulate prey for the first 24 h after being set. Counts of all fish, larval and paedomorphic *A. talpoideum*, giant salamanders, and crayfish were then tallied as the average number of individuals per trap. Only 2006 prey data were used as covariates in addition to the change in fish variable.

Data Analysis

Occupancy modeling allows for the estimation of a proportion of an area inhabited by a species (occupancy) while accounting for the probability that species may be missed or overlooked during surveys due to imperfect detection. Single-species, single-season occupancy models were constructed in program PRESENCE (MacKenzie et al., 2006) to estimate occupancy (ψ) and detectability (p) of five snake species separately in pre (2006) and post-drought (2013) years. The following model assumptions were met to avoid bias of parameter estimates 1) within years, sites were closed to changes in occupancy 2) no false presences in the data (i.e. no misidentifications) 3) no unmodeled heterogeneity in detection probability and 4) species detection histories are independent (MacKenzie et al., 2006). We attempted to use more robust multi-season models (MacKenzie et al., 2006) that allow estimation of extinction and colonization probabilities, but these models frequently failed to converge due to small sample size and low detectability.

A Principal Component Analysis (PCA) in Primer (Clarke & Gorley, 2006) was used to reduce the seven selected covariates (*see Covariates*) into two informative composite variables with orthogonal rotation (C1 and C2). Covariates were combined into components to reduce dimensionality, simplify model selection (7 variables to 2 variables), and increase statistical power without violating common rule of thumb; covariates < (0.1-0.2 x sample size; Harrell, 2001). The two components with the highest percent variation (C1 and C2) were extracted from a five component analysis. All raw covariate data was z-transformed before the PCA was conducted (Jury, 1964).

Akaike's Information Criterion (AIC) model selection was used to explore covariate effects on ψ and p for all candidate models. AICc was used for all species across all seasons by specifying the effective sample size using a conservative approach based on the number of sampling units (20 wetlands; MacKenzie, 2006). A set of sixteen models was considered in the selection process for each species in each season (Table 1) starting with the global model, the most complex model that contains the most parameters (i.e., ψ(C1,C2) p(C1,C2)). From the global model, models were constructed representing each possible combination of constant (.), C1, and C2, including the null model (ψ(.) p(.)), for occupancy and detectability (see Table 1). For 2006, an effort covariate (E) was included for p in all models to account for heterogeneity in sampling effort (see above). The global model was parametric bootstrapped 1000 times to assess model fit and c-hat was adjusted for over or underdispersion (MacKenzie & Bailey, 2004; Akaike, 1998; Burnham & Anderson, 2002). If overdispersed, models were reranked using QAIC and the number of model parameters was increased by one. For underdispersed models, c-hat was inflated to 1 and AICc ranking was used (White et al, 2001; Medeiros & Feed, 2009). Models with values < 2 AIC were considered as supported top models.

Because PRESENCE does not present derived parameters directly in the likelihood, standard errors for all parameters must use the Delta Method to calculate the variance of backtransformed estimates in order to estimate 95% confidence intervals. We used a simplified version by taking the desired untransformed regression coefficient (β) and adding or subtracting it to the untransformed standard error, then back-transforming to get the upper or lower confidence interval of the estimate.

In order to assess factors that might influence shifts in abundance of each species, raw capture rates of *N. fasciata*, *N. floridana*, and *S. pygaea*, standardized for effort, were visually examined in each year relative to wetland permanence and distance to the Savannah River floodplain.

D. Results

Aquatic trapping across 20 wetlands resulted in 242 captures of 10 species in 2006 (5250 trap-nights) and 113 captures of 10 species in 2013 (6000 trap-nights). The five species used in our analysis included *Nerodia fasciata* (2006 n = 147; 2013 n = 42 captures), *Nerodia floridana* (2006 n= 15; 2013 n = 5); *Seminatrix pygaea* (2006 n = 37; 2013 n = 27), *Farancia abacura* (2006 n = 27; 2013 n = 15) and *Regina rigida* (2006 n = 5; 2013 n = 4).

Principal component analysis yielded two factors that explained 62% of the cumulative variation in site covariates (Table 2): C1, 42.3% of variation, eigenvalue = 2.98; and C2, 19.7% of variation, eigenvalue = 1.39. Principal component one (C1) was strongly negatively correlated with wetland permanence, fish abundance, and giant salamander abundance, and positively correlated with *A. talpoideum* abundance and change in abundance of fish. Thus, wetlands with high scores for C1 were less permanent and had undergone a large change in fish abundance during drought, thus leading to lower abundance of fish and giant salamanders, but higher abundance of crayfish and *A. talpoidium*. Principal component two (C2) was strongly negatively correlated with proximity to the Savannah River floodplain and *A. talpoidium* abundance, and positively correlated with crayfish abundance. Therefore, wetlands with higher scores for C2 were closer to the Savannah River floodplain and had lower abundances of *A. talpoidium,* but higher abundance of crayfish.

Model selection revealed that for most species in both pre and post-drought years either the null model was favored and/or multiple models were favored with low individual weight (W_i) (Table 1), likely due to the relatively small number of sites we were able to sample. Two species did have heavily weighted top models in 2013 (post-drought). The top model for *N. fasciata* favored C1 ($W_i = 0.65$) for both occupancy and detectability; indicating post-drought association with wetland permanence for this species. Conversely, the top model for *R. rigida* favored C2 ($W_i = 0.66$) for both occupancy and detectability; indicating an association with distance to the Savannah River floodplain for this species.

Interspecific variation in both null model occupancy and detectability occurred in both pre and post-drought years (Fig. 2). Pre-drought detectability estimates were relatively high, ranging from $p = 0.44$ (*N. floridana*) to $p = 0.69$ (*N. fasciata*). Pre-drought, *N. fasciata* occupied nearly every wetland sampled and had the highest estimated occupancy of any species ($\psi = 0.95$). Alternatively, the congeneric *N. floridana* was estimated to only occupy one-third of the wetlands sampled ($\psi = 0.32$). *Seminatrix pygaea* was estimated to occupy approximately forty percent ($\psi = 0.41$) and *F. abacura* fifty percent ($\psi = 0.52$) of wetlands. The species with the lowest occupancy estimate pre-drought was *R. rigida* ($\psi = 0.10$).

Post-drought occupancy was generally lower than pre-drought, ranging from $\psi = 0.05\text{-}0.63$ across species. Both *Nerodia* species suffered reductions in occupancy whereas all other species did not change. *Nerodia floridana* and *N. fasciata* experienced almost identical absolute reductions in occupancy (*N. floridana*: pre-drought $\psi = 0.32$; post $\psi = 0.05$; $\Delta = -0.27$; *N. fasciata*: pre-drought $\psi = 0.95$; post psi: 0.69; $\Delta = -0.26$). However, relative to pre-drought, *N. fasciata* suffered a net reduction in occupancy of only 29%, whereas *N. floridana* was nearly locally extirpated, with a net 84% reduction in occupancy. In fact, *N. floridana* was only detected in one wetland post-drought. Significant reductions in occupancy were not observed for *F. abacura, S. pygaea,* or *R. rigida* (Fig. 2a). Detectability (*p*) decreased by approximately 50% for *N. fasciata* (pre-drought: 0.69; post: 0.33), by approximately 40% for *S. pygaea* (pre-drought: 0.57, post-drought: 0.35), and by 70% for *R. rigida* (pre-drought: 0.48, post-drought: 0.14) (Fig. 2b). *Farancia abacura* and *N. floridana* experienced no change in detectability associated with drought.

Although our occupancy analyses lacked the sample size needed to detect strong covariate relationships, examination of raw capture rates of our three most common species in relation to wetland characteristics can provide information on wetland and landscape factors that may mediate the effects of drought (Fig. 3). Prior to drought, the wetlands with the highest capture rates of *S. pygaea* were moderately permanent and closer to the Savannah River floodplain (Fig. 3c, d). *Nerodia fasciata* was captured in nearly every wetland, but wetlands with the highest capture rates were moderate or less permanent and farther from the floodplain (Fig. 3a, b). Wetlands with the highest capture rates of *N. floridana* were relatively permanent and farther from the floodplain, (Fig. 3e, f). Capture rates of all three species, decreased following drought. *Nerodia fasciata* suffered the greatest reductions in capture rate at hydrologic extremes. Alternatively, *S. pygaea* was never found in extremely permanent or ephemeral wetlands pre-drought and therefore only suffered reductions in capture rate in wetlands of moderate permanence. *Nerodia floridana* disappeared from all but one permanent wetland after the drought, but even at this wetland, capture rates were reduced by nearly 50%.

E. Discussion

We found interspecific variation in effects of drought on occupancy and detectability of semi-aquatic snake species. Specifically, the two *Nerodia* species suffered drought-induced declines in distribution and *N. floridana* was nearly extirpated from isolated wetlands across the landscape. Three species, *Seminatrix pygaea*, *Regina rigida* and *Farancia abacura* did not decline significantly in the estimated proportion of wetlands occupied across the landscape. *Nerodia fasciata, S. pygaea, and R. rigida* suffered declines in detectability. Pre-drought covariate effects on abundance and detectability were weak for all species, but snake capture rates plotted against wetland permanence and distance to floodplain showed a decline in relative abundance of *N. fasciata, S. pygaea,* and *N. floridana* across the study area. Wetlands with the highest abundances of *S. pygaea* were moderately permanent wetlands and closer to the river floodplain, whereas *N. fasciata* declined the most severely in the wetlands at the extremes of the hydrologic gradient. *Nerodia floridana* was extirpated from all but the most permanent wetland due to drought. Our results provide a unique example of how drought can influence the community composition, distribution, and relative abundance of important reptilian predators in isolated wetland ecosystems.

Estimated occupancy of *S. pygaea* was not affected by drought, a remarkable parallel to results of long-term population studies at Ellenton Bay; a ten hectare isolated wetland within our study site. For example, in the spring before a supra-seasonal drought, ~5.5 individual *S. pygaea* were captured per 100 trap nights and > 6 individuals were captured the spring following the drought, nearly 2.5 years later (Winne, 2008; Winne et al., 2006). More detailed data for Ellenton Bay suggest that this drought resilience is due to the ability of *S. pygaea* to aestivate within the dried wetland during prolonged drought, and subsequently capitalize on high productivity once the wetland refills (Winne et al., 2006). However, our study did find that detectability was reduced after drought, suggesting some effect of drought on *S. pygaea* abundance. We expect that this reduction is a result of drought-induced mortality, as indicated by a lack of large individuals of both sexes (>325 mm) after drought in 2003 (Winne et al., 2010). These large individuals likely starved due to their higher absolute metabolic rates and energy requirements than smaller individuals (Winne et al., 2010). Although larger individuals may perish during drought, our results suggest that this mortality is of minor significance to persistence of populations, given that overall occupancy rates of *S. pygaea* did not change during drought. Alternatively, emigration could explain the slight reduction in detectability that we observed; other studies have suggested that individuals emigrate from drying wetlands (Dodd, 1993; Seigel et al., 1995). However, other studies suggest terrestrial dispersal is physiologically demanding and unlikely for *S. pygaea*, especially for adults (Winne et al., 2001; Gibbons & Dorcas, 2004). Thus, our results confirm that *S. pygaea* is remarkably drought resilient, likely due to strategies like aestivation that enable most individuals to survive and occupy isolated wetlands across the landscape throughout the entire drought duration.

Similar to *S. pygaea*, *R. rigida* did not experience reductions in occupancy during drought. We know little about the ecology and life history of *R. rigida*, which is perceived to be the rarest of our focal species; very little scientific literature has been published about them (Gibbons & Dorcas, 2004). Durso et al. (2011) found that *R. rigida* had higher occupancy in wetlands closer to the Savannah River floodplain containing crayfish; a relationship that stands in our post-drought analysis. One hypothesis for the resilience of *R. rigida* to drought could be found in its close taxonomic relationship with *S. pygaea* (Pyron et al., 2013), which may suggest that *R. rigida* could also aestivate during drought. However, although perceived as highly aquatic, there are five published accounts of terrestrial activity in *R. rigida*, including individuals found up to 470 m from water (Steen et al., 2011). Thus, *R. rigida* may be more terrestrial than we think. Migration to the Savannah River floodplain, an unlikely scenario for *S. pygaea* due to desiccation risk (Winne et al., 2001) and lack of preferred food (*A. talpoideum*) in the floodplain, seems more likely for *R. rigida*. *Regina rigida* grows to a larger maximum body size than *S. pygaea*, and thus potentially has a higher capacity for terrestrial locomotion. The floodplain swamp also holds abundant populations of their preferred prey (crayfish) and its preference for wetlands close to the floodplain means that for most populations, migration to the floodplain would be comparatively shorter than for species that are more widely distributed across the landscape. Although difficult to decipher, we believe *R. rigida* likely relies on the Savannah River floodplain as refugia habitat from isolated wetlands during time of drought. Movement out of isolated wetlands and into the floodplain during drought would also explain the post-drought reduction in detectability we observed for this species.

Another species that is difficult to interpret due to lack of ecological knowledge is *F. abacura*. Its dietary preference for giant salamanders (*Siren*/*Amphiuma*) results in higher abundance in more permanent wetlands that can sustain populations of these highly-aquatic prey (Durso et al., 2011). More permanent wetlands are less likely to dry completely during drought, which could explain the lack of drought effects on either occupancy or detection probability for *F. abacura*. Additionally, *Farancia abacura* has been reported to aestivate within or near dried wetlands, similar to *S. pygaea* (Willson et al., 2006). Although reports of aestivation are anecdotal, there is substantial evidence for long-distance terrestrial movements in *F. abacura*, and it is likely that terrestrial movements are an important component of their life history (Steen et al., 2013). At least short distance migration from drying wetlands during drought has been documented, but sample sizes are small (Seigel et al., 1995; Martin, 1998; Willson et al., 2006). Since *F. abacura* is known to hibernate terrestrially, it seems likely they would also employ terrestrial aestivation, if needed. Regardless of whether *F. abacura* aestivate, migrate, or use a combination of the two, they appear to be relatively unaffected by supra-seasonal drought.

Unlike the previous species, *Nerodia fasciata* experienced declines in both occupancy and detectability during the supraseasonal drought; specifically, a ~30% reduction of occupied wetlands and ~50% reduction in mean detectability. This agrees with patterns documented at Ellenton Bay, where relative abundance using minnow traps was substantially reduced from ~4 individuals per 100 trap-nights before drought (spring 1998), to zero individuals captured in minnow traps following the supra-seasonal drought in spring 2003 (Winne, 2008). Although Seigel et al. (1995), suggested that *N. fasciata* emigrate in the direction of aquatic habitats during drying, very few *N. fasciata* immigrated back to the wetland after it refilled in 2003. This suggests high mortality during drought or failure of snakes to make the return journey (Willson et al., 2006). It is possible that *N. fasciata* migrate to permanent habitats like the Savannah River floodplain or larger creeks and remain there permanently. However, many of the wetlands we sampled were at least 1 km from permanent water; presenting a challenging journey for a species with a known maximum terrestrial dispersal of ~3 km (Luhring et al., 2011). Whatever the mechanisms, we conclude that drought causes significant declines in distribution and abundance of *N. fasciata* across the landscape.

Although *N. fasciata* are strongly affected by drought, they appear to be able to rapidly recolonize and repopulate once water-levels return to normal, a common characteristic of resilience strategists (Bond et al., 2008). For example, only a few individuals were found entering Ellenton Bay as the wetland refilled after a previous supraseasonal drought (Willson et al., 2006), but their relative abundance returned to pre-drought levels within 2.5 years (Winne, 2008). This rapid repopulation may be facilitated indirectly by the drought itself. For example, annual or periodic drying of wetlands prevents establishment of fish, producing highly suitable conditions for explosive growth of amphibian populations (Semlitsch & Brodie, 1998; Gibbons et al., 2006). This productivity results in abundant high-quality prey for *N. fasciata* (Willson & Hopkins, 2011), which fuels rapid growth, high reproductive output, and fast recovery of populations (Winne, 2008). Although *N. fasciata* inhabit these less permanent wetlands, their populations there are highly variable over time in concordance with drought. Thus, increased drought frequency could eventually cross a threshold, resulting in sustained low abundance and restricted distribution across the landscape.

Our study corroborates data from two historical drought events in demonstrating that *N. floridana* are strongly affected by supra-seasonal drought. Prior to a supra-seasonal drought in 1985, *N. floridana* were fairly common within Ellenton Bay, nearly twice as abundant as *N. fasciata* (Seigel et al., 1995). The bay dried entirely in 1988 and *N. floridana* were no longer detectable. The drought ended and the bay refilled in 1990 but *N. floridana* were not detected until five years later (1993; Seigel et al., 1995). Sampling in 1998 found *N. floridana* to still remain in the bay, but at low abundances (~1 individual per 100 trap-nights; Winne, 2008). In 1999 a supra-seasonal drought again dried Ellenton bay until 2002. Post-drought, *N. floridana* was again absent from the bay; despite intense sampling effort, they were not detected again until the third year after drought (2005; Winne, 2008). The last time *N. floridana* was captured in Ellenton bay was summer 2006, just before the supra-seasonal drought that lasted through 2012 and which is the focus of this study. Focusing at the landscape scale, we also found that *N. floridana* was strongly affected by drought. Pre-drought occupancy estimates were low (ψ = 0.32), but detectability was moderate overall (*p* =0.44), with some wetlands containing high abundances. Post-drought occupancy dropped by >80% and *N. floridana* was nearly extirpated from isolated wetlands across the landscape (ψ = 0.05). However *N. floridana* retained relatively high abundances within the one wetland where they remained (*p* = 0.59).

There are several possible factors that could explain the sensitivity of *N. floridana* to drought. Most *N. floridana* fail to emigrate from drying wetlands, especially in comparison to *N. fasciata* (Seigel et al., 1995; Willson et al., 2006). For example, of over nine years of monitoring a drift fence surrounding Ellenton bay, 359 *N. fasciata* were captured entering or exiting the bay. Only nine *N. floridana* were captured entering or leaving during that same time period, despite relatively high numbers of resident *N. floridana* within the bay (Seigel et al., 1995; Winne, 2008). The lack of dispersing *N. floridana*, especially before and after drought periods, suggests that this species may be averse to overland dispersal, possibly because the risks of leaving the wetland may be greater than remaining. This risk may be influenced by physiological characteristics such as high metabolic or evaporative water loss rates that make this species prone to desiccation. Remaining within the wetland during drought may be a successful strategy, especially if water and energy stores can outlast drought duration. For example, although Ellenton bay dried temporarily during the minor droughts of 1985 and 1987 (Fig. 1), *N. floridana* abundances remained high. However, multi-year supra-seasonal droughts may outlast this species' ability to withstand unfavorable conditions. Further research is needed to understand mechanisms that may influence the lack of dispersal and drought sensitivity of *N. floridana*.

Reliance on permanent aquatic habitat also influences the drought sensitivity of *N. floridana*. Before drought, we found *N. floridana* to be present in multiple moderate to permanent isolated wetlands, but they persisted in only one very permanent wetland at relatively high abundances. Therefore, very permanent bodies of water may act as refugia for *N. floridana* during drought. Refugia habitats are essential to drought survival for many species (Magoulick & Kobza, 2003) and may serve as source populations that facilitate population growth and recolonization of other wetlands after drought (Adams & Warren, 2005; Arthington et al., 2005). Alternatively, dynamic isolated wetlands that remain dry for a considerable time, may act as population sinks, where mortality during drought is high and habitat must be later repopulated via immigration (Dias, 1996). Supra-seasonal drought therefore, has the potential to eliminate *N. floridana* from isolated wetlands across the landscape while the most permanent wetlands, ponds, or lakes allow them to persist.

Although supra-seasonal drought is becoming increasingly common, especially in areas such as the Southeastern United States (Trenberth et al., 2007), very little is known about its ecological consequences (Bond et al., 2008) and implications for vertebrate community dynamics. Current distribution and evolution of aquatic vertebrates have been dramatically shaped by historic droughts (Douglas et al., 2003; Tarboton, 1995) and drought has resulted in extinction of approximately eight aquatic or semi-aquatic species worldwide (Cahill et al., 2012). Within North America, the Southeastern United States has the highest reptile species richness (Ricketts et al., 1999) but is also predicted to experience increases in drought frequency and intensity (Trenberth et al., 2007). Population-level impacts of drought have been documented for other taxa such as fish (e.g., Larimore et al., 1959; Trape, 2009), invertebrates (e.g. Hynes, 1958; Harrison, 2000) and birds (Cahill et al., 2012). For snakes, sea krait (*Laticauda spp.*) abundance was found to correlate with precipitation during drought (Lillywhite & Tu, 2011) and Sperry and Weatherhead (2008) found that drought reduced prey abundance, body condition, and survival of black ratsnakes (*Elaphe obsoleta*). Our study reveals that supra-seasonal drought impacts the distribution and abundance of some semi-aquatic snake species.

The extirpation or reduction of semi-aquatic snakes from isolated wetlands due to drought could have direct and indirect impacts on ecosystem dynamics. Snakes are often abundant in isolated wetlands and can play an important role as secondary or tertiary predators. For example, *N. fasciata* and *S. pygaea* reached peak densities of 171 snakes ha^{-1} of wetland habitat and combined were estimated to consume over 200 kg of amphibian prey annually in Ellenton Bay (Willson & Winne, 2016). Similarly, adult *Regina alleni* (striped crayfish snake) were estimated to consume ~10% of the crayfish population while neonates consumed >90% of the odonate population (Godley, 1980). Thus, the extirpation or reduction of snake predators in wetlands could alter abundance of prey species or the trophic structure of wetland food webs. Further, snakes could play a keystone predator role by prohibiting some species from becoming too abundant and competitively excluding other species (e.g. Jaeger, 1971). It is unknown what role snakes play as prey for higher trophic levels, although known predators like wading birds (Mushinsky, 1993), may need to shift to alternative prey resources. Ultimately, reductions in snake abundance and species richness have the potential to change dynamic ecosystem processes within isolated wetlands.

Supra-seasonal droughts may present greater risks for species and biodiversity than "normal", shorter duration droughts. Likely, severe drought is positively correlated with longer recovery time of ecosystem process, longer population recoveries, and increased probability of species extinctions (Lake, 2003). But if duration and intensity of drought increase extinction rates, and long-term droughts are becoming more common, what can be done to mitigate drought effects on biodiversity? Mitigating or managing drought effects is difficult, since droughts often span large spatial and temporal scales, and are unpredictable in timing and severity (Bond et al., 2008). One strategy is the development of long-term management plans to avoid overuse of water resources (Bond et al., 2008) that affect isolated wetlands and other aquatic habitats. Alternatively, since semi-aquatic snake species are diverse in regards to how they use a gradient of wetlands with varying hydroperiods and degrees of isolation, maintaining a large number of diverse wetland types across the landscape is likely critical to maintaining diverse communities of snakes (Roe et al., 2004) and other semi-aquatic biota. If necessary, construction of artificial wetlands could be used to mitigate wetland loss and achieve a landscape with sufficient connectivity to sustain metapopulation or source-sink dynamics. Likewise, providing high quality habitat corridors and avoiding barriers between wetlands would facilitate dispersal between wetlands.

This research provides robust support that interspecific variation in drought sensitivity observed within a single aquatic snake community (Ellenton Bay), translates to a landscape-scale. We found that snake species vary in their ability to withstand drought, a fact that likely applies to a broad range of semi-aquatic species. Why species vary differentially is unknown, and should be the priority of future research in order to identify important behavioral or physiological characteristics that mediate drought responses. Knowledge of these mechanisms will help better predict large scale shifts in distribution and abundance likely to occur as a result of climate change.

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H. Tables

Table 1. Model selection using AIC for 16 candidate models displaying weights (W_i) for five species of semi-aquatic snakes, pre and post-drought. Models with < 2 AIC values were considered as supported top models and are indicated in bold.

	Pre-drought (2006)					**Post-drought (2013)**				
	Nerodia fasciata	***Nerodia floridana***	***Seminatrix pygaea***	***Farancia abacura***	***Regina rigida***	***Nerodia fasciata***	***Nerodia floridana***	***Seminatrix pygaea***	***Farancia abacura***	***Regina rigida***
Model	W_i	W_i	W_i	W_i	W_i	W_i	W_i	W_i	W_i	W_i
ψ(.), p(E*)	**0.12**	**0.14**	0.09	**0.44**	**0.15**	0.01	**0.14**	**0.20**	**0.39**	0.01
ψ(.), p(C1,E*)	**0.18**	**0.23**	**0.21**	0.09	0.04	0.00	**0.12**	**0.21**	0.10	0.02
ψ(.), p(C2,E*)	0.03	0.05	**0.14**	0.11	0.01	0.01	**0.07**	0.05	0.12	0.01
ψ(.), p(C1,C2E*)	0.03	0.07	**0.24**	0.02	0.01	0.01	0.02	0.04	0.02	0.01
ψ(C1), p(E*)	0.03	0.03	0.05	0.13	0.01	0.00	0.04	0.05	0.12	0.01
ψ(C1), p(C1,E*)	0.03	**0.18**	0.03	0.03	**0.19**	**0.63**	**0.12**	**0.16**	0.03	0.00
ψ(C1), p(C2,E*)	0.00	0.01	0.06	0.02	0.00	0.00	**0.12**	0.01	0.03	0.00
ψ(C1), p(C1,C2,E*)	0.00	0.03	0.03	0.00	0.04	0.18	0.02	0.02	0.01	0.00
ψ(C2), p(E*)	0.05	0.04	0.02	0.09	**0.15**	0.00	0.04	0.06	0.10	0.11
ψ(C2), p(C1E*)	0.06	0.04	0.04	0.02	0.03	0.00	**0.12**	0.06	0.02	0.00
ψ(C2), p(C2,E*)	0.01	0.01	0.02	0.02	0.03	0.01	**0.12**	0.01	0.02	**0.66**
ψ(C2), p(C1,C2,E*)	0.01	0.01	0.04	0.00	0.00	0.00	0.02	0.01	0.00	0.11
ψ(C1C2), p(E*)	**0.21**	0.01	0.01	0.02	**0.27**	0.02	0.02	0.01	0.03	0.01
ψ(C1C2), p(C1,E*)	**0.19**	**0.14**	0.01	0.00	0.03	0.10	0.02	0.06	0.01	0.00
ψ(C1C2), p(C2,E*)	0.03	0.00	0.01	0.00	0.04	0.00	0.02	0.00	0.01	0.02
ψ(C1C2), p(C1,C2,E*)	0.02	0.02	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.01

Table 2. Principal component analysis results reduced seven site covariates into two composite variables: Component one (C1) was negatively correlated with wetland permanence, fish abundance, and giant salamander abundance, and positively correlated with *A. talpoideum* abundance and change in abundance of fish. Component two (C2) was negatively correlated with proximity to the Savannah River floodplain (SRF) and *A. talpoidium* abundance, and positively correlated with crayfish abundance. Change in fish abundance was the difference between 2013 and 2006 fish abundance and was a representation of each wetlands degree of hydrologic change.

	PC	
	C1	**C2**
Eigenvalues	2.98	1.39
%Variation	42.3	19.7
	Correlation	
Variable	**C1**	**C2**
Permanence	-0.438	-0.23
Distance to SRF	-0.061	-0.636
Fish abundance	-0.511	0.159
Crayfish abundance	0.244	0.633
***Ambystoma talpoidium* abundance**	0.339	-0.28
Giant Salamander abundance	-0.307	0.073
Change in Fish abundnace	0.524	-0.181

I. Figure Legends

Figure 1. Water depth (cm) readings from 1975 to 2015 at Ellenton Bay, a precipitation driven isolated wetland in the Upper Coastal Plain of South Carolina. Supraseasonal droughts are indicated with arrows in 1987-1990, 2000-2003, and 2007-2012. The focus of this study is the supraseasonal drought from2007-2012.

Figure 2. Single season, null model a) occupancy (ψ) and b) detection (*p)* probability estimates for from pre-drought 2006 (grey bars) and post drought 2013 (open bars) for fives species of semi-aquatic snakes across 20 wetlands in South Carolina. Error bars represent 95% confidence intervals.

Figure 3. The number of snake captures per 100 minnow trap nights in relation to wetland permanence or distance from the Savannah River floodplain for three species of semi-aquatic snakes: *Nerodia fasciata* (a, b), *Nerodia floridana* (c,d) and, *Seminatrix pygaea* (e,f). Each point represents capture rate at one of the twenty wetlands sampled in 2006 (open circles) and 2013 (filled circles).

J. Figures

Figure 1.

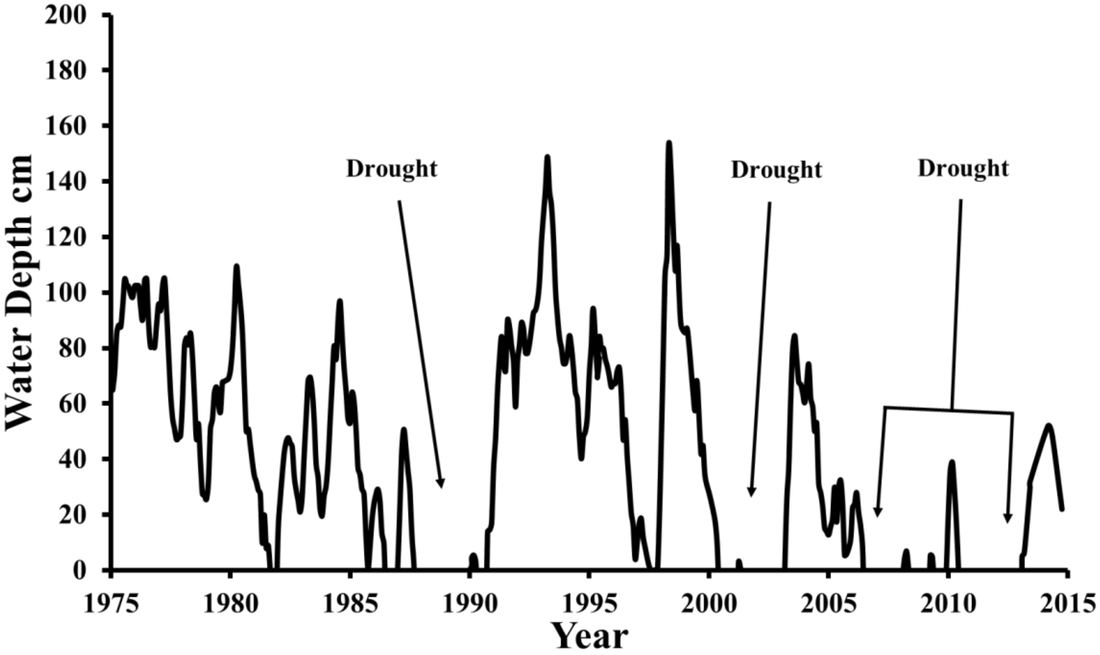


Figure 2.

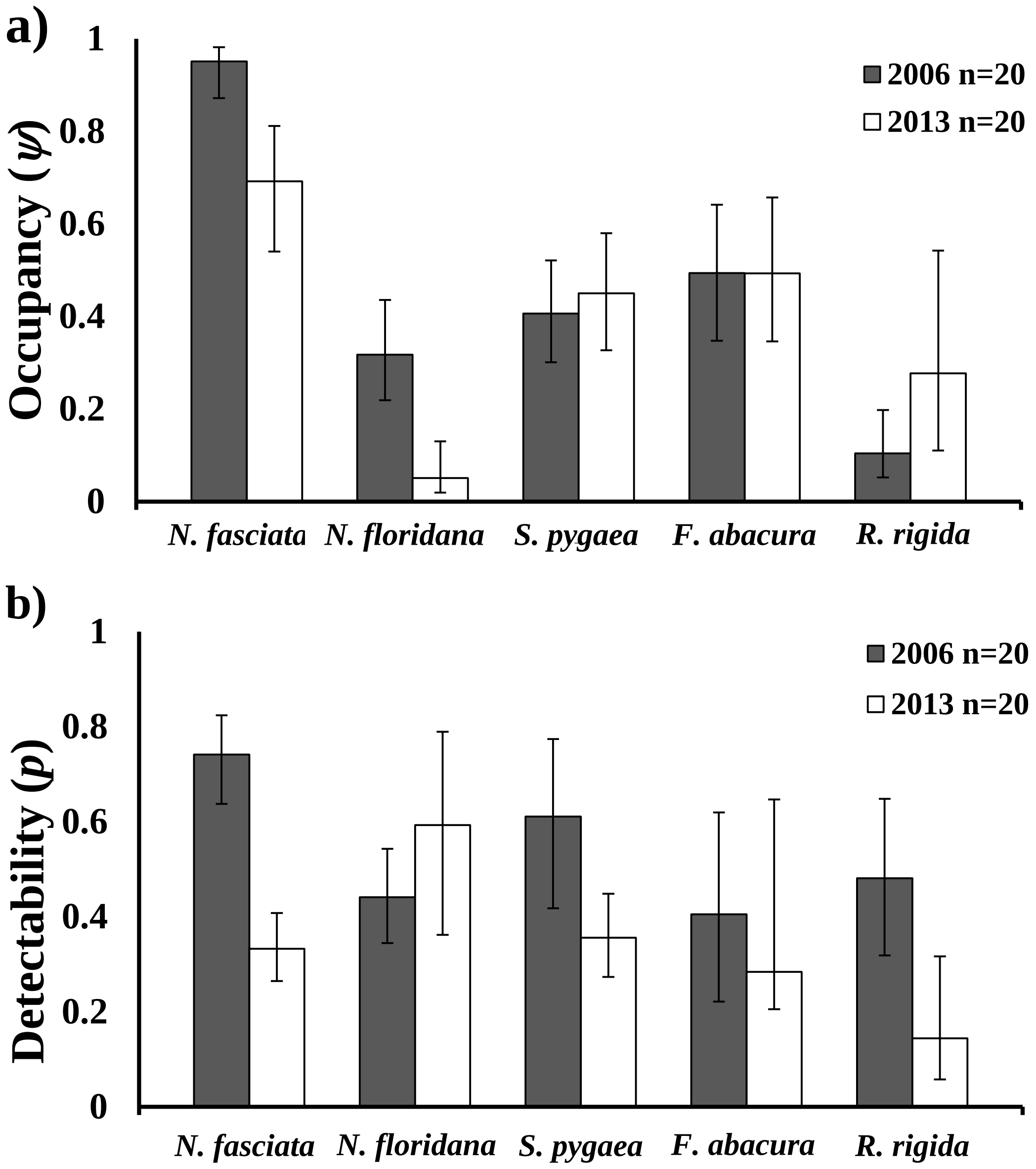
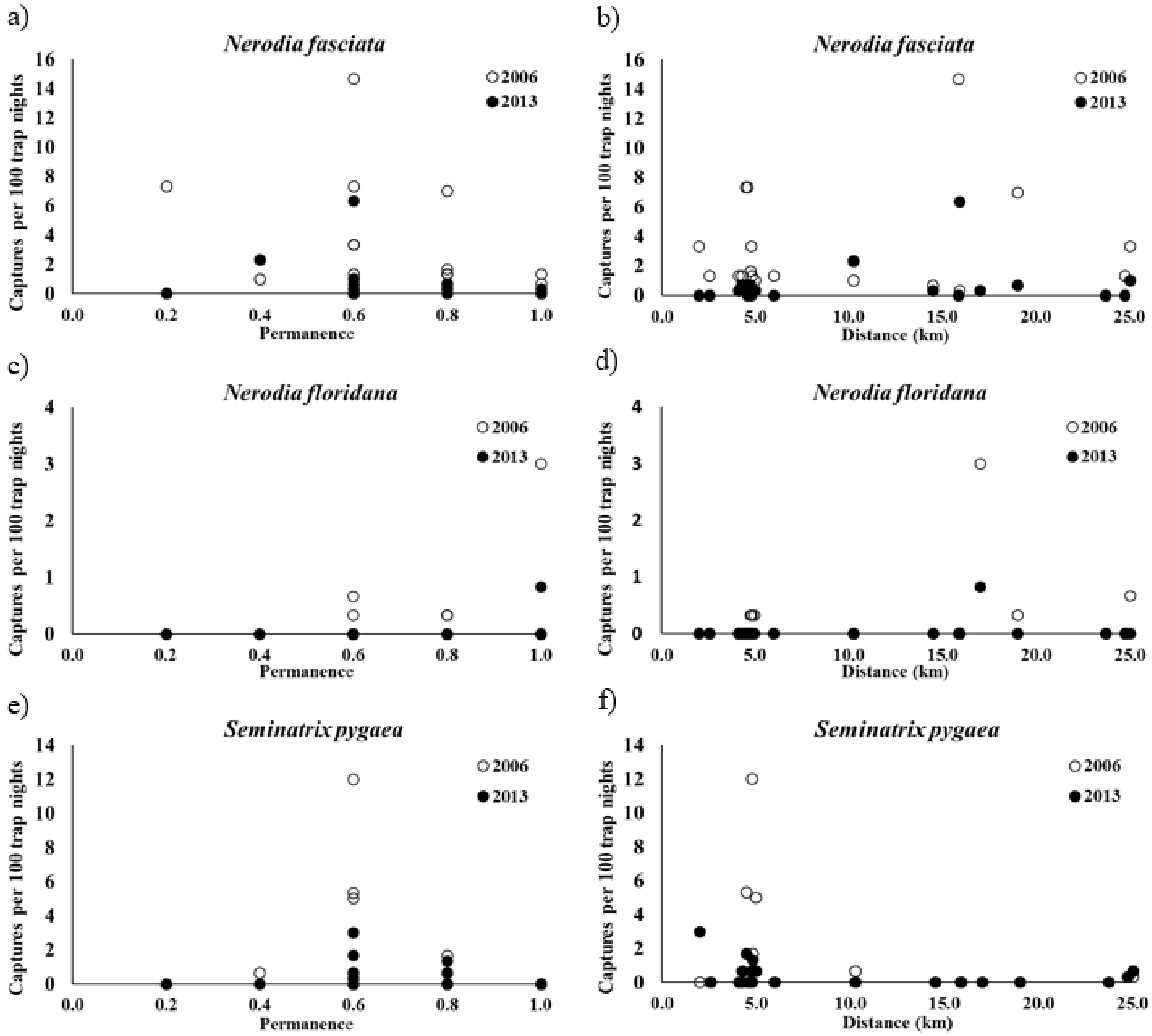

a)
Occupancy (ψ)
1
0.8
0.6
0.4
0.2
0
2006 n=20
2013 n=20
N. fasciata
N. floridana
S. pygaea
F. abacura
R. rigida
b)
Detectability (p)
1
0.8
0.6
0.4
0.2
0
2006 n=20
2013 n=20
N. fasciata
N. floridana
S. pygaea
F. abacura
R. rigida

Figure 3.


a)
Nerodia fasciata
Captures per 100 trap nights
16
14
12
10
8
6
4
2
0
0.0
0.2
0.4
0.6
0.8
1.0
Permanence
2006
2013
b)
Nerodia fasciata
Captures per 100 trap nights
0.0
5.0
10.0
15.0
20.0
25.0
Distance (km)
2006
2013
c)
Nerodia floridana
Captures per 100 trap nights
4
3
2
1
0
Permanence
2006
2013
d)
Nerodia floridana
Captures per 100 trap nights
Distance (km)
2006
2013
e)
Seminatrix pygaea
Captures per 100 trap nights
14
12
10
8
6
4
2
0
Permanence
2006
2013
f)
Seminatrix pygaea
Captures per 100 trap nights
Distance (km)
2006
2013

III. MECHANISMS THAT MEDIATE VARIATION IN RESPONSES OF SEMI-AQUAIC SNAKES TO DROUGHT: EVAPORATIVE MASS LOSS AND LOCOMOTION

A. Abstract

Understanding traits that drive species' responses to environmental variation is a critical component of understanding, predicting, and mitigating populations threated by climate change and other anthropogenic alterations to the environment. Physiological characteristics such as evaporative mass loss (EML; the rate of water and product lost through respiratory, cutaneous and ocular pathways) and locomotor performance, may mediate behavior and survival of semi-aquatic snakes faced with supra-seasonal drought. We measured rate of EML for five sympatric semi-aquatic snake species; and 2) locomotor endurance (total distance, total time, and speed traveled before exhaustion in aquatic habitats and in hydrated and dehydrated states in terrestrial habitats) using four species. We found that for EML, species grouped into three categories that did not follow taxonomic relationships. The smallest of our study species, *S. pygaea* had the highest rate of EML of any species after accounting for body size. Both *N. floridana* and *F. abacura* grouped into the moderate category, while *N. fasciata* and *R. rigida* lost mass at the slowest rates. Species also varied in their ability and willingness to move over land, suggesting that some species may be more willing or able to make terrestrial overland movements in response to environmental variation. Our results identify important mechanisms that may underpin variable responses of semi-aquatic snakes to environmental variation and better inform our understanding of species ecologies. In particular, the apparent sensitivity of *N. floridana* to drought may be driven in part by its unexpectedly high rate of EWL and reluctance to move terrestrially. This information has direct implications for future management and research, as anthropogenic impacts on environment and climatic change continue to accelerate.

B. Introduction

Stochastic environmental variation is a natural phenomenon that influences nearly every aspect of ecology, including biotic interactions (Chesson, 1986), population dynamics, life history, and community structure (Schlosser, 1990). Environmental variation drives adaptation in a wide variety of organisms by not only creating disturbances that impose natural selection, but also by facilitating the exchange of genetic variation through dispersal, that may improve the ability to resist future perturbation (Garant et al., 2007; Perron et al., 2008). One of the most important aspects of environmental variation that can occur across a landscape is the amount and frequency of available precipitation. By distributing water that is essential for sustained life, precipitation is one of the primary drivers of environmental gradients. For example, rainfall is an important factor limiting forest species distributions in Africa (Swaine, 1996). However, precipitation patterns have undergone changes both spatially and temporally. For example, over the last 100 years, annual precipitation has increased across most of North America (Trenberth et al., 2007), but in the Southeastern United States, despite increases in heavy precipitation events, decreases in annual precipitation of 1-2% per decade have been recorded (Trenberth et al., 2007).

A direct outcome of variation in precipitation are shifts in hydroperiod of aquatic habitats. Many seasonal wetlands are completely isolated from surface water, are filled by precipitation, and are emptied primarily by evapotranspiration (Sharitz, 2003). When full, isolated wetlands support high levels of biodiversity and exceptional secondary productivity, especially for amphibians (Semlitsch, 1998; Gibbons et al., 2006). For example, drying of aquatic ecosystems can reduce predator populations (e.g., Ruiz-Olmo et al., 2001), and re-wetting often enhances nutrient availability (Venterink et al., 2002), bolstering primary production (Howarth, 1988) and invertebrate populations that support amphibian larvae (Leeper

& Taylor, 1998). However, when dry, isolated wetlands become unproductive and often inhospitable for aquatic species. These dramatic changes in resource availability and habitat suitability are exacerbated by increases in drought frequency and duration (Trenberth et al., 2007). Thus, species inhabiting isolated wetlands may be unable to persist in an increasingly harsh and unpredictable environment unless they possess robust drought-survival adaptions.

Many organisms possess physiological or behavioral adaptations that allow them to persist through environmental variation (Perron et al., 2008). Wetland-dwelling species frequently cope with drought through adaptations that reduce dehydration. As a limiting resource, water plays an important role in cellular osmolarity, waste elimination, and thermoregulation (Morgan, 1984; Hill, 1989; Sawna & Coyle, 1999). Birds and reptiles use osmoregulation to reduce water loss by excreting highly concentrated uric acid (Keilen, 1959), and convert stores of fat to metabolic water (Hill, 1989). Reptiles can undergo compositional changes in lipid barriers within the skin that act as a primary barrier preventing water loss (Lillywhite & Maderson, 1982). Behaviors such as dormancy or aestivation are also common water-conserving adaptations for semi-aquatic species during periods of drought. In particular, inherently low and flexible metabolic rates enable ectotherms to utilize these energy-reducing strategies. For example, Australian eastern long-necked turtles (*Chelodina longicollis*), are known to aestivate terrestrially by lowering their metabolic rate, thereby limiting water loss (Kennett & Georges, 1990; Chessman, 1978 & 1984). In addition to aestivating, *African* lungfish (*Protopterus* spp.), Sirens (*Siren* spp.), and multiple anuran species excrete layers of mucus that dry to form a cocoon, slowing desiccation (Reno et al., 1972; Greenwood, 1986). Adaptations like these enable organisms to occupy seasonally harsh environments subject to supra-seasonal droughts, without having to abandon them altogether.

Another way species deal with drought is to avoid inhospitable habitats by moving elsewhere. Dispersal is a common adaptation to inhospitable conditions among endotherms, which have high metabolic rates and aerobic capacities conducive to extended strenuous activity (e.g., Rauhamäki et al., 2014). For example, Australian magpie geese (*Anseranas semipalmata*) are so well adapted to frequent drought that unlike many other waterfowl species, they never completely molt their primary feathers, and thus are able to fly to escape drought year-round (Romanowski, 2013). However, for smaller species with lower mobility, like many ectotherms, dispersal may be a more risky endeavor. For example, the highest documented rates of mortality in snakes occur when they travel outside their normal home ranges (Bonnet et al., 1999). Furthermore, water loss and dispersal capability may interact, such that species with high water loss rates may be constrained in their dispersal abilities and be forced to adopt strategies that do not rely on long-distance dispersal. Both directly confronting dehydration and/or moving elsewhere to avoid it are strategies that can have direct implications for the abundance and distribution of wetland-associated species in dynamic environments.

Semi-aquatic snakes offer unique opportunities to investigate variation in adaptations to drought and the implications of that variation for population and community dynamics. Semi-aquatic snakes are often abundant, diverse, serve important functional roles as predators and prey, and remain relatively understudied (Willson & Winne, 2016). Extensive long-term research in South Carolina has revealed that sympatric semi-aquatic snake species exhibit drastically different responses to supra-seasonal droughts. At one wetland, the black swamp snake (*Seminatrix pygaea*) was least effected by drought, responding by aestivating within the wetland (Willson et al., 2006; Winne et al., 2006). In contrast, the banded watersnake (*Nerodia fasciata*) suffered substantial drought induced declines in relative abundance, whereas Florida green watersnakes (*Nerodia floridana*) became locally extirpated (Willson et al., 2006; Winne, 2008; Seigel et al., 1995). A recent study revealed similar changes in distribution at a landscape scale (Vogrinc and Willson, in prep). Specifically, we documented 30% and 80% reductions in wetland occupancy for *N. fasciata* and *N. floridana*, respectively, following a supra-seasonal drought, whereas *S. pygaea, Farancia abacura* (Red-bellied Mudsnake), and *Regina rigida* (Glossy Crayfish Snake) experienced no significant change in occupancy. Although these studies provided a robust understanding of how species respond to drought at the population level, we lack a basic understanding of the physiological and behavioral mechanisms that drive differential drought responses.

In this study, we investigated two physiological characteristics that may mediate survival and behavior of semi-aquatic snakes faced with supra-seasonal drought, water loss rate and locomotor performance. Specifically, we measured rates of evaporative mass loss (EML; the rate of water and product lost through respiratory, cutaneous and ocular pathways) for five sympatric semi-aquatic snake species; and 2) locomotor endurance (total distance, total time, and average speed traveled before exhaustion in aquatic habitats, and in hydrated and dehydrated states in terrestrial habitats) using four species. We predicted that species would vary in their rates of water loss and locomotor performance, and that these physiological capabilities might relate to documented population and community dynamics related to periodic extreme droughts. For example, we predicted those species that declined the most in relative abundance during drought (*N. fasciata* and *N. floridana*) would have the highest rates of EML. We predicted that hydrated snakes would travel farther terrestrially than dehydrated snakes, and that large species known to disperse long distances (e.g., *N. fasciata* and *F. abacura*) would travel farther terrestrially than smaller species that are rarely encountered out of water (*S. pygaea*). Our results identify important mechanisms that may underpin variable responses of semi-aquatic snakes to environmental variation. This information has direct implications for future research and management of these understudied species that may be threatened by climatic change and other anthropogenic impacts to the environmental.

C. Methods

Study Site and Aquatic Trapping

We collected semi-aquatic snakes from various aquatic habitats on the Savannah River Site (SRS), in Aiken and Barnwell counties, South Carolina, from May-July, 2014. Snakes were primarily captured using plastic minnow traps (Willson et al., 2005) placed 2-3 m apart in shallow water with 3-5 cm of trap remaining above water level to ensure sufficient air for captured animals. Traps were not baited but incidental captures resulted in natural baiting of traps with fish and amphibians (Keck, 1994), which is attractive to reptilian predators. Traps were checked daily and captured snakes were removed and transported back to the Savannah River Ecology Laboratory (SREL) for processing and experiments.

All captured semi-aquatic snakes were measured (sex, snout-vent length [mm], tail length [mm], body mass [nearest 0.01 g]) and assessed for normal health and condition. Snakes in poor body condition or with open wounds, parasites, or other obvious external abnormalities were excluded from the study. Snakes captured in ecdysis were held until at least one full day after shedding occurred before being used in any experimental trial (Cohen, 1975).

Evaporative Mass Loss

In this study, our use of the term evaporative mass loss (EML) is synonymous with pulmocutaneous mass loss, which constitutes both water and metabolic gas (O_2, CO_2) lost through cutaneous, respiratory, and ocular pathways, and is commonly expressed as mg lost g^{-1} body mass h^{-1} (Mautz, 1982). Our experiment does not differentiate between water loss and metabolic gas loss, however a significant proportion of the observed mass loss is attributable to water evaporation and other studies on snakes have found metabolic gas loss to be negligible over the time scales we consider (e.g., Cohen, 1975; Mautz, 1982).

Experimental methods for EML experiments followed the general procedures of Winne et al. (2001). Snakes were retained for 7-11 days before experimental trials began to ensure that they were postabsorptive, fully hydrated, and in good health (Winne et al., 2001). During this time, snakes were housed communally in polyethylene containers of various sizes in a temperature-controlled animal room (25.5C, 12:12 photoperiod). Containers held 0.5 inches of tap water and crumpled paper towels or hide boxes for cover.

To begin EML trials, each snake was blotted dry with paper towels and massed (nearest 0.01 g on an electronic balance). Each snake was then placed individually within a rectangular steel mesh cage that limited snake activity but allowed for coiling (Winne et al. 2001). Two different cage dimensions were used depending on snake body size (23 cm x 11.5 cm x 12.5 cm, 3.25 mm mesh, for snakes < 300 mm total length; 47.5 cm x 14 cm x 11 cm, 3.25 mm mesh, for snakes > 300 mm total length). Cages containing snakes were then weighed and placed into a lighted reach-in environmental chamber (Percival Scientific Model 1-37LLVL) set at 27°C and 50% relative humidity. Up to 11 individuals were run simultaneously. Cages were removed each hour for six hours and snakes and their associated cages were weighed to the nearest 0.1 gram. Every 15 min for six hours, snakes were observed through the chamber viewing window and activity level and body position of each snake was assigned a 0-3 score: 0 = “resting” motionless with body overlapped at more than one point and head not elevated; 1 = “slightly active” motionless with head elevated, 2 = “moderately active” moving around but not actively pushing against cage; 3 = “very active” moving around and actively pushing against cage; Winne et al., 2001. Snakes were also monitored for signs of defecation that could confound measurements of EML; any snakes that defecated during the trial were excluded, re-hydrated, and re-tested >24 h later. At the end of the 6 h trial, snakes were either returned to the chamber to continue dehydration in preparation for dehydrated locomotor trials (see below) or removed from their cages and replaced back into their housing units with 0.5 inches of water in order to rehydrate until they regained their original mass.

Locomotion

Following EML measurements, we performed three types of locomotion trials: terrestrial dehydrated, terrestrial hydrated, and aquatic. We used a total sample size of 50 individual snakes of four species: *F. abacura* (n=6), *N. fasciata* (n=11), *N. floridana* (n=14), and *S. pygaea* (n=19). All snakes had been previously used in the EML experiment.

Methods for locomotor performance trials followed the general procedures of Ford and Shuttlesworth (1986) and Seigel et al. (1987) using two circular tracks, terrestrial and aquatic. The terrestrial track was made of a plywood base with an outside circumference of 5.2 m, lined with artificial grass (Astroturf) to provide traction while preventing snakes from burrowing. Aluminum flashing walls 1 m high ensured that large snakes could not escape. An aquatic track of the same dimensions was constructed from a polyurethane (1325 L; 5.2 m circumference) cattle stock tank serving as an outer wall, with a polyurethane swimming pool set inside the tank as the inner wall, weighed down by cinder blocks, and then filled with 2.5 cm of 25°C tap water. The width of both tracks was 40 cm.

All locomotor trials were conducted between 800 and 1800 h in a temperature controlled room at 25°C and each individual snake performed one trial per day. Beginning at a starting line, snakes were individually raced around the track by lightly tapping the tail tip with a soft bristle brush. The snake was then prompted to continuously crawl around the circular track until it no longer responded by advancing forward in response to ten light taps of the tail (Arnold & Bennett, 1988). During the trial, the total number of laps crawled by the snake was recorded and time was measured to the nearest 0.1 sec with a handheld stopwatch. Total distance was calculated by multiplying circumference of the track by the number of laps plus any additional distance moved past the starting point. Any trial in which the snake immediately assumed a defensive position and refused to crawl in response to light tapping was considered unsuccessful and the snake was retested the following day. If the snake continued to assume defensive positions for three consecutive trials, that locomotion trial type was considered complete and that individual snake proceeded to the next trial type the following day.

Snakes were first tested for terrestrial locomotion under dehydrated conditions (90% of hydrated body mass). This allowed dehydrated locomotion trials to be performed immediately after the conclusion of EML experiments. Depending on the size of the snake, some individuals required additional time in the environmental chamber in order to reach the dehydration threshold of 90% of initial body mass (10% body mass lost). If a dehydrated snake was not successful on its first trial, it was allowed to rehydrate for at least 12 h, and then was placed back into the environmental chamber, dehydrated to 90% of hydrated body mass, and re-tested.

Following dehydrated terrestrial trials, snakes were allowed to rehydrate in 1 cm of tap water for 12 h and each snake was weighed to confirm it had returned to approximately its original body mass. They then proceeded to hydrated terrestrial trials, and finally aquatic trials, allowing 24 h between trials. Thus, the entire timeline of experimental trials for each animal lasted between 3 and 13 days, depending on how many trials were not successful. At the termination of the experiment, snakes were returned to their original capture location.

Analyses

Total EML was calculated for each individual snake by subtracting its final mass (after six hours in the environmental chamber) from its initial mass. To compare mass loss among snake species, while accounting for differences in body size, an ANCOVA was performed, with log-transformed total body mass lost (g) as the dependent variable and initial mass (g) as the covariate. A post hoc comparison (Tukey's test) was then used to assess differences among species pairs with a Bonferonni-corrected α of 0.005. A non-parametric Kruskal-Wallace test was used to compare the mean sum of activity scores across individuals among species. A post hoc multiple comparison with a Bonferonni-corrected α of 0.005 was used to assess differences among species pairs. For locomotion, a two-way ANOVA with main effects of species and trial type (terrestrial dehydrated, terrestrial hydrated, and aquatic), plus an interaction, was performed for each of the three dependent variables measured (total time, speed, and total distance). All analyses were performed in R 2.14.2, using the "car" package (Fox, 2011) for ANCOVA and, unless otherwise stated, statistical significance was recognized at $\alpha < 0.05$.

D. Results

Aquatic Trapping

Trapping and one incidental capture yielded a total of 122 semi-aquatic snakes of five species that were suitable for EML experiments. Body size ranges and sample sizes for the five species were as follows: (*Nerodia fasciata*; n = 31, SVL = 234 - 674 mm; *Nerodia floridana* = 22, SVL = 247 - 610 mm; *Seminatrix pygaea* = 34, SVL = 232 - 328 mm; *Farancia abacura* = 22, SVL = 445 - 1096 mm; *Regina rigida* = 13, SVL = 204 - 545 mm.

Evaporative Mass Loss

Absolute rates of evaporative mass loss depended strongly on body size (ANCOVA, initial mass, $F_{4, 121}$= 157.31 $p < 0.01$) and differed substantially among species (species, $F_{4, 121}$= 7.03, $p<0.01$), but we detected no species-by-body size interaction ($F_{4, 121}$= 2.09, $p = 0.08$; Fig 1). Post hoc tests indicated that *N. fasciata* did not differ from *R. rigida* (Tukey's, $MS_{112} = 0.01$, $p = 0.92$), but all other species pairs differed significantly from one another (all $p < 0.005$). Accounting for body size, species fell into three distinct groups, reflecting high, moderate, or low rates of EML. The smallest of our study species, *Seminatrix pygaea* had the highest EML rate of any species, even after correcting for body size. For example, a 300 mm SVL *S. pygaea* lost mass approximately 1.72 and 3.77 times faster than an *N. floridana* and an *N. fasciata* of the same size, respectively. *Nerodia floridana* and *F. abacura* grouped into the moderate category, losing approximately two times more mass than an *N. fasciata* of the same size. The low EML category included *N. fasciata* and *R. rigida* which did not differ in rate of mass loss.

Activity scores differed significantly among species (Kruskal-Wallace Test; df = 4, $\chi^2 =60.11$ $p<0.01$). Three species, *S. pygaea, N. fasciata,* and *N. floridana* exhibited similarly high activity levels [*N. floridana*: mean summed activity score (se) = 41.68 (3.17); *S. pygaea*: 53.23 (2.05); *N. fasciata*: 43.12 (3.7)] and were substantially more active than *F. abacura* and *R. rigida* that had similarly low activity scores [*F. abacura*: 12.5 (2.35); *R. rigida*: 17.53 (2.25)]

Locomotion

Regardless of locomotion trial type, species differed in total time (ANOVA; $F_{3, 131}$=5.32, p< 0.01), distance ($F_{3, 131}$=2.81, p= 0.04), and speed ($F_{3, 131}$=7.91, p<0.01) prior to exhaustion (Fig 2). Across species, distance ($F_{2, 131}$=9.44, p<0.01) and speed ($F_{2, 131}$= 167.66, p<0.01) differed among locomotion trial types, but total time did not ($F_{2, 131}$= 0.85, p= 0.42). A species-by-trial type interaction was only significant for speed ($F_{6, 131}$= 3.69, p<0.01). In general, *S. pygaea* and *N. fasciata* performed similarly in aquatic and terrestrial hydrated trials, moving farther and longer than *F. abacura* and *N. floridana,* despite high variation. For all species, individuals swam more quickly than they crawled terrestrially. Terrestrial hydrated trials did not differ from dehydrated trials in speed, total time, or distance, except for *S. pygaea,* which moved shorter distances and times in dehydrated trials than in hydrated trials.

At least a few individuals of all five species displayed persistent defensive behaviors in response to terrestrial locomotion trials, but none showed these behaviors during aquatic trials. *Nerodia floridana* frequently refused to crawl terrestrially (70% of terrestrial trials; Fig 3), instead exhibiting strong defensive responses that included body coiling, striking, and sometimes lunging vigorously. Unlike *N. fasciata*, *N. floridana* would rarely abandon its defensive position and continue crawling. A few individuals of both *F. abacura* and *S. pygaea* curled into a ball in response to the bristle brush stimuli. *Seminatrix pygaea* successfully completed 90% of all trials and *F. abacura* and *N. fasciata* were always successful within three trial attempts across all locomotion trial types.

E. Discussion

We assessed evaporative mass loss (EML) and locomotor performance of sympatric semi-aquatic snake species inhabiting isolated wetlands that are subject to periodic drying. For EML, species grouped into three categories that did not follow taxonomic affinities. The smallest of our study species, *S. pygaea* had the highest rate of EML of any species after accounting for body size. Both *N. floridana* and *F. abacura* grouped into the moderate category, while *N. fasciata* and *R. rigida* lost mass at the slowest rates. Species also varied in their ability and willingness to move over land, suggesting that some species may be more willing or able to make terrestrial overland movements in response to environmental variation than others. Interspecific variation in EML and locomotor performance may be influenced by multiple proximate factors. We discuss these potential mechanisms in an ecological context, specifically how interspecific differences in physiological characteristics relate to observed population trends and conservation implications.

Evaporative Mass Loss

Farancia abacura had the highest absolute rate of water loss of any species and after correcting for body size, fell into the moderate EWL category. We suspect that body morphology contributes strongly to the relatively high water loss rate observed in this species. *Farancia abacura* is long and slender in body morphology, unlike our other species which are all relatively stout. This body form may allow *F. abacura* to consume elongate prey, occupy fossorial burrows, or better maneuver in muddy habitat. However, it results in high surface-area-to-volume-ratio that is positively correlated to water loss (Gans et al., 1968).

After accounting for body size, the EML rate of *S. pygaea* was at least two times higher than any other species, and comparable to rates measured for this species previously (Winne et al., 2001). This high EML rate may reflect a highly aquatic ecology, where physiologically preventing EML by investing in resources like skin lipids would be energetically wasteful (Cohen, 1975). High lipid barrier permeability can permit cutaneous respiration, as seen in other aquatic or semi-aquatic snake species (Standaert & Johansen, 1974; Heatwole & Seymour, 1978). However, this adaptation to aquatic lifestyle may then constrain terrestrial activity, as much mass is lost cutaneously. In fact, there are many examples supporting a relationship between habitat use and EML. In reptiles, rates of water loss are often most strongly correlated with habitat aridity or microhabitat use (Cohen, 1975; Mautz, 1982). For example, a meta-analysis of 120 squamate species found that those inhabiting mesic environments had the highest rates of evaporative water loss (Cox & Cox, 2015). This relationship is largely explained by the lipid mesolayer beneath the skin that acts as the primary barrier against water loss (Lillywhite & Maderson et al., 1982). Although previous snake studies primarily investigated terrestrial species across moisture gradients, we believe a correlation between habitat use and water loss may also hold true for semi-aquatic snakes. For example, *S. pygaea* is rarely encountered out of water, is thought to be the most highly aquatic North American snake, and has the highest EML rate of any species in our community. This supports the idea that interspecific differences in barrier permeability relate to the evaporative stress of varying habitats chosen by species (Lillywhite et al., 2009).

Regina rigida had the lowest EML rate of any species, a surprising result given that *R. rigida* is closely related to *S .pygaea* (Pyron et al., 2013). One possible explanation for this disparity is activity, which is positively correlated with mass loss (Dmi'el, 1972; Cohen, 1975). We found that *R. rigida* was significantly less active than *S. pygaea* during EML trials. However, we believe activity likely is not the primary factor influencing this difference because of the magnitude of the EML difference and the fact that Winne et al. (2001) found activity had no effect on EML. Likewise, we also do not expect morphology to be the driver of the low EML rates we observed in *R. rigida* relative to *S. pygaea*; these species are generally similar in body shape and the individuals we tested overlapped broadly in body size (Fig. 1). Perhaps the most likely explanation for these surprising results is that our perception that *R. rigida* has a highly aquatic lifestyle is incorrect. *Regina rigida* is one of the least studied North American snakes and is traditionally thought to be highly aquatic, due to its rarity and a lack of terrestrial observations (Gibbons & Dorcas, 2004; Steen et al. 2011). Given that habitat use frequently correlates with EWL, it is possible that *R. rigida* is more terrestrial than has been thought (Steen et al. 2011). The low rates of water loss in *R. rigida* are unexpected, intriguing, and warrant further investigation.

Another surprising result was the difference in EML between *Nerodia* species. *Nerodia floridana* lost mass at approximately twice the rate of *N. fasciata*, despite these species being closely related and sharing similar morphologies. This disparity in water loss between *Nerodia* species further supports the notion that closely-related species do not always share similar rates of water loss, despite the suggestion by some authors that water loss rate may be phylogenetically conserved (Lahav & Dmi'el, 1996; Minnich, 1979). As with *S. pygaea* and *R. rigida*, high rates of EML in *N. floridana* may reflect microhabitat use. The ecology of *N. floridana* is also poorly understood, resulting in the perception *N. floridana* and *N. fasciata* are ecologically similar (Gibbons & Dorcas, 2004). However, the difference in EML we observed, in conjunction with differential sensitivity to drought (Seigel et al., 1995; Willson et al., 2006; Vogrinc and Willson, in prep), suggests that these species may differ in terms of their ecologies and habitat preferences. *Nerodia floridana* may therefore be more aquatic than *N. fasciata,* as its presumably more permeable lipid barrier may be better suited to a highly aquatic lifestyle. More aquatic habitat use is further supported by a preference for fish as prey by *N. floridana* which are most common in permanent water bodies (Durso & Willson, 2011).

Locomotion

Despite logistical challenges and high variability among individuals, several patterns emerged from our locomotor performance experiments. All species readily swam in aquatic trials at higher speeds than they crawled terrestrially, similar to a study on semi-aquatic sea kraits (*Laticaudidae*) (Shine et al., 2003). In hydrated terrestrial trials, *S. pygaea* traveled farther and longer, but slower in average speed (m/s) than both *N. floridana* and *F. abacura*, our two largest species. However, relative to body size (body lengths/sec) *S. pygaea* also swims faster than any other species tested. This aquatic proficiency may reflect adaptations of *S. pygaea* to a highly aquatic lifestyle and the absence of conflicting requirements of terrestrial locomotion (Shine et al., 2003). Terrestrial hydrated trials did not differ from dehydrated trials in speed, total time to exhaustion, or distance for all species but *S. pygaea* (except sample size was low). This suggests that dehydration may have little influence on dispersal capacity, or that our dehydration threshold of 10% may have been too conservative. However, high variation and unequal sample size for all trial types makes interpretation of these results difficult. For both terrestrial trials, *N. floridana* frequently refused to crawl terrestrially, with most terrestrial trials ending in a defensive behavior. This suggests that *N. floridana* may be reluctant to make overland movements to escape drought, possibly because of their high rate of water loss or low mobility on land.

Implications for Drought Survival

A species' vulnerability to environmental change depends on a number of factors (Huey et al., 2012), especially physiological processes (Williams et al., 2008). Although, most studies have investigated temperature sensitivity rather than water loss, examples of physiological traits playing an important role in sensitivity to environmental change or stochasticity can be found in a variety of taxonomic groups. For example, many tropical ectotherms (e.g., insects and lizards) are highly sensitive to temperature shifts since they live close to their optimal temperatures (Deutsch et al., 2008; Chown, et al., 2002; Sinervo et al., 2010). Bats are particularly sensitive to shifts in ambient temperature that influence energy requirements necessary for successful hibernation (Humphries et al., 2002), and small bodied frog species are more vulnerable than larger species (Tracy et al., 2010). Our results indicate that physiological constraints and behavior of semi-aquatic snakes can influence a species' sensitivity to variation in precipitation.

Results of our EML and locomotion experiments can be useful in interpreting species' responses to drought. Previous research at population and landscape scales has shown that *R. rigida, F. abacura,* and *S. pygaea* are resilient to drought, experiencing no declines in occupancy but declines in detectability for *R. rigida* and *S. pygaea* (Vogrinc and Willson, in prep; Winne, 2008; Seigel et al., 1995). Conversely, both *Nerodia* species suffer reductions in occupancy and detectability following supraseasonal droughts and *N. floridana* are locally extirpated from all but the most permanent wetlands (Vogrinc and Willson, in prep). We believe that the high EWL rate of *N. floridana* and its apparent reluctance to move terrestrially may partially explain this species sensitivity to drought. Siegel et al. (1995) captured few *N. floridana* leaving a wetland during dry-down and used a drift-fence encircling a wetland to deduce that *N. floridana* likely remained within the wetland, rather than dispersing or migrating. Our terrestrial locomotion experiments support this conclusion. Although they readily swam in aquatic trials, *N. floridana* frequently refused to make terrestrial movements, suggesting that they may feel uncomfortable on land, possibly due to the constraints of elevated EWL rate. Even those *N. floridana* that did crawl terrestrially in our trials, exhibited lower endurance than *N. fasciata*. Being reluctant to migrate, *Nerodia floridana* may remain within drying wetlands in attempt to wait out droughts. However, if droughts are too long or severe, their physiological limits may be exceeded, and they may perish. Conversely, the relatively lower rate of EWL and willingness to move overland may be key contributing factors allowing *N. fasciata* to seek refuge during droughts, recolonize, and repopulate rapidly (Winne, 2008).

If high rates of EWL may contribute to the sensitivity of *N. floridana* to drought, why don't we see similar patterns in *S. pygaea* or *F. abacura*? One hypothesis is that other species may be able to compensate for physiological parameters through behavior. For example, the desert dwelling *Spalerosophis diadema* (Diadem snake), had cutaneous water loss (CWL) and skin resistance ($R_{s)}$ levels similar to the semi-aquatic *Natrix,* presumably due to alleviated constraints (lower temperatures) of nocturnal behavior (Dmi'el., 1985). In our study, *Seminatrix pygaea* have high EML but suffer little during droughts, and are likely unable to make considerable overland movements without dehydrating (Dorcas & Gibbons, 2004; Winne, 2008). *Seminatrix pygaea* may be so constrained by its physiology that there has been selection against dispersal during drought. They therefore use aestivation, a unique behavioral strategy that apparently makes them well-adapted to isolated habitats that may be prone to drought (Winne, 2008). Thus, *S. pygaea* can be classified as having resistance traits that allow them to 'sit out' drought due to a desiccation resistant life history stage (Bond et al., 2008). The other species from our community potentially using this strategy to persist despite moderate EML rates is *F. abacura*, which have anecdotally been reported to aestivate (Willson et al., 2006). However, EML may not act as a significant behavioral constraint for *F. abacura*, since they exhibited the fastest terrestrial movement in our locomotion experiments and have been regularly documented to make extensive terrestrial movements (Steen, 2013). Therefore, large body size and fast movement over short distances might compensate for the moderate water loss of *F. abacura.*

Climatic changes are expected to result in range shifts and possible local extinctions for a variety of species (Chen et al., 2011) and changes in drought appear to have implications for the distribution and abundance of semi-aquatic snakes. This study has highlighted the importance of understanding species physiological and behavioral mechanisms that may mediate differential drought responses. However, additional research is needed to understand the physiological processes that limit these species and how they influence behavioral adaptations and population dynamics. For example, simulating wetland dry-down and drought in a laboratory setting could yield substantial insight into species' behavioral responses, potential plasticity in skin lipid composition, and limits of aestivation for species like *S. pygaea*. Alternatively, field studies that directly assess behavioral responses of different species (e.g., migration, dispersal, and aestivation) would provide a final critical parameter necessary to unlock complex relationships physiology, behavior, and drought survival. Ultimately, identification of physiological characteristics that could act as critical mechanisms prohibiting or facilitating drought survival is imperative to making informed management decisions for species threatened by environmental change.

F. References

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H. Figure Legends

Figure 1. Total body mass lost over 6 h at 27°C and 50% relative humidity, relative to initial mass, for five species of semi-aquatic snakes; *Seminatrix pygaea* n= 34 (y = 0.2787x - 0.1736), *Farancia abacura* n= 22 (y = 0.8026x - 1.135), *Nerodia floridana* n= 22 (y = 0.6449x - 0.8528), *Nerodia fasciata* = 31(y = 0.6125x - 1.1082) and *Regina rigida* n=13(y = 0.5588x - 0.9588).

Figure 2. Locomotor endurance of four semi-aquatic snake species under three conditions: aquatic, hydrated terrestrial, and dehydrated terrestrial. a) The average speed traveled around a constructed circular track; b) total distance covered before exhaustion (snake no longer responds to ten light tap of the tail with a brush); c) the duration of locomotion prior to exhaustion. Numbers above bars represent sample sizes for each species.

Figure 3. Percentage of locomotion trials (aquatic, terrestrial, and dehydrated terrestrial combined), that resulted in three failed attempts (never successful), failed on the first, but successful on second or third trials (eventually successful), or successful the first trial, for four species of semi-aquatic snake. Numbers above bars represent sample sizes for each species.

I. Figures

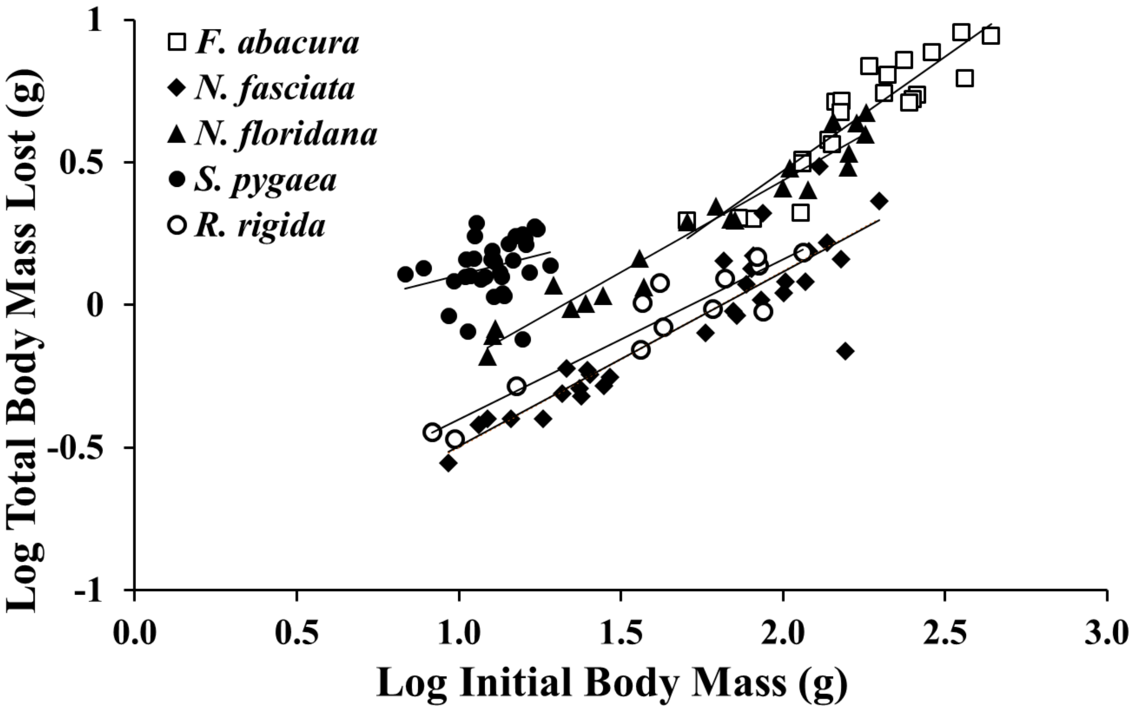


Figure 1.

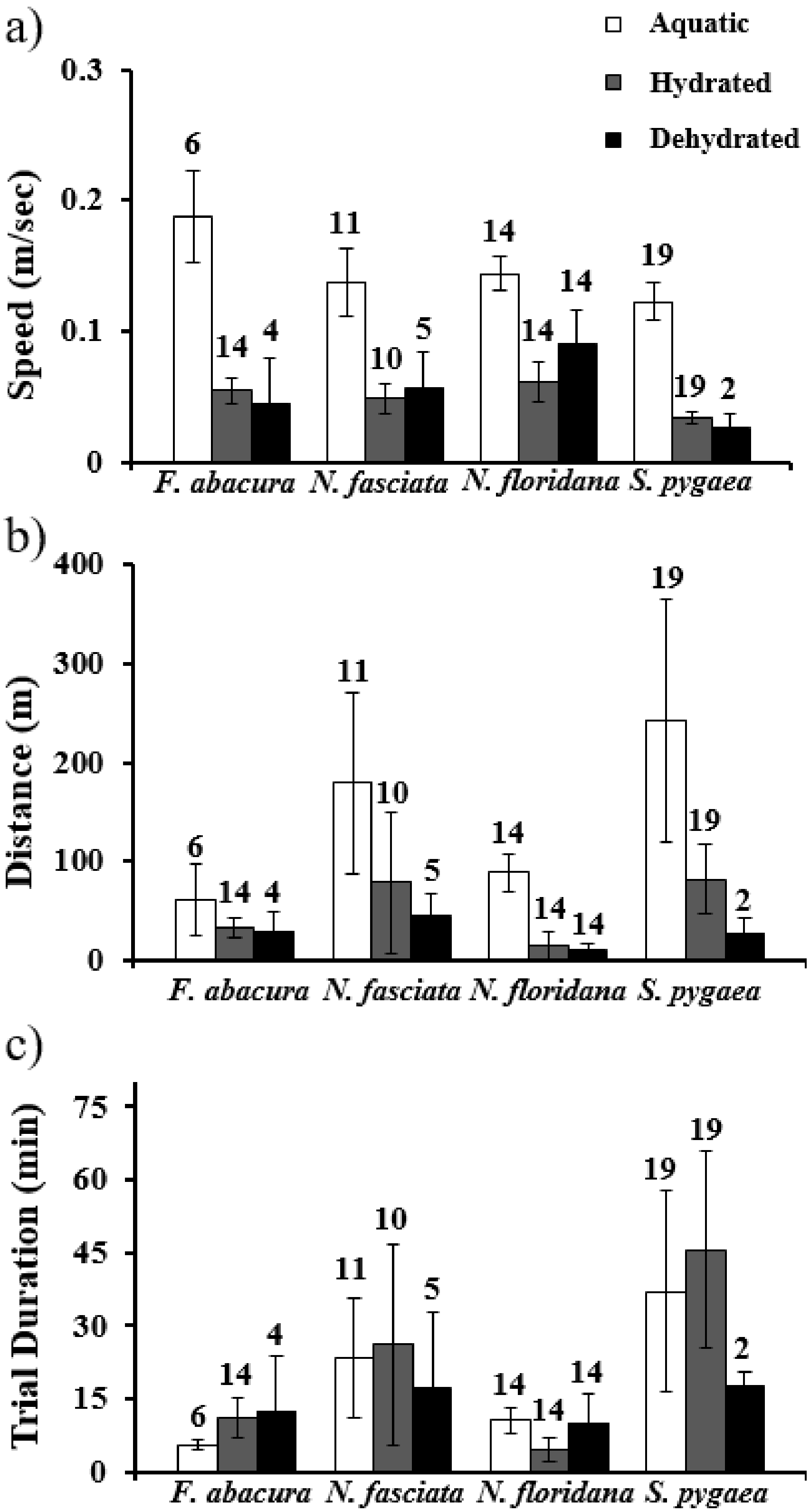

a)
□ Aquatic
■ Hydrated
■ Dehydrated
Speed (m/sec)
0.3
0.2
0.1
0
6
14
4
11
10
5
14
14
14
19
19
2
F. abacura
N. fasciata
N. floridana
S. pygaea
b)
Distance (m)
400
300
200
100
0
6
14
4
11
10
5
14
14
14
19
19
2
F. abacura
N. fasciata
N. floridana
S. pygaea
c)
Trial Duration (min)
75
60
45
30
15
0
6
14
4
11
10
5
14
14
14
19
19
2
F. abacura
N. fasciata
N. floridana
S. pygaea

Figure 2.

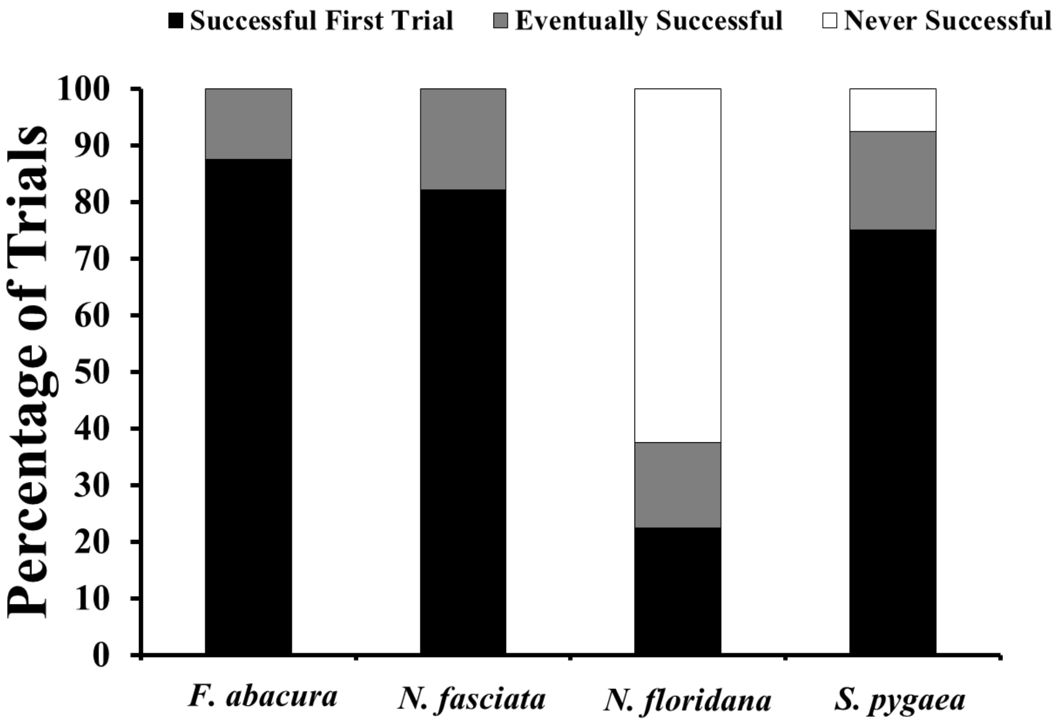

■ Successful First Trial
▨ Eventually Successful
☐ Never Successful
Percentage of Trials
100
90
80
70
60
50
40
30
20
10
0
F. abacura
N. fasciata
N. floridana
S. pygaea

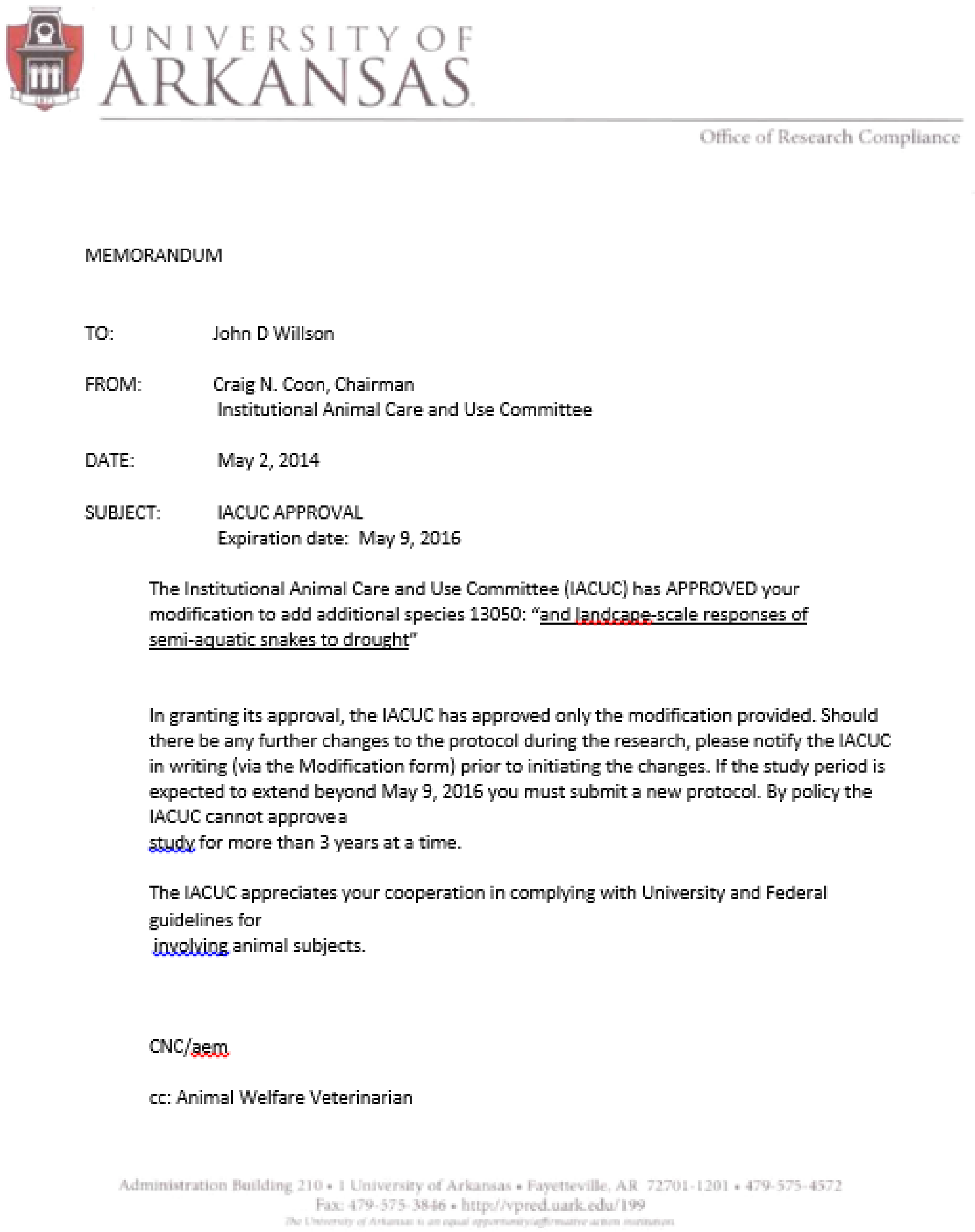
Figure 3.

IV. Conclusion

This thesis presents two studies investigating the responses of semi-aquatic snakes to drought in order to better understand large-scale effects of drought on distribution, abundance and species composition and mechanisms that mediate these species specific drought effects. In chapter one, we found that drought-related population dynamics of semi-aquatic snakes species observed at one wetland are repeatable at landscape-scales. Snake species were found to differ drastically in their drought responses, as some species were unaffected (*F. abacura*) or experienced minor reductions in detectability (*S. pygaea* and *R. rigida*.). Conversely, some species were declined substantially in both occupancy and detectability (*N. fasciata*) while another (*N. floridana*) became nearly extirpated in isolated wetlands across the landscape. This study highlights that supraseasonal drought is a significant stochastic event that can have serious implications for species' persistence and community dynamics. This is especially true for species that responded poorly like *N. floridana*, since drought frequency and intensity is predicted to increase due to climate change.

In chapter two, we found that physiological characteristics like EML and locomotor performance vary among species and likely are important in mediating drought responses of semi-aquatic snakes. Specifically, we found that differences in EML did not group out by taxonomic affinities but likely by each species habitat use. We found that species like *N. floridana* that had high water loss compared to a congeneric, also failed to make overland moments in terrestrial locomotor trials, likely due to a more highly aquatic lifestyle than was traditionally thought. Therefore a species locomotor ability and EML rate my act to prohibit or facilitate drought resilience or resistance for certain species.

In conclusion, we found that focal scale studies translate to the landscape scale and that some species of semi-aquatic snake species respond more ‘resistantly’ or ‘resiliently’ than others. These differences are likely driven by interspecific variation in physiological characteristics like EML and locomotor performance. These studies are the first of their kind, and build a foundation for one of the most thorough investigations of the effects of environmental variation on a community of organisms. This information will be useful for predicting drought responses for other groups of semi-aquatic species that might be vulnerable to changes in drought frequency and other anthropogenic effects on the environment.



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MEMORANDUM

TO: John D Willson

FROM: Craig N. Coon, Chairman
Institutional Animal Care and Use Committee

DATE: May 2, 2014

SUBJECT: IACUC APPROVAL
Expiration date: May 9, 2016

The Institutional Animal Care and Use Committee (IACUC) has APPROVED your modification to add additional species 13050: "and landcape-scale responses of semi-aquatic snakes to drought"

In granting its approval, the IACUC has approved only the modification provided. Should there be any further changes to the protocol during the research, please notify the IACUC in writing (via the Modification form) prior to initiating the changes. If the study period is expected to extend beyond May 9, 2016 you must submit a new protocol. By policy the IACUC cannot approve a
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The IACUC appreciates your cooperation in complying with University and Federal guidelines for
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cc: Animal Welfare Veterinarian

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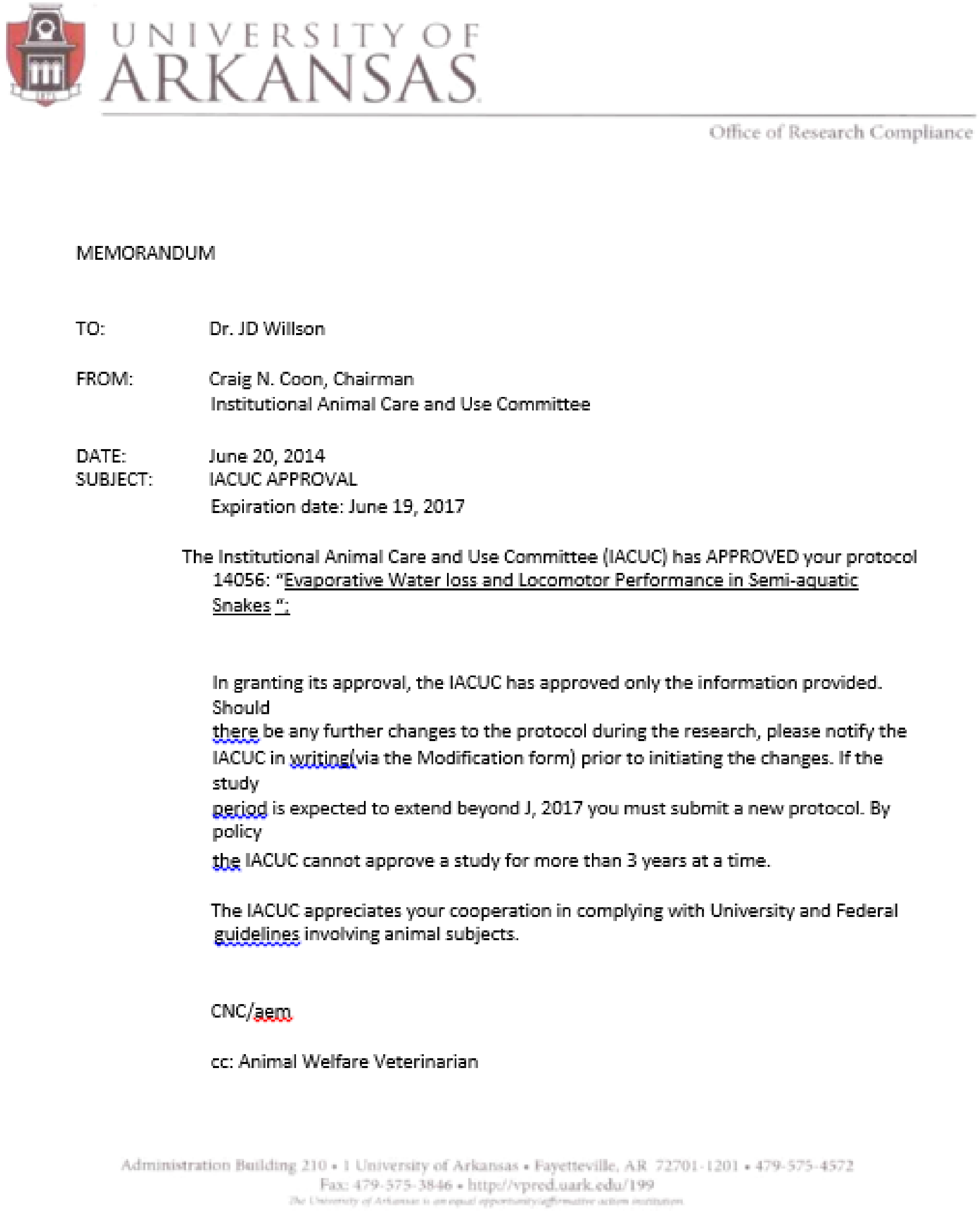

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TO: Dr. JD Willson

FROM: Craig N. Coon, Chairman
Institutional Animal Care and Use Committee

DATE: June 20, 2014
SUBJECT: IACUC APPROVAL
Expiration date: June 19, 2017

The Institutional Animal Care and Use Committee (IACUC) has APPROVED your protocol 14056: "Evaporative Water loss and Locomotor Performance in Semi-aquatic Snakes ";

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