ORIGINAL RESEARCH

Landscape-Scale Effects of Supra-Seasonal Drought on Semi-Aquatic Snake Assemblages

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Abstract

Climate change is predicted to alter the frequency and intensity of precipitation events, placing stress on freshwater aquatic ecosystems and their associated wildlife. Thus, understanding interspecific variation in drought sensitivity and the repeatability of those responses across heterogeneous landscapes is critical. Semi-aquatic snakes serve important roles within aquatic ecosystems and several species are threatened. Yet, little is known about the effects of drought on semi-aquatic snake populations or assemblages. We systematically trapped 20 isolated wetlands in South Carolina before (2006) and after (2013) a multi-year supra-seasonal drought to determine drought-induced shifts in occupancy and detection for five semi-aquatic snake species. Our results confirm that supra-seasonal drought differentially affects semi-aquatic snake species across landscape scales. Specifically, site occupancy decreased dramatically following drought for banded watersnakes (*Nerodia fasciata*) (0.95 to 0.69) and Florida green watersnakes (*Nerodia floridana*) (0.32 to 0.05), but was relatively unchanged for black swamp snakes (*Seminatrix pygaea*), mudsnakes (*Farancia abacura*) and glossy crayfish snakes (*Regina rigida*). Species lacking adaptations that make them resistant or resilient to drought may become locally extirpated if climate change projections are realized or landscapes are degraded or fragmented in ways that prevent drought recovery.

Keywords Climate change · Communities · Environmental stochasticity · Occupancy modeling · Stochasticity · Wetlands

Introduction

Anthropogenic impacts to climate contribute to rapid environmental changes that have altered ecosystems and eliminated species across the globe (Allen et al. 2010). At least one vertebrate extinction is attributed to climate change (Pounds et al.

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1999), and the most conservative climate warming scenarios estimate that approximately 18% of species are committed to extinction by 2050 (Thomas et al. 2004). One undesirable consequence of global climate change is increased frequency of supra-seasonal drought. Multiple lines of evidence suggest that drought frequency, intensity, and duration will increase in the future in many regions (Dai 2011; Seneviratne et al. 2012; Ficklin et al. 2015). 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. 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 and Bradley 2002). Metapopulation dynamics can also be altered, as drought influences movement behavior, which, in turn, can alter rates of dispersal and colonization (Walls et al. 2013a). Finally, as the available surface

water across a landscape is limited, wildlife is forced to concentrate, increasing the severity of competition and probability of predation and disease transmission (Kock 2005).

Drought inflicts considerable stress on a variety of organisms, especially those that are closely tied to aquatic systems. Species regularly confronted with drought possess traits that allow them to either persist throught drought (resistance) or recolonize and repopulate after drought-induced declines (resilience) (Lake 2000). However, projected increases in drought intensity may be too extreme for even "drought-tolerant" species to withstand (Bond et al. 2008). Population-level impacts of drought have been documented for some taxa, such as fishes (e.g., Larimore et al. 1959; Trape 2009), invertebrates (e.g., Hynes 1958; Harrison 2000), amphibians (Walls et al. 2013b), and birds (e.g., Cahill et al. 2013). Among snakes, sea krait (*Laticauda* spp.) abundance correlates with precipitation during drought (Lillywhite and Tu 2011) and drought reduced prey abundance, body condition, and survival of ratsnakes (*Pantherophis obsoletus*) in Texas (Sperry and Weatherhead 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 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; Winne et al. 2006). However, due to their low detectability, little is known about the responses of snake populations and assemblages to supra-seasonal drought events.

More than two decades of previous herpetological research at Ellenton Bay, a 10 ha 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 has experienced multiple periodic droughts including three multi-year supra-seasonal droughts (Fig. 1). We found that, at this wetland, highly aquatic black swamp snakes (*Seminatrix pygaea*) were least impacted by drought, exhibiting resistance by aestivating within the wetland and exhibiting little change in relative abundance over multi-year droughts (Willson et al. 2006; Winne et al. 2006). Conversely, banded watersnake (*Nerodia fasciata*) populations severely declined, but exhibited resilience by quickly recovering through rapid reproduction and recruitment when the drought ended (Willson et al. 2006). Exhibiting neither resistance nor resilience, Florida green watersnakes (*Nerodia floridana*) became locally extirpated, were not detected for three years post-drought, and never regained their pre-drought relative abundance (Seigel et al. 1995; Willson et al. 2006). Thus, previous research has documented dramatic interspecific variation in both behavioral and population responses to drought at one wetland study site. However, it is unknown if these patterns are location-specific, or if they occur broadly across the landscape.
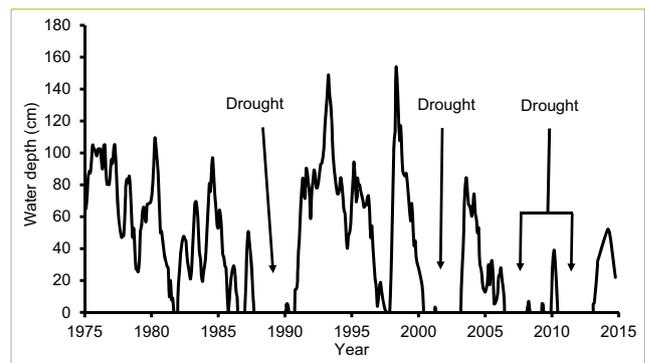

Fig. 1 Water depth (cm) readings from 1975 to 2015 at Ellenton Bay, a precipitation driven isolated wetland in the Upper Coastal Plain of South Carolina. Supra-seasonal droughts are indicated with arrows in 1987–1990, 2000–2003, and 2007–2012. The focus of this study is the supra-seasonal drought from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

In this study, we investigated variation in landscape-scale effects of drought on distribution and abundance of five sympatric semi-aquatic snake species—*N. fasciata*, *N. floridana*, *S. pygaea*, mud snakes (*Farancia abacura*), and glossy crayfish snakes (*Regina rigida*). We systematically sampled semi-aquatic snakes at 20 wetlands before and after an intense supra-seasonal drought occurring from 2007 to 2012 and used an occupancy modeling framework (MacKenzie et al. 2006) to estimate pre- and post-drought species-specific detection probability (p) and site occupancy (ψ). We also investigated landscape and wetland characteristics (e.g., hydroperiod, distance to perminant water) that may influence shifts in abundance and distribution associated with drought. Based on previous research at Ellenton Bay (Willson et al. 2006; Winne et al. 2006), we expected that *Nerodia* spp., especially *N. floridana*, would be particularly sensitive to drought and decline in occupancy across the landscape, whereas occupancy of other species, especially *S. pygaea*, would not change during drought. Likewise, we expected declines in *Nerodia* spp. to be most severe in wetlands with short hydroperiods that were long distances from refuges such as the floodplain of the Savannah River. Our study represents the first landscape-scale analysis of drought effects on snake assemblages and highlights the importance of understanding species' responses to environmental variation that may be exacerbated by climate change.

Methods

Study Sites

We sampled 20 freshwater wetlands located on the US Department of Energy's (DOE) Savannah River Site (SRS) in 2006 (pre-drought; Fig. 1) and 2013 (post-drought) for semi-aquatic snakes. From 2007 to 2012 the SRS experienced the

most severe drought in at least the past three decades, which left most isolated wetlands dry for at least several months (Fig. 1). The SRS encompasses nearly 932 km^2 within the Upper Coastal Plain of South Carolina (Aiken and Barnwell Counties), USA, and includes a variety of habitats such as bald cypress swamp, pine and hardwood forest, black water creeks, Carolina bays, and other freshwater wetlands (Davis and Janecek 1997). 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 undisturbed and unfragmented habitats in comparison to surrounding landscape. However, previous DOE activities resulted in radiological contamination of some areas of the site.

We selected 20 wetlands for sampling that ranged between 5 and 150 ha and represented a hydrological gradient from semi-permanent to permanent. All wetlands conformed to the following criteria: 1) open canopy, 2) surface water or precipitation fed, 3) <1 mile from access (road), 4) non-radiologically contaminated, and 5) within SRS boundaries. We included many of the wetlands within the landscape that met our criteria and we considered them to be representative of wetlands on the SRS (e.g., Thompson and Seber 1996; MacKenzie et al. 2005). Most of the wetlands in our study dried at least temporarily during the 2007–2012 drought. In our dataset, wetlands with the shortest hydroperiods were completely dry for a least eight consecutive months during this period.

Field Methods

We sampled all wetlands during May and June in 2006 (pre-drought; Durso et al. 2011) and 2013 (post-drought). We captured snakes using unbaited plastic minnow traps (model 700, Gator Buckets, Ladoga, IN) which are effective for capturing semi-aquatic snakes (Willson et al. 2008). In both years, we set one array of 60 traps 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, we set traps at these five wetlands with half of the standard effort: 30 traps for 5 nights (150 trap-nights). We accounted for this heterogeneity in effort by incorporating a sampling covariate for effort into model selection in 2006. Initial efforts to scale trapping effort more closely to wetland area in 2006 introduced so many missing values into the data that models often failed to converge. We placed traps 2–3 m apart in shallow water at the vegetated periphery of each wetland, leaving ~5 cm of trap above water to provide air for captured animals. We checked traps daily, measured captured snakes (sex, snout-vent length [mm], body mass [nearest 0.01 g on a digital balance]), and released all snakes at their capture location.

Covariates

We measured seven site covariates (Table 1) based on perceived importance and previous research (Durso et al. 2011). We measured distance to the Savannah River floodplain from the center of the wetland of interest to the nearest boundary of the floodplain, using ArcGIS (ESRI 2011). Based on a combination of historical hydrological data for some wetlands and our own observations of wetland hydrology between 1998 and 2013, we ranked the permanence of each wetland as follows: 1 (never dries), 0.80 (only dries during supra-seasonal droughts), 0.60 (only dries periodically), 0.40 (typically dries annually but stays filled in wet years), 0.20 (dries annually).

We generated four site covariates representing wetland prey community composition based on the relative abundance of prey captured in minnow traps. Specifically, we allowed minnow traps to accumulate prey for the first 24 h after being set and counted all larval and paedomorphic A. talpoideum, giant salamanders (Siren and Amphiuma), crayfish, and fishes captured. We used average counts of each prey group in 2006 as a site covariate, but excluded Eastern mosquitofish (Gambusia holbrooki) from fish counts due to their very small size (making them unimportant as prey for most snakes) and highly variable abundances that swamped out general patterns of abundance of other fishes. Detection probabilities of prey groups estimated in 2006 exceeded 0.90 (Durso et al. 2011). We created a fifth prey covariate representing change in prey community during drought by subtracting pre-drought fish relative abundances (2006) from post-drought fish relative abundances (2013). We focused on fishes for this covariate

Table 1 Principal component analysis results reducing seven site covariates into two composite variables

	Component	
	C1	C2
Eigenvalues	3.0	1.4
% Variation	42.3	19.7
	Correlation	
Variable	C1	C2
Permanence	**−0.44**	−0.23
Distance to Savannah River Floodplain	−0.06	**−0.64**
Fish relative abundance	**−0.51**	0.16
Crayfish relative abundance	0.24	**0.63**
Ambystoma talpoideum relative abundance	**0.34**	−0.28
Giant salamander relative abundance	**−0.31**	0.07
Change in fish relative abundance	**0.52**	−0.18

Change in fish abundance was the difference between 2013 and 2006 fish relative abundance and was a representation of each wetland's degree of hydrologic change. We considered variables with correlations of >0.30 to be strong contributors to each component (indicated in bold)

because they were much more strongly affected by wetland drying than amphibians.

Data Analysis

Occupancy modeling allows estimation of the probability that a site is inhabited by a species (occupancy) while accounting for the probability that species may be missed or overlooked during surveys due to imperfect detection. We constructed single-species, single-season occupancy models in program PRESENCE (Hines 2006) to estimate occupancy (ψ) and detection (p) of five snake species separately in pre- (2006) and post-drought (2013) years.

We used a Principal Component Analysis (PCA) in Primer (Clarke and Gorley 2006) to reduce the seven selected covariates (*see Covariates*) into two informative composite variables with orthogonal rotation (C1 and C2). We combined covariates into components to reduce dimensionality, simplify model selection (2 variables instead of 7), and increase statistical power without violating common rules of thumb (number of covariates <10–20% of sample size; Harrell 2001). We extracted the two components with the highest percent variation (C1 and C2) from a five component analysis and considered variables with correlations of >0.30 to be strong contributors to each component. We z-transformed all raw covariate data before conducting the PCA (Jury 1964).

We used Akaike's Information Criterion (AIC) for model selection to explore covariate effects on ψ and p for all candidate models. We used AIC_c for all species across both seasons by specifying the effective sample size using a conservative approach based on the number of sampling units (20 wetlands; MacKenzie et al. 2006). We considered a set of sixteen models in the selection process for each species in each season (Table 2) 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, we constructed models representing each possible combination of constant (.), C1, and C2, including the null model (ψ(.) p(.)), for occupancy and detection (see Table 2). For 2006, we included an effort covariate (E) for p in all models to account for heterogeneity in sampling effort (see above). To assess model fit we used 1000 parametric bootstraps of the global model and adjusted c-hat for over or underdispersion (Akaike 1973; Burnham and Anderson 2002; MacKenzie and Bailey 2004). We reranked overdispersed models using $QAIC_c$ and increased the number of model parameters by one. For underdispersed models, we inflated c-hat to 1 and used AIC_c ranking (MacKenzie et al. 2006). Models with values <2 ΔAIC 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 back-transformed estimates to estimate 95% confidence intervals (CI). We used a simplified version by adding or subtracting (1.95 * the untransformed standard error) from the untransformed regression coefficient (β), then back-transforming from the logit scale to get the upper or lower 95% CI of the estimate. We inferred significant differences based on non-overlapping 95% CIs.

In order to assess factors that might influence shifts in relative abundance of each species, we qualitatively compared capture rates of *N. fasciata*, *N. floridana*, and *S. pygaea*, standardized for effort (i.e., counts divided by number of trap-nights sampled), to wetland permanence and distance to the Savannah River floodplain in each year. Ideally, studies aimed at understanding variation in abundance should account for imperfect detection by using capture-mark-recapture, or similar approaches, to estimate individual capture probability. The approach used in our study (i.e., low effort across many sites) precluded the use of mark recapture, but given significant correlations between capture rates and estimated abundances found in other studies of semi-aquatic snakes (King et al. 2006, Willson & Winne, unpubl. data), we believe that these rates are meaningful indicators of abundance in our system.

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 were *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 1): C1, 42.3% of variation (eigenvalue = 3.0) and C2, 19.7% of variation (eigenvalue = 1.49). 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 fishes and giant salamanders, but higher abundance of *A. talpoideum*. Principal component two (C2) was strongly negatively correlated with distance to the Savannah River floodplain and positively correlated with crayfish abundance. Therefore, wetlands with higher scores for C2 were closer to the Savannah River floodplain and had 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

Table 2 AIC model selection for five species of semi-aquatic snakes, pre- (2006) and post-drought (2013)

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

Models within <2 AIC were considered to be supported top models and are indicated in bold

ψ = site occupancy, p = detection probability, E = effort covariate, $C1$ = first component, $C2$ = second component, W_i = AIC weight

*The effort covariate was included in all models to account for the effect of unequal sampling effort on detection probability

(Wi; Table 2), likely due to the relatively small number of sites we were able to sample. Two species had heavily weighted top models in 2013 (post-drought). The top model for *N. fasciata* favored C1 ($W_i = 0.65$) for both occupancy and detection; 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 detection; indicating an association with crayfish and the Savannah River floodplain for this species.

Interspecific variation in both null model occupancy and detection occurred in both pre- and post-drought years (Fig. 2). Pre-drought detection 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* occupied nearly one-third of the wetlands sampled ($\psi = 0.32$). *Seminatrix pygaea* was estimated to occupy approximately 40% ($\psi = 0.41$) and *F. abacura* 50% ($\psi = 0.52$) of wetlands. The species with the lowest occupancy estimate pre-drought was *R. rigida* ($\psi = 0.10$).

Both *Nerodia* species suffered reductions in occupancy from pre- to post-drought seasons, whereas all other species did not change (Fig. 2a). *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 ψ: 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 very permanent wetland post-drought. Significant reductions in occupancy were not observed for *F. abacura, S. pygaea,* or *R. rigida* (Fig. 2a). Detection (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 detection associated with drought.

Although our occupancy analyses lacked the power 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 close to the Savannah River floodplain (Fig. 3c, d). *Nerodia fasciata* was captured in nearly every wetland, but wetlands with the highest capture rates were moderately permanent and far from
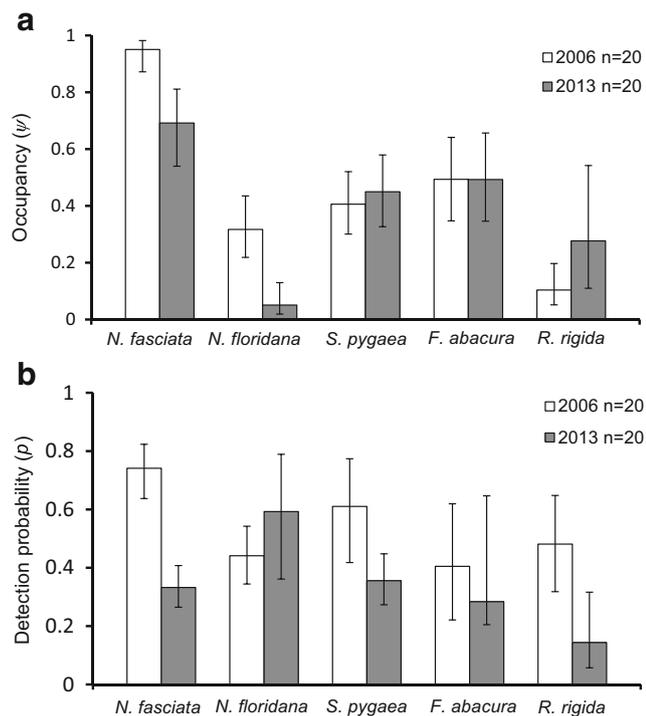
Fig. 2 Single season, null model a) occupancy (ψ) and b) detection (p) probability estimates for pre-drought 2006 (open bars) and post drought 2013 (grey bars) for five species of semi-aquatic snakes across 20 wetlands in South Carolina. *N. fasciata* = *Nerodia fasciata* (banded watersnake), *N. floridana* = *Nerodia floridana* (Florida green watersnake), *S. pygaea* = *Seminatrix pygaea* (black swamp snake), *F. abacura* = *Farancia abacura* (mud snake), *R. rigida* = *Regina rigida* (glossy crayfish snake). Error bars represent 95% confidence intervals

the floodplain (Fig. 3a, b). Wetlands with the highest capture rates of *N. floridana* were relatively permanent and far 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 (i.e., very ephemeral and very permanent wetlands). 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%.

Discussion

We found interspecific variation in the effects of drought on occupancy and detection 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*, showed no change in occupancy following the drought. Pre-drought covariate effects on abundance and

detection 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 both extremes of the hydrologic gradient. 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 result that mirrors long-term population studies at Ellenton Bay. For example, relative abundance of *S. pygaea* remained virtually unchanged (~5.5 vs. ~6.5 captures per 100 trap night) at Ellenton Bay before and after a supra-seasonal drought which dried the wetland for most of 2000 and 2001 (Willson et al. 2006; Winne 2008). More detailed data for Ellenton Bay suggest that this drought resistance 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 (Willson et al. 2006; Winne et al. 2010). However, our current study found that detection was reduced after drought, suggesting some effect of drought on *S. pygaea* abundance or behavior. 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). 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 of *S. pygaea* did not change following drought. Alternatively, emigration could explain the slight reduction in detection that we observed; select studies have suggested that individuals emigrate from drying wetlands (Dodd 1992; Seigel et al. 1995). However, other studies suggest that terrestrial dispersal is physiologically demanding and unlikely for *S. pygaea*, especially for adults (Winne et al. 2001). Thus, our results confirm that *S. pygaea* is remarkably drought resistant, likely due to strategies such as 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 (Gibbons and 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 resistance of *R. rigida* to drought could be found in its close taxonomic relationship with *S. pygaea* (McVay and Carstens 2013), which may
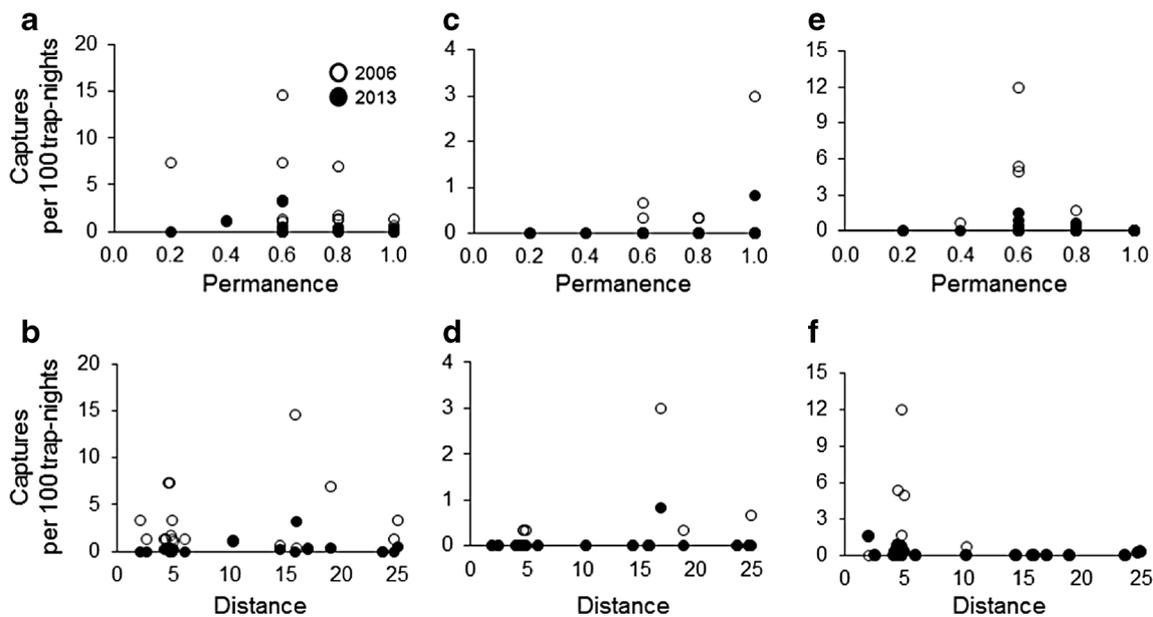
Fig. 3 Relative abundance (effort-corrected capture rate) of snakes in relation to wetland permanence and distance from the Savannah River floodplain for three species of semi-aquatic snakes: (**a**, **b**) *Nerodia fasciata*, (**c**,**d**) *Nerodia floridana*, and (**e**,**f**) *Seminatrix pygaea,* before (2006) and after (2013) supra-seasonal drought. Each point represents capture rate at one of the 20 wetlands sampled in 2006 (open circles) and 2013 (filled circles)

suggest that *R. rigida* could also aestivate during drought. However, *R. rigida* has been found to exhibit terrestrial activity far from water (Steen et al. 2011), suggesting that this species may at times be more terrestrial than we usually perceive. Migration to the Savannah River floodplain, an unlikely scenario for *S. pygaea* due to small body size, high desiccation risk (Winne et al. 2001), and lack of preferred food (*A. talpoideum*) in the floodplain, seems more likely for *R. rigida.* Movement of some or many individuals out of isolated wetlands and into the floodplain during drought would also explain the observed post-drought reduction in detection.

Little is known about *F. abacura,* but its dietary preference for giant salamanders (*Siren* spp./*Amphiuma* spp.) is thought to be the primary reason for their higher abundance in more permanent wetlands, which sustain populations of these highly-aquatic prey (Durso et al. 2013). 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*. Like *S. pygaea*, *Farancia abacura* has been reported to aestivate within or near dried wetlands (Willson et al. 2006). Although reports of aestivation are anecdotal, short distance migration from drying wetlands during drought has also been documented, although sample sizes are small (Seigel et al. 1995; Martin 1998; Willson et al. 2006; Steen et al. 2013). Additionally, the maximum size of *F. abacura* exceeds that sampled by minnow traps (Willson et al. 2008), so it is possible that large individuals could go undetected until recruitment of juvenile

snakes into the population occurs. However, Winne et al. (2006) showed that post-drought survival of aestivating large female *S. pygaea* was lower than that of smaller females, so we would predict that large *F. abacura*, which are >300% larger than the largest *S. pygaea*, are at greater risk of perishing if they remain in dried wetlands during drought. Regardless of whether *F. abacura* aestivate, migrate, or use a combination of the two strategies, they appear to be relatively unaffected by supra-seasonal drought.

Unlike the above drought-resilient species, *Nerodia fasciata* experienced declines in both occupancy and detection during the supra-seasonal drought; specifically, ~30% reduction in occupancy and ~50% mean reduction in detection. We interpret the reduction in detection probability of *N. fasicata* to be an indication of population declines at sites where they persisted. 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; Winne et al. 2010). 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. Although *N. fasciata* are strongly affected by drought, they

appear to be able to rapidly repopulate once water-levels return to normal (Winne 2008), a common characteristic of resilience (Bond et al. 2008).

Our study corroborates data from two historical drought events 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). Subsequent supra-seasonal droughts resulted in *N. floridana* declining substantially, eventually to the point of becoming no longer detectable and perhaps locally extirpated (Willson et al. 2006). We found that *N. floridana* was also strongly affected by drought at the landscape scale. Pre-drought occupancy estimates were low ($\psi = 0.32$), but detection 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 ($\psi = 0.05$). However, *N. floridana* retained relatively high abundances within the one wetland where they persisted, as indicated by high detection probability ($p = 0.59$).

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, 359 *N. fasciata* were captured entering or exiting Ellenton Bay over nine years. 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). The lack of dispersing *N. floridana*, especially before and after drought periods, suggests that this species may be averse to overland dispersal. Although remaining within the wetland during drought may be beneficial for short periods (e.g., droughts can lead to concentration of prey; Canton et al. 1984), the results of our study suggest that supra-seasonal droughts may outlast this species' ability to withstand unfavorable conditions. Indeed, the only wetland in our study where *N. floridana* persisted rarely, if ever, dries. It is possible that permanent bodies of water act as refugia for *N. floridana* during drought. Refugia habitats are essential to drought survival for many species (Magoulick and Kobza 2003) and may serve as source populations that facilitate population growth and recolonization of other wetlands following drought (Adams and Warren 2005; Arthington et al. 2005). We suggest that capture biases against very large individuals (Willson et al. 2008) are unlikely to be responsible for the apparent extirpation of *N. floridana* at most wetlands, because the largest individuals are the most likely to perish during times of food scarcity (Wikelski and Trillmich 1997; Winne et al. 2006).

Given that the southeastern United States is predicted to experience increases in drought frequency and intensity (Ficklin et al. 2015; Feng et al. 2016), efforts may be needed to protect sensitive wetland-associated species like *N. floridana*. 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 to mitigate effects on biodiversity 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, because semi-aquatic snake species are diverse in their habitat preferences and responses to drought, maintaining a large number of diverse wetland types across the landscape is likely critical to maintaining diverse assemblages of snakes (Roe et al. 2004). If necessary, construction of artificial wetlands could be used to mitigate wetland loss and achieve a landscape with sufficient connectivity to sustain meta-population dynamics (Amezaga et al. 2002). Finally, providing high quality habitat corridors and avoiding barriers between wetlands would facilitate dispersal between wetlands (Roe and Georges 2007). Without intervention, changes in drought frequency and intensity may drive both local (Walls et al. 2013a) and species extinctions (Cahill et al. 2013).

References

Adams SB, Warren ML (2005) Recolonization by warmwater fishes and crayfishes after severe drought in upper coastal plain hill streams. Transaction of American Fish Society 134:1173–1192

Akaike H (1973) Information theory and an extension of the maximum likelihood principle. In: Petrov B, Csáki F (eds) second international symposium on information theory. Akademiai Kidao, Budapest, Tsahkadsor, Armenia, USSR, pp 267–281

Allen CD, Macalady AK, Chenchouni H, Bachelet D, McDowell N, Vennetier M, Kitzberger T, Rigling A, Breshears DD, Hogg ET (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. Forest Ecology Management 259:660–684

Amezaga J, Santamaría L, Green AJ (2002) Biotic wetland connectivity—supporting a new approach for wetland policy. Acta Oecologica 23:213–222

Arthington AH, Balcombe SR, Wilson GA, Thoms MC, Marshall J (2005) Spatial and temporal variation in fish-assemblage structure in isolated waterholes during the 2001 dry season of an arid-zone floodplain river, Cooper Creek, Australia. Marine and Freshwater Research 56:25–35

Bigler C, Kulakowski D, Veblen TT (2005) Multiple disturbance interactions and drought influence fire severity in Rocky Mountain subalpine forests. Ecology 86:3018–3029

Bond NR, Lake P, Arthington AH (2008) The impacts of drought on freshwater ecosystems: an Australian perspective. Hydrobiologia 600:3–16

Burnham KP, Anderson DR (2002) Model selection and multi-model inference: a practical information-theoretic approach. Springer, New York

Cahill AE, Aiello-Lammens ME, Fisher-Reid MC, Hua X, Karanewsky CJ, Ryu HY, Sbeglia GC, Spagnolo F, Waldron JB, Warsi O (2013) How does climate change cause extinction? Proceeding of the Royal Society Biological Science Series B 280:20121890

Canton SP, Cline LD, Short R, Ward JV (1984) The macroinvertebrates and fish of a Colorado stream during a period of fluctuating discharge. Freshwater Biology 14:311–316

Clarke KR, Gorley RN (2006) PRIMER v6. United Kingdom

Dai A (2011) Drought under global warming: a review. Wiley Interdisciplinary Reviews: Climate Change 2:45–65

Davis CE, Janecek LL (1997) DOE research set-aside areas of the Savannah River site. Savannah River Ecology Laboratory, Aiken, South Carolina

Dodd CK (1992) Biological diversity of a temporary pond herpetofauna in north Florida sandhills. Biodiversity and Conservation 1:125–142

Durso AM, Willson JD, Winne CT (2011) Needles in haystacks: estimating detection probability and occupancy of rare and cryptic snakes. Biological Conservation 144:1508–1515

Durso AM, Willson JD, Winne CT (2013) Habitat influences diet overlap in aquatic snake assemblages. Journal of Zoology (London) 291:185–193

ESRI (2011) ArcGIS desktop: release 10. Environmental Systems Research Institute, Redlands, California

Feng D, Beighley E, Hughes R, Kimbro D (2016) Spatial and temporal variations in eastern U.S. hydrology: responses to global climate variability. Journal of the American Water Resources Association 52:1089–1108

Ficklin DL, Maxwell JT, Letsinger SL, Gholizadeh H (2015) A climatic deconstruction of recent drought trends in the United States. Environmental Research Letters 10:044009

Gibbons JW, Dorcas ME (2004) North American Watersnakes: a natural history. University of Oklahoma, Norman, Oklahoma, USA

Harrell F (2001) Regression modeling strategies: with applications to linear models, logistic regression, and survival analysis. Springer, Cham, Switzerland

Harrison RD (2000) Repercussions of El Niño: drought causes extinction and the breakdown of mutualism in Borneo. Proceeding of the Royal Society Biological Science Series B 267:911–915

Hines JE (2006) PRESENCE - software to estimate patch occupancy and related parameters 2.4 edition. United States geological survey, Patuxent wildlife research center, Laurel, Maryland

Hynes H (1958) The effect of drought on the fauna of a small mountain stream in Wales. Verh Internat Verein. Theor Angew Limnol 8:826–833

Jury E (1964) Theory and application of the Z-transform method. John Wiley and Sons, Inc., New York

King RB, Queral-Regil A, Stanford KM (2006) Population size and recovery criteria of the threatened Lake Erie watersnake: integrating multiple methods of population estimation. Herpetological Monographs 20:83–104

Knight D (1987) Parasites, lightning, and the vegetation mosaic in wilderness landscapes. In: Turner M, Bogucki D, Bormann F, Box E, Bratton S, Dolan R, Dunn C, Forman R, Gruendling G, Guntenspergen G, Hayes T, Leitner L, Meentenmeyet V, Morrison D, Nassauer J, Odum W, Pace W III, Remillard M, Riskind D, Risser P, Sharpe D, Smith T III, Stearns F, Turner M, Westmacott R (eds) Landscape heterogeneity and disturbance. Springer, New York, pp 59–83

Kock R (2005) What is this infamous "wildlife/livestock disease interface?" a review of current knowledge for the African continent. In: Osofsky SA (ed) Conservation and development interventions at the wildlife/livestock Interface: implications for wildlife, livestock and human health. IUCN species survival commission, Margate, United Kingdom, pp 1–13

Lake P (2000) Disturbance, patchiness, and diversity in streams. Journal of North American Benthological Society 19:573–592

Lake P (2003) Ecological effects of perturbation by drought in flowing waters. Freshwater Biology 48:1161–1172

Larimore RW, Childers WF, Heckrotte C (1959) Destruction and re-establishment of stream fish and invertebrates affected by drought. Transactions of the American Fisheries Society 88:261–285

Lillywhite HB, Tu M-C (2011) Abundance of sea kraits correlates with precipitation. PLoS One 6:e28556

MacKenzie DI, Bailey LL (2004) Assessing the fit of site-occupancy models. Journal of Agricultural, Biological, and Environmental Statistics 9:300–318

MacKenzie DI, Nichols JD, Sutton N, Kawanishi K, Bailey LL (2005) Improving inferences in population studies of rare species that are detected imperfectly. Ecology 86:1101–1113

MacKenzie DI, Nichols JD, Royle JA, Pollock KH, Bailey LL, Hines JE (2006) Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Academic Press, San Diego

Magoulick DD, Kobza RM (2003) The role of refugia for fishes during drought: a review and synthesis. Freshwater Biology 48:1186–1198

Martin CA (1998) An ecological profile of the western mud snake (Farancia abacura reinwardtii). MS thesis, Stephen F. Austin State University, Nacogdoches, Texas, USA

McVay JD, Carstens B (2013) Testing monophyly without well-supported gene trees: evidence from multi-locus nuclear data conflicts with existing taxonomy in the snake tribe Thamnophiini. Molecular Phylogenetics and Evolution 68:425–431

Pough FH (1980) The advantages of ectothermy for tetrapods. The American Naturalist 115:92–112

Pounds JA, Fogden MPL, Campbell JH (1999) Biological response to climate change on a tropical mountain. Nature 398:611–615

Rhind S, Bradley J (2002) The effect of drought on body size, growth and abundance of wild brush-tailed phascogales (Phascogale tapoatafa) in south-western Australia. Wildlife Research 29:235–245

Roe JH, Georges A (2007) Heterogeneous wetland complexes, buffer zones, and travel corridors: landscape management for freshwater reptiles. Biological Conservation 135:67–76

Roe JH, Kingsbury BA, Herbert NR (2004) Comparative water snake ecology: conservation of mobile animals that use temporally dynamic resources. Biological Conservation 118:79–89

Seigel RA, Gibbons JW, Lynch TK (1995) Temporal changes in reptile populations: effects of a severe drought on aquatic snakes. Herpetologica 51:424–434

Seneviratne SI, Nicholls N, Easterling D, Goodess CM, Kanae S, Kossin J, Luo Y, Marengo J, McInnes K, Rahimi M, Reichstein M, Sorteberg A, Vera C, Zhang X (2012) Changes in climate extremes and their impacts on the natural physical environment. In: Field CB, Barros V, Stocker TF, Qin D, Dokken DJ, Ebi KL, Mastrandrea MD, Mach KJ, Plattner G-K, Allen SK, Tignor M, Midgley PM (eds) Managing the risks of extreme events and disasters to advance climate change adaptation. A special report of working groups I and II of the Intergovernmental Panel on Climate Change (IPCC). Cambridge University Press, Cambridge, pp 109–230

Sperry JH, Weatherhead PJ (2008) Prey-mediated effects of drought on condition and survival of a terrestrial snake. Ecology 89:2770–2776

Steen DA, Stiles JA, Stiles SH, Guyer C, Pierce JB, Rudolph DC, Smith LL (2011) Regina rigida (glossy crayfish snake). Terrestrial Movements Herpetol Rev 42:102

Steen DA, Stevenson DJ, Beane JC, Willson JD, Aresco MJ, Godwin J, Graham SP, Smith L, Howze J, Rudolph DC, Pierce J, Lee J,

Gregory B, Jensen J, Stiles S, Stiles J, Nazdrowicz N, Guyer C (2013) Terrestrial movements of the red-bellied Mudsnake (*Farancia abacura*) and rainbow snake (*F. erytrogramma*). Herpetological Review 44:208–213

Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, Collingham YC, Erasmus BF, De Siqueira MF, Grainger A, Hannah L (2004) Extinction risk from climate change. Nature 427: 145–148

Thompson S, Seber G (1996) Adaptive sampling. John Wiley & Sons, New York

Trape S (2009) Impact of climate change on the relict tropical fish fauna of central Sahara: threat for the survival of Adrar mountains fishes, Mauritania. PLoS One 4:e4400

Walls SC, Barichivich WJ, Brown ME, Scott DE, Hossack BR (2013a) Influence of drought on salamander occupancy of isolated wetlands on the southeastern coastal plain of the United States. Wetlands 33: 345–354

Walls SC, Barichivich WJ, Brown ME (2013b) Drought, deluge and declines: the impact of precipitation extremes on amphibians in a changing climate. Biology 2:399–418

Wikelski M, Trillmich F (1997) Body size and sexual size dimorphism in marine iguanas fluctuate as a result of opposing natural and sexual selection: an island comparison. Evolution 51:922–936

Willson JD, Winne CT, Dorcas ME, Gibbons JW (2006) Post-drought responses of semi-aquatic snakes inhabiting an isolated wetland: insights on different strategies for persistence in a dynamic habitat. Wetlands 26:1071–1078

Willson JD, Winne CT, Keck MB (2008) Empirical tests of biased body size distributions in aquatic snake captures. Copeia 2008:401–408

Winne CT (2008) *Seminatrix pygaea*, A model of ecological resilience in dynamic habitats. Ph. D. dissertation, University of Georgia, Athens, Georgia, USA

Winne CT, Ryan TJ, Leiden Y, Dorcas ME (2001) Evaporative water loss in two natricine snakes, *Nerodia fasciata* and *Seminatrix pygaea*. Journal of Herpetology 35:129–133

Winne CT, Willson JD, Gibbons JW (2006) Income breeding allows an aquatic snake *Seminatrix pygaea* to reproduce normally following prolonged drought-induced aestivation. The Journal of Animal Ecology 75:1352–1360

Winne CT, Willson JD, Gibbons JW (2010) Drought survival and reproduction impose contrasting selection pressures on maximum body size and sexual size dimorphism in a snake, *Seminatrix pygaea*. Oecologia 162:913–922