



Influence of Drought on Salamander Occupancy of Isolated Wetlands on the Southeastern Coastal Plain of the United States

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Abstract In the southeastern U.S., changes in temperature and precipitation over the last three decades have been the most dramatic in winter and spring seasons. Continuation of these trends could negatively impact pond-breeding amphibians, especially those that rely on winter and spring rains to fill seasonal wetlands, trigger breeding, and ensure reproductive success. From 2009 to 2012, we monitored Spring and Fall presence of aquatic stages (larval and paedomorphic, gilled adult) of a winter-breeding amphibian (the mole salamander, *Ambystoma talpoideum*) and used multi-season models to estimate occupancy, local colonization and extinction. Seasonal estimates of occupancy, corrected for imperfect detection, declined from 22.3 % of ponds in Spring 2009 to 9.9 % in Fall 2012. Our best supported model suggested that changes in occupancy were driven by increased rates of extinction that corresponded with drought-related drying of ponds. Based on uncertainty in climate change projections for the Southeast, we present a conceptual model of predicted changes in wetland hydroperiods across a landscape with projected decreases and

increases in future precipitation. Such precipitation changes could alter wetland hydroperiods, facilitate extinctions of species adapted to short, intermediate or long hydroperiod environments and, ultimately, modify the composition of amphibian communities within freshwater wetland ecosystems.

Keywords Climate change · Drought · Mole salamander · Occupancy dynamics · Pond-breeding amphibians · Wetland hydrology

Introduction

Climate change is anticipated to be one of the most significant drivers of ecological change in the forthcoming century (Lawler et al. 2009). Freshwater wetlands, especially those that are ephemeral and hydrologically isolated from other freshwater systems, are especially vulnerable to the impact of climate change (Brooks 2009) because of their shallow depths, dependence on rainfall, and connection (if one exists) to a shallow groundwater system. Isolated wetlands are critical to the persistence of aquatic biodiversity in many regions, including the southeastern United States. For this region, general circulation models (e.g., the Hadley Centre Model and the Canadian Climate Centre Model: National Assessment Synthesis Team 2000) project that temperatures will increase and the intensity of droughts during future La Niña phases will strengthen; indeed, the percentage of the Southeast experiencing moderate to severe drought has increased over the last three decades (Karl et al. 2009). Hydrologic responses to drought have the potential to be a significant driving force behind losses of freshwater wetlands, their ecosystem function, and the biological resources they harbor. The prevalence and diversity of isolated wetlands across many landscapes and watersheds, particularly in the South Atlantic and Gulf Coast regions

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of the U.S. (Comer et al. 2005), make them valuable in identifying and forecasting the effects of drought and other climate change phenomena on wetland-associated wildlife and, therefore, relevant to adaptive management of water resources.

One scenario under prolonged drought conditions is that evapotranspiration losses from freshwater wetlands could exceed potential increases in precipitation, resulting in shortened wetland hydroperiods (the number of days in a year a wetland retains water). In turn, decreases in hydroperiod will likely lead to an increased frequency of reproductive failure for many species that breed in these habitats, such as amphibians (Brooks 2004), for which freshwater wetlands provide critical habitat. Amphibian populations are declining on a global scale (Houlahan et al. 2000; Stuart et al. 2004), but locally they can be extremely abundant and are therefore suitable “vectors” for transferring biomass and energy from isolated wetlands (larval habitat) to surrounding terrestrial habitat (juvenile and adult habitat) (Gibbons et al. 2006; Regester et al. 2006, 2008; Earl et al. 2011). The roles of amphibians in these ecosystems offer insight into the potential consequences of climate change should the ecosystem services amphibians provide be lost from wetlands and the surrounding terrestrial environment. Amphibians, then, along with the hydrology of the freshwater wetlands they inhabit, can serve as valuable indicators of the potential impacts of climate change.

As part of the U.S. Geological Survey’s Amphibian Research and Monitoring Initiative (Muths et al. 2005), we initiated long-term monitoring of the mole salamander, *Ambystoma talpoideum*, a generalist species that breeds in seasonal, semi-permanent, and permanent wetlands. Our objective was to assess whether changes in site occupancy for aquatic stages (larval and paedomorphic, gilled adult) of the mole salamander were associated with changes in local drought and wetland hydrology. In an occupancy modeling framework (MacKenzie et al. 2006), the primary hypothesis we tested was that estimates of occupancy varied as a consequence of the effects of drought on extinction probabilities. Under a scenario of ongoing drought, long-hydroperiod breeding sites could dry prematurely, causing local extinction to increase and occurrence to decrease. Alternatively, shortened hydroperiods of permanent and semi-permanent wetlands, due to an extended, local drought, could eliminate populations of fish and other predators, thus creating suitable breeding habitat for mole salamanders (sensu Werner et al. 2009). Under this drought scenario, occupancy could remain relatively constant, or even increase, assuming the effects of drought on the terrestrial habitat do not restrict inter-pond connectivity, dispersal and colonization of new sites, and that the population response (in terms of colonization) is sufficient to counteract local extinctions. In contrast, during episodes of increased precipitation (as projected by climate models

developed by the Hadley Centre: National Assessment Synthesis Team 2000), local colonization and occurrence could increase or at least remain stable as formerly short hydroperiod wetlands transition into ones of longer hydroperiod, thus creating additional suitable breeding habitat for mole salamanders on the landscape (Fig. 1).

Methods

Study Species

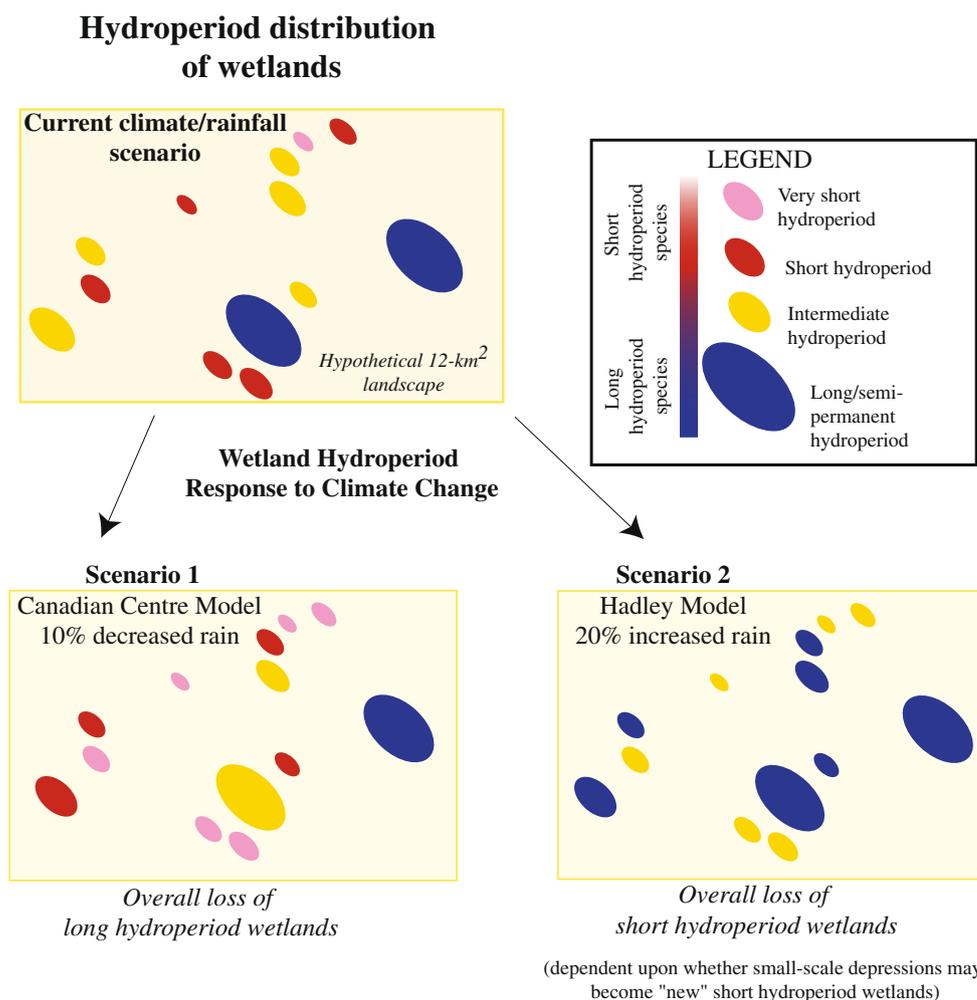
On the Atlantic and Gulf Coastal Plain of the southeastern U.S., *A. talpoideum* breeds primarily from December to March, depending on the onset of winter rains. In landscapes with temporary ponds that dry annually, larvae are capable of metamorphosing in 4–5 months (Semlitsch 1985; SCW, pers. obs.) and populations consist of predominantly metamorphosed, terrestrial adults. In contrast, paedomorphic adults predominate in fishless, permanent and semi-permanent ponds, where they can persist for 14–15 months (Patterson 1978). Such variation is thought to be adaptive in the face of environmental uncertainty (Wilbur and Collins 1973); pond drying influences the expression of these alternative life history strategies, although its propensity to do so varies among populations (Semlitsch et al. 1990). In this study, we focused on the pond-associated larval and paedomorph stages because these individuals are typically more abundant, persist in the aquatic environment for relatively long periods of time and, thus, are more detectable (resulting in more precise parameter estimates) than terrestrial adults when a drift fence is not available to intercept migrating adults.

The mole salamander can be a keystone species in some communities (Fauth 1999) and, at some localities, constitutes the primary prey item for at least one dietary specialist (Willson et al. 2010). Thus, environmental changes that influence the occurrence of mole salamanders within communities may potentially affect the rest of the community as well. At our study site in the Florida panhandle, this species declined significantly in terrestrial habitats over a 28-yr period but is not yet of conservation concern (Dodd et al. 2007). The mole salamander is ecologically similar to other pond-breeding salamanders, which makes it a useful “surrogate” for species that are of conservation concern. Monitoring the biological responses of a relatively common surrogate species to climate change is an important first step for devising management options for rare species of conservation concern that also breed in freshwater wetlands.

Study Area

St. Marks National Wildlife Refuge (SMNWR) is located in the panhandle region of northwest Florida, U.S. (Fig. 2), an

Fig. 1 Conceptual model of predicted changes in wetland hydroperiods across a landscape with projected decreases (Canadian Model) and increases (Hadley Model) in future precipitation

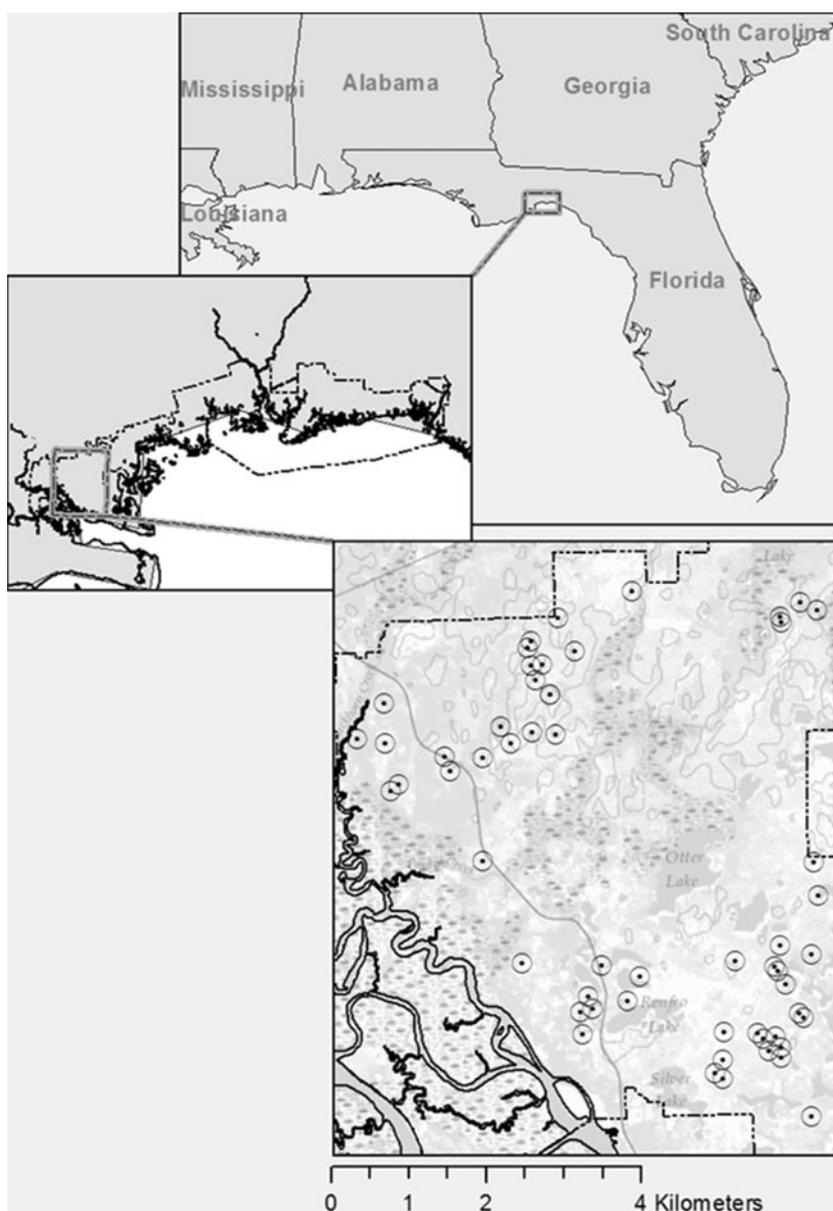


area reported to be one of the five richest biodiversity hotspots in North America (Blaustein 2008). Three management units (St. Marks, Wakulla and Panacea) comprise the refuge and extend 72 km along the Gulf Coast in Taylor, Jefferson and Wakulla counties. The refuge consists of 27,500 ha of diverse terrestrial (sandhills, flatwoods and hammocks) and wetland (freshwater wetlands and marsh) habitats. Within the refuge boundaries there are either historically or currently three amphibians of conservation concern and four other salamander species that have been identified as possibly being in decline (Dodd et al. 2007).

Initially we randomly selected 45 ponds (identified using National Wetland Inventory maps) at SMNWR, Wakulla County, Florida and, from 2009 to 2011, sampled them for *A. talpoideum* (Fig. 2). In spring 2012 we added 15 ponds to increase our sample size. Ponds were of short, intermediate and long hydroperiods and occurred in sandhill and long-leaf pine (*Pinus palustris*) savanna habitat, as well as areas dominated by cypress (*Taxodium* sp.), blackgum (*Nyssa* sp.) and titi (*Cyrilla* sp. and *Cliftonia* sp.) (Walls et al. 2011). Normal high-water pond areas ranged from 0.01 to 1.6 ha. Ponds were

sampled during two periods, corresponding to Spring and Fall, each year, resulting in a total of eight sampling timeframes (Spring 2009=30 March-3 April, 20–24 April; Fall 2009=13–16 and 19–23 October; Spring 2010=12–16 and 19–23 April; Fall 2010=4–8 and 19–21 October; Spring 2011=30 March-1 April and 4–8 April; Fall 2011=17–21 October; Spring 2012=26–30 March and 2–5 April; and Fall 2012=15–25 October). In 2009 and 2010, we sampled each pond with four modified commercial crayfish traps (2.5 cm mesh, Lee Fisher International, Tampa, Florida, U.S., lined with 4 mm Vexar[®]) (Johnson and Barichivich 2004). We placed traps in $\leq 0.5 - 0.6$ m of water, for two trap nights per pond (without moving traps between nights), resulting in eight trap-nights/site/season or 16 total trap-nights/site/calendar year. These traps were efficient in capturing all but the smallest of larvae (e.g., hatchlings: $\bar{x} \pm 1$ SD total length=11.47 \pm 1.79 mm: Walls and Altig 1986). Thus, in 2011 and 2012 we experimented with alternative trap types to determine whether use of a different type of trap (one that ensured capture of smaller individuals) would affect detection probability. In 2011 we supplemented our crayfish traps with four aluminum screen funnel traps (76 \times 20 cm) in each pond. In

Fig. 2 Location of SMNWR along the Gulf Coast region of NW FL (*top*); boundaries of SMNWR (dotted line) (*middle*); and locations of 60 wetlands sampled on SMNWR for mole salamanders (*bottom*)



2012, we used 10 minnow traps (0.48 cm² white plastic mesh) only in each pond. The number and identity of all amphibians captured was recorded daily, along with snout-vent length (SVL, in mm) of all mole salamanders captured. All salamanders were released near their point of capture after tail-clipping.

Statistical Analyses

We used an information-theoretic, model-selection framework to fit a set of candidate models that represented hypotheses about how *A. talpoideum* occupancy changed during our study. In particular, we focused on the consequences of drought on pond-level extinction rates. We represented drought using the Palmer Hydrological Drought Index (PHDI: a measure of the long-term hydrological

impacts of drought) for Northwest Florida (Division 01, National Climatic Data Center 2012), as our observations indicated that dry conditions during the course of our study shortened pond hydroperiods. Indeed, over the eight seasons we sampled, the percentage of ponds that were dry at the time of sampling ranged from 0 to 44.4 %. For estimating the effect of drought on Spring-time occupancy, we used monthly PHDI values averaged over the previous 6 months (October to April). For Fall samples, we used the average PHDI value from April to September.

We used Program PRESENCE (v. 5.5; <http://www.mbr-pwrc.usgs.gov/software/presence.html>) to fit five multi-season models that described occupancy dynamics in our study system (MacKenzie et al. 2006). Preliminary analyses indicated that season, but not trap type, influenced detection probability. Thus, season was included

as a covariable of detection in all models. The first model we fit estimated probability of site occupancy (Ψ) the first season and assumed colonization and extinction were constant during the study. This unconditional equilibrium model assumed changes in site occupancy were random rather than being related to the previous occupancy state (MacKenzie et al. 2006). The remaining four models were fitted using the explicit dynamics parameterization, in which extinction and colonization rates are estimated to describe the processes driving changes in occupancy. Extinction (ε_t) is the probability that a site occupied in season t is unoccupied in season $t+1$. Colonization (γ_t) is the probability that an unoccupied site in season t is occupied in season $t+1$. For the explicit dynamics models, we modeled colonization in three ways. We either assumed colonization was constant for all intervals during the study, limited colonization to winter interval only but assumed the rate was equal in all winters, or limited colonization to winter intervals but allowed it to vary among years. We limited colonization to winter months in two models because, for this winter-breeding species, there was no expectation that salamanders would colonize ponds between Spring and Fall. We modeled extinction either as a function of drought or assumed it was constant during the study.

These models may be expressed as follows: 1) The probability a pond was occupied did not depend on its occupancy status in the previous season (non-Markovian model), and colonization and extinction were constant (i.e., population at equilibrium) in the intervals between samples: $\Psi(\text{Spring09}), \gamma(\cdot), \{\varepsilon=1-\gamma\}, p(\text{season})$; 2) the probability a pond was occupied depended upon its occupancy status in the previous season (Markovian model), but colonization and extinction were constant in the intervals between samples: $\Psi(\text{Spring09}), \gamma(\cdot), \varepsilon(\cdot), p(\text{season})$; 3) the probability a pond was occupied depended on its occupancy status in the previous season, colonization was constant in all intervals, but extinction depended on PHDI: $\Psi(\text{Spring09}), \gamma(\cdot), \varepsilon(\text{PHDI}), p(\text{season})$; 4) the probability a pond was occupied depended on its occupancy status in the previous season, colonization was constant but occurred only during the winter interval between Fall and Spring samples, and extinction depended on PHDI: $\Psi(\text{Spring09}), \gamma(\text{Summer} = 0), \varepsilon(\text{PHDI}), p(\text{season})$; and 5) the probability a pond was occupied depended on its occupancy status in the previous season, colonization occurred only during the winter interval but varied among years, and extinction depended on PHDI: $\Psi(\text{Spring09}), \gamma(\text{Summer} = 0, \text{year}), \varepsilon(\text{PHDI}), p(\text{season})$.

We evaluated the fit of these five models using Akaike's Information Criterion (AIC) and weighed the relative support of each using AIC weights (ω ; Burnham and Anderson

2002). We estimated occupancy, detection probability, colonization, and extinction rates from our best-fit model.

Results

Our best-supported model indicated that the probability a pond was occupied depended on its occupancy status in the previous season, that colonization did not occur during summer months but was a constant rate across all winters, and that extinction was a function of drought (Table 1). The 2-year drought during our study was associated with greater extinction rates ($b_{\text{PHDI}} = -0.306$, $\text{se} = 0.178$) and a decline in occupancy from an initial estimate of 0.223 (0.063) in Spring 2009 to 0.099 (0.037) in Fall 2012 (Fig. 3). Estimated seasonal detection probabilities from our top-ranked model ranged from 0.037 ($\text{se} = 0.017$) to 0.273 (0.049), with no recaptures of marked salamanders.

The second-best model was similar to the top-ranked model except the former held colonization constant across all intervals between samples, including during Summer. Greater support for the top-ranked model illustrates the importance of modifying colonization to reflect the natural history of the study animal (i.e., that colonization in this species is evidenced by reproduction in the winter). The model that constrained colonization to Winter but allowed the rate to vary among years had less support (Table 1). While the remaining equilibrium models received the least support, the conditional parameterization was competitive with the top three models (based on Δ AIC values). The two models based on constant rates of colonization and extinction across the study period received the least support (Table 1).

Discussion

Our results indicate that estimates of the probability of occurrence in mole salamanders decreased over the course of our study due to an increase in the probability of extinction, rather than a decrease in the probability of colonization. This increase in local extinction rate may be due to drought-induced pond drying (thus rendering ponds unavailable for sampling), or could represent an actual demographic change. Our best-supported model indicated that this increase in estimated extinction probability was driven by an increase in the severity of drought (as measured by PHDI) over time, although we caution that there could be other factors that coincide with this trend.

These results provide support for our prediction that, under a scenario of ongoing drought, local extinction increases and occurrence decreases as long-hydroperiod breeding sites dry prematurely. The populations we sampled

Table 1 Models used to describe changes in occupancy of the mole salamander, *Ambystoma talpoideum*, in 60 ponds sampled between 2009 and 2012 at St. Marks National Wildlife Refuge, Florida. Models are ranked according to relative differences in AIC from the top-ranked model and model weights (ω). K is the number of parameters in each

model, $-2l$ is twice the negative log-likelihood, ψ is the estimated (se) probability of occurrence, γ is the estimated (se) probability of colonization, and ε is the estimated (se) probability of extinction. “Summer = 0” indicates colonization occurred only during winter intervals

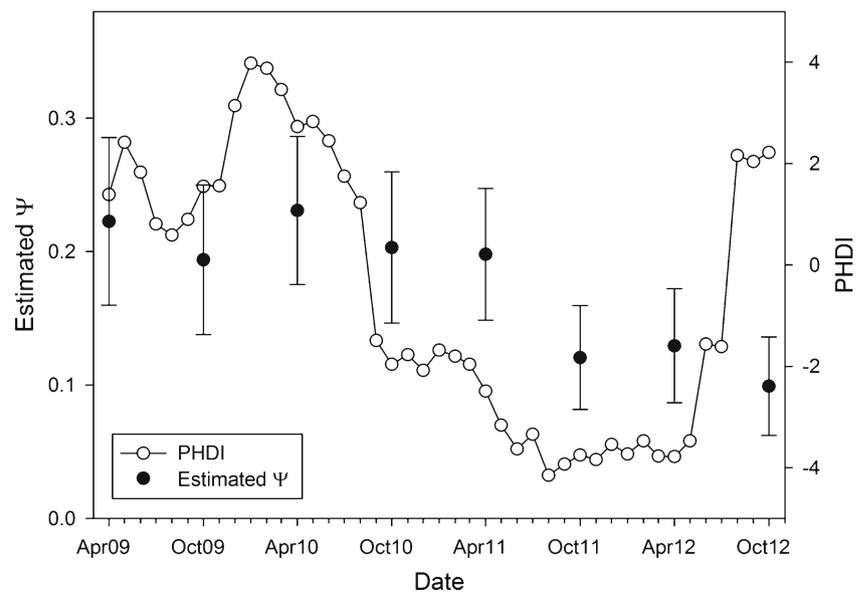
Model	Δ AIC	ω	K	$-2l$	Ψ_{Spring09}	Season	γ	ε
$\Psi(\text{Spring09}), \gamma(\text{Summer}=0), \varepsilon(\text{PHDI}), p(\text{season})$	0.00	0.50	12	831.73	0.2227 (0.0629)	Summer09	0 ^a (–)	0.1294 (0.0706)
						Winter09/10	0.0659 (0.0278)	0.0833 (0.0666)
						Summer10	0 ^a (–)	0.1207 (0.0705)
						Winter10/11	0.0659 (0.0278)	0.2836 (0.0775)
						Summer11	0 ^a (–)	0.3907 (0.1218)
						Winter11/12	0.0659 (0.0278)	0.4078 (0.1305)
$\Psi(\text{Spring09}), \gamma(\cdot), \varepsilon(\text{PHDI}), p(\text{season})$	1.30	0.26	12	833.03	0.2100 (0.0631)	Summer09	0.0316 (0.0136)	0.1210 (0.0672)
						Winter09/10	0.0316 (0.0136)	0.0747 (0.0609)
						Summer10	0.0316 (0.0136)	0.1121 (0.0666)
						Winter10/11	0.0316 (0.0136)	0.2848 (0.0832)
						Summer11	0.0316 (0.0136)	0.4019 (0.1332)
						Winter11/12	0.0316 (0.0136)	0.4207 (0.1426)
$\Psi(\text{Spring09}), \gamma(\text{Summer}=0, \text{year}), \varepsilon(\text{PHDI}), p(\text{season})$	2.73	0.13	14	830.46	0.2216 (0.0626)	Summer09	0 ^a (–)	0.1335 (0.0726)
						Winter09/10	0.0961 (0.0543)	0.0894 (0.0710)
						Summer10	0 ^a (–)	0.1253 (0.0729)
						Winter10/11	0.0714 (0.0493)	0.2743 (0.0745)
						Summer11	0 ^a (–)	0.3703 (0.1161)
						Winter11/12	0.0270 (0.0328)	0.3857 (0.1247)
$\Psi(\text{Spring09}), \gamma(\cdot), \varepsilon(\cdot), p(\text{season})$	3.17	0.12	11	836.90	0.2097 (0.0631)	Summer09	0.0300 (0.0128)	0.2140 (0.0684)
						Winter09/10	0.0300 (0.0128)	0.2140 (0.0684)
						Summer10	0.0300 (0.0128)	0.2140 (0.0684)
						Winter10/11	0.0300 (0.0128)	0.2140 (0.0684)
						Summer11	0.0300 (0.0128)	0.2140 (0.0684)
						Winter11/12	0.0300 (0.0128)	0.2140 (0.0684)
$\Psi(\text{Spring09}), \gamma(\cdot), \{\varepsilon=1-\gamma\}, p(\text{season})$	86.04	0.00	3	921.77	0.2276 (0.0704)	Summer09	0.2128 (0.0327)	0.7872 ^b
						Winter09/10	0.2128 (0.0327)	0.7872 ^b
						Summer10	0.2128 (0.0327)	0.7872 ^b
						Winter10/11	0.2128 (0.0327)	0.7872 ^b
						Summer11	0.2128 (0.0327)	0.7872 ^b
						Winter11/12	0.2128 (0.0327)	0.7872 ^b
Summer12	0.2128 (0.0327)	0.7872 ^b						

^a This parameter fixed to 0; ^b this parameter derived

continued to show the effects of drought (in terms of a decline in occupancy) even after SMNWR was impacted by Tropical Storm Debby in June 2012. This tropical storm inundated the area over a 6-day period with 735.55 mm of rain, of which 76 % occurred on a single day (Remote Automated Weather Station [RAWS] U.S. Climate Archive of the Western Regional Climate Center, St. Marks [West], FL station). This tropical cyclone may likely have been a “drought buster”

(Maxwell et al. 2012); it resulted in a 500-year + average recurrence interval for maximum 48-hour rainfall amounts (<http://blog.citizen.apps.gov/SERFCJournal/2012/06/500-year-rainfall-event/>, accessed 2 July 2012). In October 2012, only 6 of 60 ponds (10 %) were dry during our Fall sampling; however, it is not known whether this deluge occurred in time to refill drying ponds and prevent larval and paedomorph mortality and/or increased metamorphosis. Our future

Fig. 3 Palmer Hydrological Drought Index (PHDI) for Northwest Florida (Division 01) from April 2009 to October 2012, along with estimated probabilities of occurrence (ψ ; ± 1 se) in the mole salamander, *Ambystoma talpoideum*, on six sampling periods during this time. Values of PHDI below 0 indicate drought conditions



monitoring will focus on the long-term effects of this flood, which could either increase occupancy on the landscape if favorable aquatic habitat was created by this event or, alternatively, could cause a decline in occupancy due to adult mortality in the flooded terrestrial habitat and/or the introduction of predatory fishes into formerly fishless ponds.

Importance of Wetland Hydroperiod for Pond-breeding Amphibians

Hydroperiod is one of the most important wetland-level features associated with the presence of amphibians and species richness (Mattfeldt et al. 2009; Zipkin et al. 2012). Wetland hydroperiod influences site occupancy and persistence of amphibians both directly (i.e., via the timing of pond-filling and the length of time water is available for larval development) and indirectly (i.e., through effects on predatory and competitive interactions; Wilbur 1987; Pechmann et al. 1989; Skelly 1997). The hydrologic variation that is the essence of a seasonal wetland includes differences among wetlands across a landscape, and within a wetland among years (Comer et al. 2005). Most pond-breeding amphibian species have adaptations to subsets of conditions along the hydroperiod continuum; i.e., there are “short-hydroperiod,” “intermediate hydroperiod,” and “long hydroperiod” species (Snodgrass et al. 2000; Babbitt et al. 2003; Fig. 1).

At the single population/species level, differences in life-history traits, larval periods and breeding phenology result in varied threshold relationships between successful reproduction (i.e., the production of juveniles) and the hydroperiod needed for larval development. The minimum threshold is constrained largely by physical factors — when does the wetland fill, for how long, and when does it dry? For example, at a long-term study site in South Carolina the minimum

hydroperiod necessary to produce juveniles may range from 30 days for some species (e.g., eastern narrow-mouthed toad, *Gastrophryne carolinensis*) to 154 days for others (e.g., eastern tiger salamander, *Ambystoma tigrinum*; Daszak et al. 2005). Similarly, in Rhode Island, different species of amphibians require ponds to be inundated for 125 days to at least 580 days (Paton and Crouch 2002). For a particular species, if the wetland does not hold water for a sufficient period during the appropriate season then the result is catastrophic reproductive failure (Semlitsch et al. 1996; Taylor et al. 2006). If reproductive failure occurs frequently relative to the life span of the species, then local extinctions occur (i.e., at the site-level and, potentially, regional level as well) (Taylor et al. 2006). For those individuals that metamorphose successfully from a drying wetland, decreasing hydroperiod may have indirect effects in the form of reduced body size at metamorphosis which, in turn, influences correlates of fitness such as age and size at first reproduction (Smith 1987; Semlitsch et al. 1988). Insufficient rainfall and shortened hydroperiod have been associated with catastrophic reproductive failure in a variety of pond-breeding amphibians (Semlitsch 1987; Dodd 1993, 1994, 1995; Richter et al. 2003; Palis et al. 2006; Taylor et al. 2006), metamorphosis at smaller body sizes and the potential local elimination of paedomorphosis (McMenamin and Hadly 2010). As much as 90 % of a population of *A. talpoideum* may skip breeding in a drought year (Kinkead and Otis 2007), lowering the reproductive output of that population in such years. Similarly, breeding probabilities for female *A. tigrinum* may be reduced by >50 % in drought years (Church et al. 2007). Such climate-induced complete or partial reproductive failure is a likely contributor to population declines in several species of amphibians (Daszak et al. 2005; Taylor et al. 2006). For instance, in an ongoing 34-yr study where breeding adults are censused each year, *A.*

talpoideum numbers declined from thousands of breeding females in the late 1970s to mid-1980s (when wetland hydroperiods were generally long; Semlitsch et al. 1996) to several hundred by the early 2000s (Daszak et al. 2005) and fewer than 40 since 2007 (DES, unpublished data). At this South Carolina site, juvenile recruitment has occurred in *A. talpoideum* only once in the last 14 years due to hydroperiods less than the 142 day minimum necessary to complete larval development at this wetland.

The occurrence and persistence of some species at a wetland are also affected by a second threshold that occurs at the transition point(s) from intermediate hydroperiods to long, semi-permanent, or permanent wetlands. Whereas physical factors largely constrain reproductive success and larval survival at the minimum hydroperiod threshold, biotic factors (especially competition and predation) play the predominant roles at longer hydroperiods (sensu Wellborn et al. 1996; Snodgrass et al. 2000). Snodgrass et al. (2000) sampled 25 isolated wetlands and found the highest species richness in wetlands with 8–10 month hydroperiods. Longer hydroperiod wetlands, both with and without fish, were relatively species-depauperate. In addition to fish species that are good colonizers, widely distributed, and highly predatory, such as green sunfish (*Lepomis cyanellus*) and redfin pickerel (*Esox americanus*), invertebrates and other vertebrate species (e.g., other amphibians, aquatic snakes and turtles) may play important roles as predators on the overall amphibian community in southeastern isolated wetlands (Fauth 1999; Gibbons et al. 2006). The relationship of reproductive success to hydroperiod at the population/wetland level shapes community level patterns, as wetlands of varied hydroperiods harbor different species. For some amphibian communities, species richness and total numbers of metamorphosing juveniles are likely to change with hydroperiod, with highest numbers often observed at intermediate hydroperiods (Pechmann et al. 1989; Snodgrass et al. 2000; Babbitt 2005). Thus, as climate change affects seasonal wetland hydroperiods, the cascade of effects on the amphibian community is likely to be substantial. For many species, a long-term shift to an inappropriate hydroperiod may eliminate a wetland as a population source as effectively as ditching, filling, or other anthropogenic disturbances.

Impact of Climatic Variation on Amphibians in the Southeastern U.S

Evaluating how local extinction and colonization may influence occupancy helps researchers to understand population declines and to prioritize which species-specific life history characteristics (e.g., adult survival and reproduction versus juvenile dispersal and colonization) should be targeted in a broad, landscape-level monitoring effort. The results of our monitoring indicate that short-term drought may be driving

local extinctions of pond-associated life history stages of *A. talpoideum*. We presently are unable to evaluate whether this impact on aquatic stages may affect terrestrial adults, although Dodd et al. (2007) demonstrated a decline of terrestrial *A. talpoideum* in this same geographic area 8–10 years earlier. High survivorship and temporary emigration of adults could buffer against the loss of larvae and pedomorphs due to environmental uncertainty in the aquatic habitat (sensu Price et al. 2012). The relatively short-term nature of our monitoring also limits the inferences we can draw regarding long-term climate change. In the absence of such longer-term data, we present a conceptual model (Fig. 1) to illustrate a mechanism by which either drier or wetter conditions will likely alter the overall amphibian assemblage in the Southeast. A drier climate, as predicted by Canadian Climate Centre Atmosphere–ocean General Circulation Models (AOGCMs), will presumably truncate all ranges of current hydroperiods. In contrast, a wetter future climate in the Southeast, as simulated by AOGCMs developed by the Hadley Centre in the United Kingdom (National Assessment Synthesis Team 2000), may conceivably increase the number of wetlands in the long-term, including adding wetlands that currently do not exist or have hydroperiods that are presently too short to be of benefit to amphibians (Fig. 1). During wet years, currently short-hydroperiod wetlands may disappear as all sites become persistently inundated (Fig. 1) and potentially colonized by aquatic predators, thus increasing local extinctions of amphibians adapted to ephemeral habitats and altering the species composition of amphibian assemblages at these sites (Babbitt and Tanner 2000; Babbitt et al. 2003; Werner et al. 2007). During dry years, wetlands with currently long hydroperiods may shift to short or intermediate hydroperiods (Fig. 1), potentially eliminating aquatic predators, increasing extinctions of species adapted to permanent or semi-permanent wetlands and, again, altering the species' associations of these hydrologically-modified wetlands. Last, in dry years local colonizations may increase as individuals disperse from drying wetlands to those that still retain water.

Many parts of the Southeast have experienced an increase in the occurrence of heavy downpours, yet the percentage of the region experiencing moderate to severe drought has also increased (Karl et al. 2009). Over the last decade (2002–2011), the Florida panhandle has experienced some of the wettest, as well as some of the driest, months recorded since 1895 (as measured by PHDI: Northwest Florida, Division 01; National Climatic Data Center 2012), including a 500-yr flood associated with Tropical Storm Debby in June 2012. These paradoxically-opposing climatic patterns – that of an intensified hydrologic cycle of both drought and deluge - illustrate the highly complex manner in which a changing climate may affect various freshwater habitats and the amphibians they harbor.

Several pond-breeding amphibians of conservation concern occur on federal lands in the southeastern U.S. By predicting how relatively common focal species like the mole salamander respond to hydrologic shifts resulting from climate change, we can approximate how other species of conservation concern may be affected. Continued monitoring of temporal variation in drought and other environmental conditions associated with site occupancy will aid in understanding the potential impact that future climate change may have on pond-breeding amphibians.

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