

Landscape-scale effects of supra-seasonal drought on semi-aquatic snake assemblages

Philip N. Vogrin^a, Andrew M. Durso^b, Christopher T. Winne^c, and John D. Willson^{a*}

^aDepartment of Biological Sciences, University of Arkansas, Fayetteville, AR 72701, USA
(pnvogrin@email.uark.edu)

^bDepartment of Biology, Utah State University, Logan, UT 84322, USA (amdurso@gmail.com)

^cSavannah River Ecology Laboratory, Aiken, SC 29802, USA (ctwinne@gmail.com)

*Corresponding Author: Department of Biological Sciences, University of Arkansas, Fayetteville, AR 72701, USA; jwillson@uark.edu; phone: 479-575-2647; fax: 479-575-4010

1 **Abstract**

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

18 **Keywords**

19 Climate change, communities, environmental stochasticity, occupancy modeling, stochasticity,
20 wetlands

21 **Introduction**

22 Anthropogenic impacts to climate contribute to rapid environmental changes that have
23 altered ecosystems and eliminated species across the globe (Allen et al. 2010). At least one
24 vertebrate extinction is attributed to climate change (Pounds et al. 1999), and the most
25 conservative climate warming scenarios estimate that approximately 18% of species are
26 committed to extinction by 2050 (Thomas et al. 2004). One undesirable consequence of global
27 climate change is increased frequency of supra-seasonal drought. Multiple lines of evidence
28 suggest that drought frequency, intensity, and duration will increase in the future in many regions
29 (Dai 2011; Seneviratne et al. 2012; Ficklin et al. 2015). Defined as long, irregular, and

30 unpredictable periods of below average rainfall (Lake 2003), supra-seasonal drought can strongly
31 influence the magnitude of other stochastic disturbance events. Prolonged drought desiccates
32 dead and decaying organic materials, increasing their flammability and fire risk (Knight 1987;
33 Bigler et al. 2005). Drought can also reduce the available water, food, and habitat resources
34 within an ecosystem, thereby influencing survival, growth, and reproduction of wildlife. For
35 example, brush-tailed phascogales (*Phascogale tapoatafa*) suffered 15-25% reductions in body
36 size and a one-third reduction in species detection probability during drought (Rhind and Bradley
37 2002). Meta-population dynamics can also be altered, as drought influences movement behavior,
38 which, in turn, can alter rates of dispersal and colonization (Walls et al. 2013a). Finally, as the
39 available surface water across a landscape is limited, wildlife is forced to concentrate, increasing
40 the severity of competition and probability of predation and disease transmission (Kock 2005).

41 Drought inflicts considerable stress on a variety of organisms, especially those that are
42 closely tied to aquatic systems. Species regularly confronted with drought possess traits that
43 allow them to either persist through drought (resistance) or recolonize and repopulate after
44 drought-induced declines (resilience) (Lake 2000). However, projected increases in drought
45 intensity may be too extreme for even “drought-tolerant” species to withstand (Bond et al. 2008).
46 Population-level impacts of drought have been documented for some taxa, such as fishes (e.g.,
47 Larimore et al. 1959; Trape 2009), invertebrates (e.g., Hynes 1958; Harrison 2000), amphibians
48 (Walls et al. 2013b), and birds (e.g., Cahill et al. 2013). Among snakes, sea krait (*Laticauda*
49 spp.) abundance correlates with precipitation during drought (Lillywhite and Tu 2011) and
50 drought reduced prey abundance, body condition, and survival of ratsnakes (*Pantherophis*
51 *obsoletus*) in Texas (Sperry and Weatherhead 2008). Of the organisms vulnerable to climatic
52 changes in aquatic environments, semi-aquatic snakes fall into a peculiar category in regards to
53 their ability to confront change. Semi-aquatic snakes that rely on aquatic habitats for shelter and
54 food can withstand long periods of starvation due to low metabolic demands (Pough 1980), but
55 exhibit limited vagility due to physiological characteristics such as high rates of evaporative
56 water loss and small body size (Winne et al. 2001; Winne et al. 2006). However, due to their low
57 detectability, little is known about the responses of snake populations and assemblages to supra-
58 seasonal drought events.

59 More than two decades of previous herpetological research at Ellenton Bay, a 10 ha
60 isolated semi-permanent wetland in the Coastal Plain of the southeastern United States, has
61 yielded insight into the influence of drought on semi-aquatic snake population and community
62 dynamics. Since 1974, Ellenton Bay has experienced multiple periodic droughts including three
63 multi-year supra-seasonal droughts (Fig. 1). We found that, at this wetland, highly aquatic black
64 swamp snakes (*Seminatrix pygaea*) were least impacted by drought, exhibiting resistance by
65 aestivating within the wetland and exhibiting little change in relative abundance over multi-year
66 droughts (Willson et al. 2006; Winne et al. 2006). Conversely, banded watersnake (*Nerodia*
67 *fasciata*) populations severely declined, but exhibited resilience by quickly recovering through
68 rapid reproduction and recruitment when the drought ended (Willson et al. 2006). Exhibiting
69 neither resistance nor resilience, Florida green watersnakes (*Nerodia floridana*) became locally
70 extirpated, were not detected for three years post-drought, and never regained their pre-drought
71 relative abundance (Seigel et al. 1995; Willson et al. 2006). Thus, previous research has
72 documented dramatic interspecific variation in both behavioral and population responses to
73 drought at one wetland study site. However, it is unknown if these patterns are location-specific,
74 or if they occur broadly across the landscape.

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

90 and highlights the importance of understanding species' responses to environmental variation
91 that may be exacerbated by climate change.

92 **Methods**

93 *Study Sites*

94 We sampled 20 freshwater wetlands located on the US Department of Energy's (DOE)
95 Savannah River Site (SRS) in 2006 (pre-drought; Fig. 1) and 2013 (post-drought) for semi-
96 aquatic snakes. From 2007-2012 the SRS experienced the most severe drought in at least the past
97 three decades, which left most isolated wetlands dry for at least several months (Fig. 1). The SRS
98 encompasses nearly 932 km² within the Upper Coastal Plain of South Carolina (Aiken and
99 Barnwell Counties), USA, and includes a variety of habitats such as bald cypress swamp, pine
100 and hardwood forest, black water creeks, Carolina bays, and other freshwater wetlands (Davis
101 and Janecek 1997). The Savannah River forms the western boundary of the site, with an
102 extensive floodplain composed of semi-permanent water and lowland forest. The SRS
103 encourages management (fire), conservation (set aside areas), and research, while limiting
104 anthropogenic impacts, resulting in relatively undisturbed and unfragmented habitats in
105 comparison to surrounding landscape. However, previous DOE activities resulted in radiological
106 contamination of some areas of the site.

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

116 *Field Methods*

117 We sampled all wetlands during May and June in 2006 (pre-drought; Durso et al. 2011)
118 and 2013 (post-drought). We captured snakes using unbaited plastic minnow traps (model 700,
119 Gator Buckets, Ladoga, IN) which are effective for capturing semi-aquatic snakes (Willson et al.
120 2008). In both years, we set one array of 60 traps each night for five consecutive nights (300
121 trap-nights) per wetland; thus one array-night (60 trap-nights) represented one sampling unit. In
122 2006, five wetlands had dried sufficiently that they could not accommodate the full array of 60
123 traps. Thus, we set traps at these five wetlands with half of the standard effort: 30 traps for 5
124 nights (150 trap-nights). We accounted for this heterogeneity in effort by incorporating a
125 sampling covariate for effort into model selection in 2006. Initial efforts to scale trapping effort
126 more closely to wetland area in 2006 introduced so many missing values into the data that
127 models often failed to converge. We placed traps 2-3 m apart in shallow water at the vegetated
128 periphery of each wetland, leaving ~5 cm of trap above water to provide air for captured animals.
129 We checked traps daily, measured captured snakes (sex, snout-vent length [mm], body mass
130 [nearest 0.01 g on a digital balance]), and released all snakes at their capture location.

131 *Covariates*

132 We measured seven site covariates (Table 1) based on perceived importance and previous
133 research (Durso et al. 2011). We measured distance to the Savannah River floodplain from the
134 center of the wetland of interest to the nearest boundary of the floodplain, using ArcGIS (ESRI
135 2011). Based on a combination of historical hydrological data for some wetlands and our own
136 observations of wetland hydrology between 1998 and 2013, we ranked the permanence of each
137 wetland as follows: 1 (never dries), 0.80 (only dries during supra-seasonal droughts), 0.60 (only
138 dries periodically), 0.40 (typically dries annually but stays filled in wet years), 0.20 (dries
139 annually).

140 We generated four site covariates representing wetland prey community composition
141 based on the relative abundance of prey captured in minnow traps. Specifically, we allowed
142 minnow traps to accumulate prey for the first 24 h after being set and counted all larval and
143 paedomorphic *A. talpoideum*, giant salamanders (*Siren* and *Amphiuma*), crayfish, and fishes
144 captured. We used average counts of each prey group in 2006 as a site covariate, but excluded
145 Eastern mosquitofish (*Gambusia holbrooki*) from fish counts due to their very small size
146 (making them unimportant as prey for most snakes) and highly variable abundances that

147 swamped out general patterns of abundance of other fishes. Detection probabilities of prey
148 groups estimated in 2006 exceeded 0.90 (Durso et al. 2011). We created a fifth prey covariate
149 representing change in prey community during drought by subtracting pre-drought fish relative
150 abundances (2006) from post-drought fish relative abundances (2013). We focused on fishes for
151 this covariate because they were much more strongly affected by wetland drying than
152 amphibians.

153 *Data Analysis*

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

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

168 We used Akaike's Information Criterion (AIC) for model selection to explore covariate
169 effects on ψ and p for all candidate models. We used AIC_c for all species across both seasons by
170 specifying the effective sample size using a conservative approach based on the number of
171 sampling units (20 wetlands; MacKenzie et al. 2006). We considered a set of sixteen models in
172 the selection process for each species in each season (Table 2) starting with the global model, the
173 most complex model that contains the most parameters (i.e., $\psi(C1,C2)p(C1,C2)$). From the
174 global model, we constructed models representing each possible combination of constant (.), C1,
175 and C2, including the null model ($\psi(.)p(.)$), for occupancy and detection (see Table 2). For

176 2006, we included an effort covariate (E) for p in all models to account for heterogeneity in
177 sampling effort (see above). To assess model fit we used 1000 parametric bootstraps of the
178 global model and adjusted c -hat for over or underdispersion (Akaike 1973; Burnham and
179 Anderson 2002; MacKenzie and Bailey 2004). We reranked overdispersed models using QAIC_c
180 and increased the number of model parameters by one. For underdispersed models, we inflated c -
181 hat to 1 and used AIC_c ranking (MacKenzie et al. 2006). Models with values $< 2 \Delta AIC$ were
182 considered as supported top models.

183 Because PRESENCE does not present derived parameters directly in the likelihood,
184 standard errors for all parameters must use the Delta Method to calculate the variance of back-
185 transformed estimates to estimate 95% confidence intervals (CI). We used a simplified version
186 by adding or subtracting (1.95 * the untransformed standard error) from the untransformed
187 regression coefficient (β), then back-transforming from the logit scale to get the upper or lower
188 95% CI of the estimate. We inferred significant differences based on non-overlapping 95% CIs.

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

199 **Results**

200 Aquatic trapping across 20 wetlands resulted in 242 captures of 10 species in 2006 (5250
201 trap-nights) and 113 captures of 10 species in 2013 (6000 trap-nights). The five species used in
202 our analysis were *Nerodia fasciata* (2006 $n = 147$; 2013 $n = 42$ captures), *Nerodia floridana*
203 (2006 $n = 15$; 2013 $n = 5$), *Seminatrix pygaea* (2006 $n = 37$; 2013 $n = 27$), *Farancia abacura*
204 (2006 $n = 27$; 2013 $n = 15$), and *Regina rigida* (2006 $n = 5$; 2013 $n = 4$).

205 Principal component analysis yielded two factors that explained 62% of the cumulative
206 variation in site covariates (Table 1): C1, 42.3% of variation (eigenvalue = 3.0) and C2, 19.7% of
207 variation (eigenvalue = 1.49). Principal component one (C1) was strongly negatively correlated
208 with wetland permanence, fish abundance, and giant salamander abundance, and positively
209 correlated with *A. talpoideum* abundance and change in abundance of fish. Thus, wetlands with
210 high scores for C1 were less permanent and had undergone a large change in fish abundance
211 during drought, thus leading to lower abundance of fishes and giant salamanders, but higher
212 abundance of *A. talpoideum*. Principal component two (C2) was strongly negatively correlated
213 with distance to the Savannah River floodplain and positively correlated with crayfish
214 abundance. Therefore, wetlands with higher scores for C2 were closer to the Savannah River
215 floodplain and had higher abundance of crayfish.

216 Model selection revealed that for most species in both pre- and post-drought years either
217 the null model was favored and/or multiple models were favored with low individual weight (W_i ;
218 Table 2), likely due to the relatively small number of sites we were able to sample. Two species
219 had heavily weighted top models in 2013 (post-drought). The top model for *N. fasciata* favored
220 C1 ($W_i = 0.65$) for both occupancy and detection; indicating post-drought association with
221 wetland permanence for this species. Conversely, the top model for *R. rigida* favored C2 ($W_i =$
222 0.66) for both occupancy and detection; indicating an association with crayfish and the Savannah
223 River floodplain for this species.

224 Interspecific variation in both null model occupancy and detection occurred in both pre-
225 and post-drought years (Fig. 2). Pre-drought detection estimates were relatively high, ranging
226 from $p = 0.44$ (*N. floridana*) to $p = 0.69$ (*N. fasciata*). Pre-drought, *N. fasciata* occupied nearly
227 every wetland sampled and had the highest estimated occupancy of any species ($\psi = 0.95$).
228 Alternatively, the congeneric *N. floridana* occupied nearly one-third of the wetlands sampled (ψ
229 $= 0.32$). *Seminatrix pygaea* was estimated to occupy approximately 40% ($\psi = 0.41$) and *F.*
230 *abacura* 50% ($\psi = 0.52$) of wetlands. The species with the lowest occupancy estimate pre-
231 drought was *R. rigida* ($\psi = 0.10$).

232 Both *Nerodia* species suffered reductions in occupancy from pre- to post-drought
233 seasons, whereas all other species did not change (Fig. 2a). *Nerodia floridana* and *N. fasciata*

234 experienced almost identical absolute reductions in occupancy (*N. floridana*: pre-drought $\psi =$
235 0.32; post $\psi = 0.05$; $\Delta = -0.27$; *N. fasciata*: pre-drought $\psi = 0.95$; post $\psi = 0.69$; $\Delta = -0.26$).
236 However, relative to pre-drought, *N. fasciata* suffered a net reduction in occupancy of only 29%,
237 whereas *N. floridana* was nearly locally extirpated, with a net 84% reduction in occupancy. In
238 fact, *N. floridana* was only detected in one very permanent wetland post-drought. Significant
239 reductions in occupancy were not observed for *F. abacura*, *S. pygaea*, or *R. rigida* (Fig. 2a).
240 Detection (p) decreased by approximately 50% for *N. fasciata* (pre-drought: 0.69; post: 0.33), by
241 approximately 40% for *S. pygaea* (pre-drought: 0.57, post-drought: 0.35), and by 70% for *R.*
242 *rigida* (pre-drought: 0.48, post-drought: 0.14) (Fig. 2b). *Farancia abacura* and *N. floridana*
243 experienced no change in detection associated with drought.

244 Although our occupancy analyses lacked the power needed to detect strong covariate
245 relationships, examination of raw capture rates of our three most common species in relation to
246 wetland characteristics can provide information on wetland and landscape factors that may
247 mediate the effects of drought (Fig. 3). Prior to drought, the wetlands with the highest capture
248 rates of *S. pygaea* were moderately permanent and close to the Savannah River floodplain (Fig.
249 3c, d). *Nerodia fasciata* was captured in nearly every wetland, but wetlands with the highest
250 capture rates were moderately permanent and far from the floodplain (Fig. 3a, b). Wetlands with
251 the highest capture rates of *N. floridana* were relatively permanent and farther from the
252 floodplain, (Fig. 3e, f). Capture rates of all three species decreased following drought. *Nerodia*
253 *fasciata* suffered the greatest reductions in capture rate at hydrologic extremes (i.e., very
254 ephemeral and very permanent wetlands). Alternatively, *S. pygaea* was never found in extremely
255 permanent or ephemeral wetlands pre-drought and therefore only suffered reductions in capture
256 rate in wetlands of moderate permanence. *Nerodia floridana* disappeared from all but one
257 permanent wetland after the drought, but even at this wetland, capture rates were reduced by
258 nearly 50%.

259 Discussion

260 We found interspecific variation in the effects of drought on occupancy and detection of
261 semi-aquatic snake species. Specifically, the two *Nerodia* species suffered drought-induced
262 declines in distribution and *N. floridana* was nearly extirpated from isolated wetlands across the
263 landscape. Three species, *Seminatrix pygaea*, *Regina rigida*, and *Farancia abacura*, showed no

264 change in occupancy following the drought. Pre-drought covariate effects on abundance and
265 detection were weak for all species, but snake capture rates plotted against wetland permanence
266 and distance to floodplain showed a decline in relative abundance of *N. fasciata*, *S. pygaea*, and
267 *N. floridana* across the study area. Wetlands with the highest abundances of *S. pygaea* were
268 moderately permanent wetlands and closer to the river floodplain, whereas *N. fasciata* declined
269 the most severely in the wetlands at both extremes of the hydrologic gradient. Our results
270 provide a unique example of how drought can influence the community composition,
271 distribution, and relative abundance of important reptilian predators in isolated wetland
272 ecosystems.

273 Estimated occupancy of *S. pygaea* was not affected by drought, a result that mirrors long-
274 term population studies at Ellenton Bay. For example, relative abundance of *S. pygaea* remained
275 virtually unchanged (~5.5 vs. ~6.5 captures per 100 trap night) at Ellenton Bay before and after a
276 supra-seasonal drought which dried the wetland for most of 2000 and 2001 (Willson et al. 2006;
277 Winne 2008). More detailed data for Ellenton Bay suggest that this drought resistance is due to
278 the ability of *S. pygaea* to aestivate within the dried wetland during prolonged drought, and
279 subsequently capitalize on high productivity once the wetland refills (Willson et al. 2006; Winne
280 et al. 2010). However, our current study found that detection was reduced after drought,
281 suggesting some effect of drought on *S. pygaea* abundance or behavior. We expect that this
282 reduction is a result of drought-induced mortality, as indicated by a lack of large individuals of
283 both sexes (>325 mm) after drought in 2003 (Winne et al. 2010). Although larger individuals
284 may perish during drought, our results suggest that this mortality is of minor significance to
285 persistence of populations, given that overall occupancy of *S. pygaea* did not change following
286 drought. Alternatively, emigration could explain the slight reduction in detection that we
287 observed; select studies have suggested that individuals emigrate from drying wetlands (Dodd
288 1992; Seigel et al. 1995). However, other studies suggest that terrestrial dispersal is
289 physiologically demanding and unlikely for *S. pygaea*, especially for adults (Winne et al. 2001).
290 Thus, our results confirm that *S. pygaea* is remarkably drought resistant, likely due to strategies
291 such as aestivation that enable most individuals to survive and occupy isolated wetlands across
292 the landscape throughout the entire drought duration.

293 Similar to *S. pygaea*, *R. rigida* did not experience reductions in occupancy during
294 drought. We know little about the ecology and life history of *R. rigida*, which is perceived to be
295 the rarest of our focal species (Gibbons and Dorcas 2004). Durso et al. (2011) found that *R.*
296 *rigida* had higher occupancy in wetlands closer to the Savannah River floodplain containing
297 crayfish; a relationship that stands in our post-drought analysis. One hypothesis for the resistance
298 of *R. rigida* to drought could be found in its close taxonomic relationship with *S. pygaea* (McVay
299 and Carstens 2013), which may suggest that *R. rigida* could also aestivate during drought.
300 However, *R. rigida* has been found to exhibit terrestrial activity far from water (Steen et al.
301 2011), suggesting that this species may at times be more terrestrial than we usually perceive.
302 Migration to the Savannah River floodplain, an unlikely scenario for *S. pygaea* due to small body
303 size, high desiccation risk (Winne et al. 2001), and lack of preferred food (*A. talpoideum*) in the
304 floodplain, seems more likely for *R. rigida*. Movement of some or many individuals out of
305 isolated wetlands and into the floodplain during drought would also explain the observed post-
306 drought reduction in detection.

307 Little is known about *F. abacura*, but its dietary preference for giant salamanders (*Siren*
308 spp./*Amphiuma* spp.) is thought to be the primary reason for their higher abundance in more
309 permanent wetlands, which sustain populations of these highly-aquatic prey (Durso et al. 2013).
310 More permanent wetlands are less likely to dry completely during drought, which could explain
311 the lack of drought effects on either occupancy or detection probability for *F. abacura*. Like *S.*
312 *pygaea*, *Farancia abacura* has been reported to aestivate within or near dried wetlands (Willson
313 et al. 2006). Although reports of aestivation are anecdotal, short distance migration from drying
314 wetlands during drought has also been documented, although sample sizes are small (Seigel et al.
315 1995; Martin 1998; Willson et al. 2006; Steen et al. 2013). Additionally, the maximum size of *F.*
316 *abacura* exceeds that sampled by minnow traps (Willson et al. 2008), so it is possible that large
317 individuals could go undetected until recruitment of juvenile snakes into the population occurs.
318 However, Winne et al. (2006) showed that post-drought survival of aestivating large female *S.*
319 *pygaea* was lower than that of smaller females, so we would predict that large *F. abacura*, which
320 are >300% larger than the largest *S. pygaea*, are at greater risk of perishing if they remain in
321 dried wetlands during drought. Regardless of whether *F. abacura* aestivate, migrate, or use a
322 combination of the two strategies, they appear to be relatively unaffected by supra-seasonal
323 drought.

324 Unlike the above drought-resilient species, *Nerodia fasciata* experienced declines in both
325 occupancy and detection during the supra-seasonal drought; specifically, ~30% reduction in
326 occupancy and ~50% mean reduction in detection. We interpret the reduction in detection
327 probability of *N. fasciata* to be an indication of population declines at sites where they persisted.
328 This agrees with patterns documented at Ellenton Bay, where relative abundance using minnow
329 traps was substantially reduced from ~4 individuals per 100 trap-nights before drought (spring
330 1998), to zero individuals captured in minnow traps following the supra-seasonal drought in
331 spring 2003 (Winne 2008; Winne et al. 2010). Although Seigel et al. (1995) suggested that *N.*
332 *fasciata* emigrate in the direction of aquatic habitats during drying, very few *N. fasciata*
333 immigrated back to the wetland after it refilled in 2003. This suggests high mortality during
334 drought or failure of snakes to make the return journey (Willson et al. 2006). It is possible that *N.*
335 *fasciata* migrate to permanent habitats like the Savannah River floodplain or larger creeks and
336 remain there permanently. Although *N. fasciata* are strongly affected by drought, they appear to
337 be able to rapidly repopulate once water-levels return to normal (Winne 2008), a common
338 characteristic of resilience (Bond et al. 2008).

339 Our study corroborates data from two historical drought events demonstrating that *N.*
340 *floridana* are strongly affected by supra-seasonal drought. Prior to a supra-seasonal drought in
341 1985, *N. floridana* were fairly common within Ellenton Bay, nearly twice as abundant as *N.*
342 *fasciata* (Seigel et al. 1995). Subsequent supra-seasonal droughts resulted in *N. floridana*
343 declining substantially, eventually to the point of becoming no longer detectable and perhaps
344 locally extirpated (Willson et al. 2006). We found that *N. floridana* was also strongly affected by
345 drought at the landscape scale. Pre-drought occupancy estimates were low ($\psi = 0.32$), but
346 detection was moderate overall ($p = 0.44$), with some wetlands containing high abundances. Post-
347 drought occupancy dropped by >80% and *N. floridana* was nearly extirpated from isolated
348 wetlands across the landscape ($\psi = 0.05$). However, *N. floridana* retained relatively high
349 abundances within the one wetland where they persisted, as indicated by high detection
350 probability ($p = 0.59$).

351 There are several possible factors that could explain the sensitivity of *N. floridana* to
352 drought. Most *N. floridana* fail to emigrate from drying wetlands, especially in comparison to *N.*
353 *fasciata* (Seigel et al. 1995; Willson et al. 2006). For example, 359 *N. fasciata* were captured

354 entering or exiting Ellenton Bay over nine years. Only nine *N. floridana* were captured entering
355 or leaving during that same time period, despite relatively high numbers of resident *N. floridana*
356 within the bay (Seigel et al. 1995). The lack of dispersing *N. floridana*, especially before and
357 after drought periods, suggests that this species may be averse to overland dispersal. Although
358 remaining within the wetland during drought may be beneficial for short periods (e.g., droughts
359 can lead to concentration of prey; Canton et al. 1984), the results of our study suggest that supra-
360 seasonal droughts may outlast this species' ability to withstand unfavorable conditions. Indeed,
361 the only wetland in our study where *N. floridana* persisted rarely, if ever, dries. It is possible that
362 permanent bodies of water act as refugia for *N. floridana* during drought. Refugia habitats are
363 essential to drought survival for many species (Magoulick and Kobza 2003) and may serve as
364 source populations that facilitate population growth and recolonization of other wetlands
365 following drought (Adams and Warren 2005; Arthington et al. 2005). We suggest that capture
366 biases against very large individuals (Willson et al. 2008) are unlikely to be responsible for the
367 apparent extirpation of *N. floridana* at most wetlands, because the largest individuals are the
368 most likely to perish during times of food scarcity (Wikelski and Trillmich 1997; Winne et al.
369 2006).

370 Given that the southeastern United States is predicted to experience increases in drought
371 frequency and intensity (Ficklin et al. 2015; Feng et al. 2016), efforts may be needed to protect
372 sensitive wetland-associated species like *N. floridana*. Mitigating or managing drought effects is
373 difficult, since droughts often span large spatial and temporal scales, and are unpredictable in
374 timing and severity (Bond et al. 2008). One strategy to mitigate effects on biodiversity is the
375 development of long-term management plans to avoid overuse of water resources (Bond et al.
376 2008) that affect isolated wetlands and other aquatic habitats. Alternatively, because semi-
377 aquatic snake species are diverse in their habitat preferences and responses to drought,
378 maintaining a large number of diverse wetland types across the landscape is likely critical to
379 maintaining diverse assemblages of snakes (Roe et al. 2004). If necessary, construction of
380 artificial wetlands could be used to mitigate wetland loss and achieve a landscape with sufficient
381 connectivity to sustain meta-population dynamics (Amezaga et al. 2002). Finally, providing high
382 quality habitat corridors and avoiding barriers between wetlands would facilitate dispersal
383 between wetlands (Roe and Georges 2007). Without intervention, changes in drought frequency

384 and intensity may drive both local (Walls et al. 2013a) and species extinctions (Cahill et al.
385 2013).

386

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605 **Table 1** Principal component analysis results reducing seven site covariates into two composite
 606 variables. Change in fish relative abundance was the difference between 2013 and 2006 fish
 607 abundance and was a representation of each wetland's degree of hydrologic change. We
 608 considered variables with correlations of >0.30 to be strong contributors to each component
 609 (indicated in bold).

610

	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
<i>Ambystoma talpoideum</i> relative abundance	0.34	-0.28
Giant salamander relative abundance	-0.31	0.07
Change in fish relative abundance	0.52	-0.18

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623 **Table 2** AIC model selection for five species of semi-aquatic snakes, pre- (2006) and post-
624 drought (2013). Models within < 2 AIC were considered to be supported top models and are
625 indicated in bold. ψ = site occupancy, p = detection probability, E = effort covariate, $C1$ = first
626 component, $C2$ = second component, W_i = AIC weight. * The effort covariate was included in all
627 models to account for the effect of unequal sampling effort on detection probability.
628

Model	Pre-drought (2006)					Post-drought (2013)				
	<i>Nerodia fasciata</i>	<i>Nerodia floridana</i>	<i>Seminatrix pygaea</i>	<i>Farancia abacura</i>	<i>Regina rigida</i>	<i>Nerodia fasciata</i>	<i>Nerodia floridana</i>	<i>Seminatrix pygaea</i>	<i>Farancia abacura</i>	<i>Regina rigida</i>
$\psi(\cdot), p(E^*)$	0.12	0.14	0.09	0.44	0.15	0.01	0.14	0.20	0.39	0.01
$\psi(\cdot), p(C1, E^*)$	0.18	0.23	0.21	0.09	0.04	0.00	0.12	0.21	0.10	0.02
$\psi(\cdot), p(C2, E^*)$	0.03	0.05	0.14	0.11	0.01	0.01	0.07	0.05	0.12	0.01
$\psi(\cdot), p(C1, C2, E^*)$	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
$\psi(C1C2), p(E^*)$	0.21	0.01	0.01	0.02	0.27	0.02	0.02	0.01	0.03	0.01
$\psi(C1C2), p(C1, E^*)$	0.19	0.14	0.01	0.00	0.03	0.10	0.02	0.06	0.01	0.00
$\psi(C1C2), p(C2, E^*)$	0.03	0.00	0.01	0.00	0.04	0.00	0.02	0.00	0.01	0.02
$\psi(C1C2), p(C1, C2, E^*)$	0.02	0.02	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.01

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630

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

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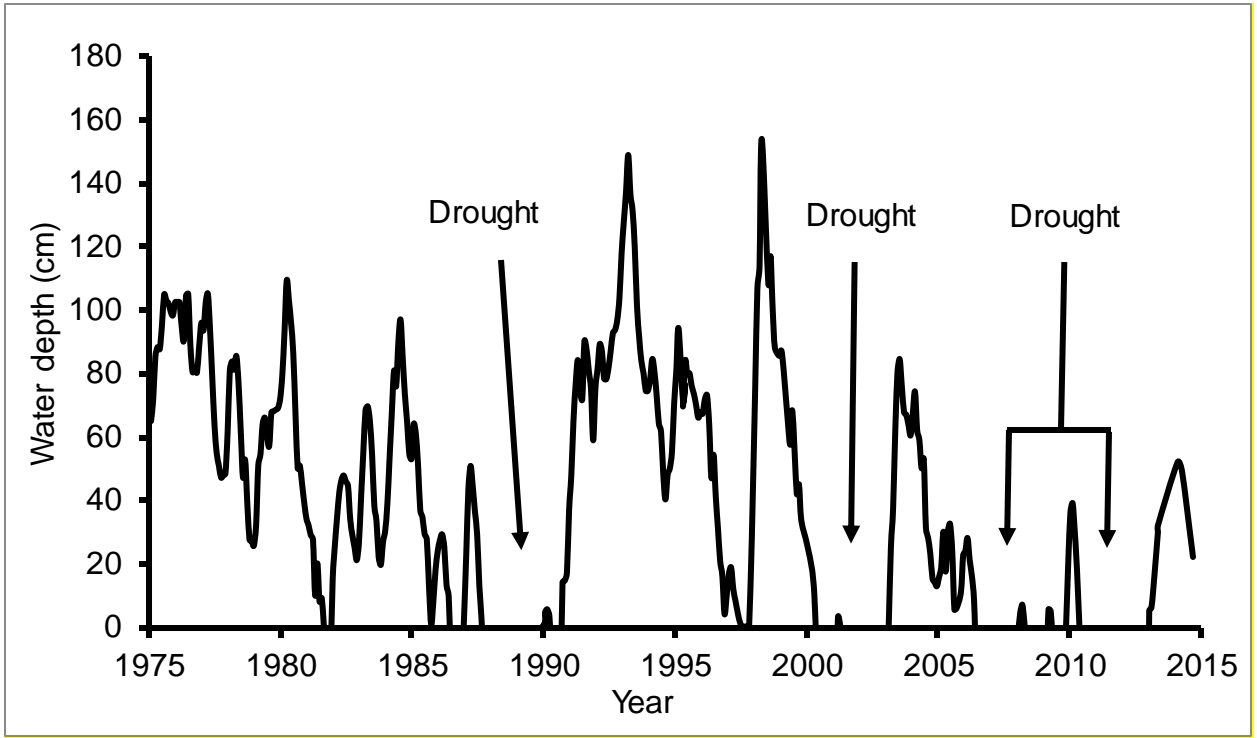
636 **Figure 2** Single season, null model a) occupancy (ψ) and b) detection (p) probability estimates
637 for pre-drought 2006 (open bars) and post drought 2013 (grey bars) for five species of semi-
638 aquatic snakes across 20 wetlands in South Carolina. *N. fasciata* = *Nerodia fasciata* (banded
639 watersnake), *N. floridana* = *Nerodia floridana* (Florida green watersnake), *S. pygaea* =
640 *Seminatrix pygaea* (black swamp snake), *F. abacura* = *Farancia abacura* (mud snake), *R. rigida*
641 = *Regina rigida* (glossy crayfish snake). Error bars represent 95% confidence intervals

642

643 **Figure 3** Relative abundance (effort-corrected capture rate) of snakes in relation to wetland
644 permanence and distance from the Savannah River floodplain for three species of semi-aquatic
645 snakes: (a, b) *Nerodia fasciata*, (c,d) *Nerodia floridana*, and (e,f) *Seminatrix pygaea*, before
646 (2006) and after (2013) supra-seasonal drought. Each point represents capture rate at one of the
647 20 wetlands sampled in 2006 (open circles) and 2013 (filled circles)

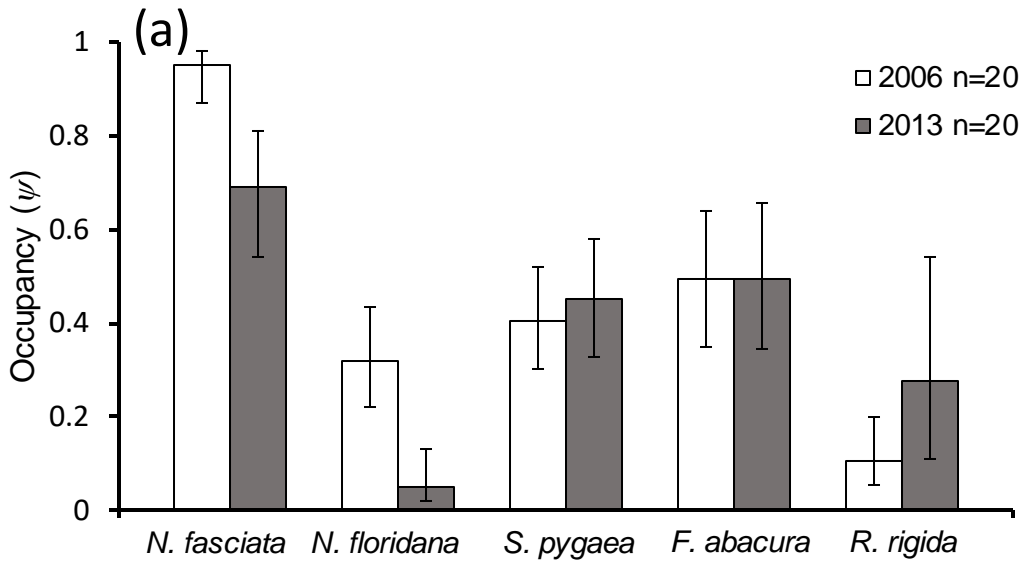
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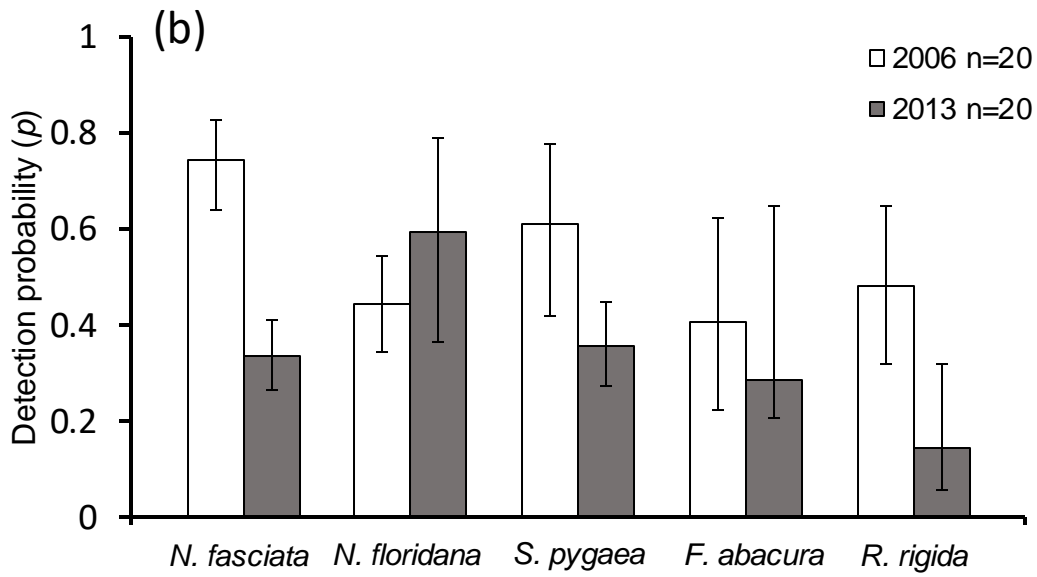


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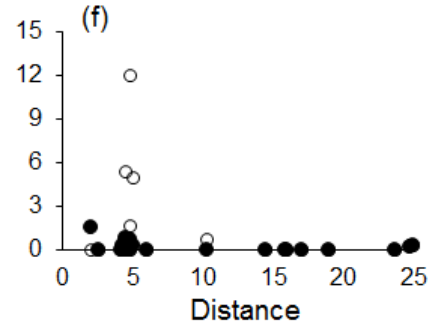
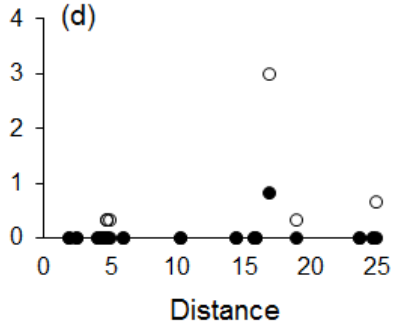
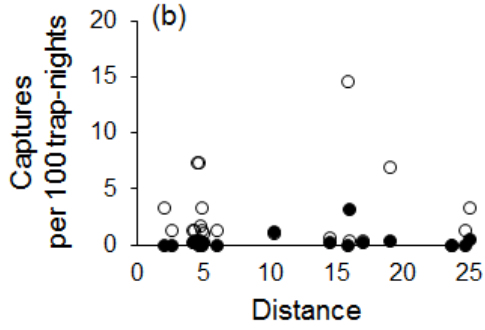
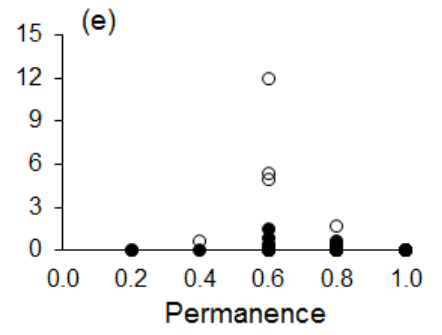
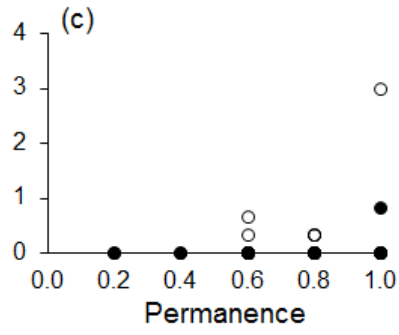
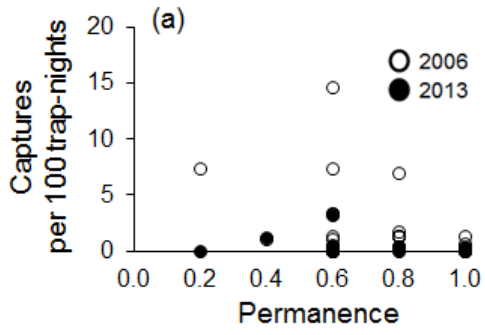
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