
RAINS FROM SUCCESSIVE HURRICANES REDUCE NESTING SUCCESS OF THE MARBLED SALAMANDER (*AMBYSTOMA OPACUM*)

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Abstract.—Current models predict that the intensity of extreme weather will increase as climate change progresses. Indeed, 2020 brought a record number of tropical storms to the Southeastern U.S. The effect of these storms is a conservation concern for amphibians because they depend on aquatic habitats for reproduction. I studied the effect of three subsequent hurricanes on the nesting success of Marbled Salamanders (*Ambystoma opacum*) in Tuskegee National Forest, Alabama, USA. In autumn, females migrate to nesting grounds, lay eggs terrestrially and guard them until seasonal rains flood the nest causing eggs to hatch. Rains from Hurricane Sally brought the salamanders into the breeding grounds, but rains from Hurricane Delta drove them back out, leaving the nesting area flooded before eggs could be laid. Most nests were constructed on the periphery of the semi-flooded nesting grounds, and subsequent seasonal rains flooded nests before the eggs were ready to hatch. Rains from Hurricane Zeta maintained high water levels. Of 28 nests, three were successful. Two nests were never covered in water (i.e., 100% egg mortality), and the rest were flooded prematurely. Concomitant lab studies demonstrated that premature flooding of nests reduces hatching success, indicating that increased hurricane frequency can harm salamander populations even if they are relatively far from the coast. Few studies have focused on the effects of hurricanes on salamanders; thus, additional research is warranted because the Southeastern U.S. is a hotspot for both salamander diversity and hurricane activity.

Key Words.—amphibian decline; climate change; cyclones; developmental plasticity; developmental rate; egg survival; embryo physiology; nesting behavior

INTRODUCTION

Due to global climate change, the frequency of high-intensity hurricanes may increase in the future (Emanuel 2013; Knutson et al. 2020), and these storms could negatively affect wildlife. For example, sea turtles, fishes, and rays exhibited marked behavioral changes after subsequent category 5 hurricanes, potentially due to detrimental changes in water temperature, oxygen availability, or food resources (Matley et al. 2019). Additionally, a meta-analysis using 286 study sites of Caribbean coral reefs showed that coral cover is reduced by an average of about 17% during the year following a hurricane (Gardner et al. 2005). Much existing research is focused on coastal or river ecosystems due to concerns over flooding caused by both rising sea levels and greater storm surges (Mallin and Corbett 2006; Walls et al. 2019); however, tropical storms inundate the landscape, even long after making landfall, and future storms may have higher rainfall rates (Knutson et al. 2020). Increased precipitation from hurricanes may negatively impact populations even if they reside far from the coast. For example, flooding caused by torrential rains from Hurricane Agnes destroyed

nests of Painted Turtles (*Chrysemys picta*), causing low recruitment in subsequent years (Ernst 1974). Because this extreme weather can adversely affect a diversity of taxa (Moreno and Møller 2011; Maxwell et al. 2019) and threaten species of conservation concern (Walls et al. 2019), there is an urgent need to understand how altered weather patterns impact both coastal and inland ecosystems. Such work is particularly timely considering that variation in precipitation may increase in the future (Chou et al. 2013; Konapala et al. 2020).

Studies of hurricanes are often focused on plants, but many studies have considered invertebrates, birds, fish, and mammals; relatively few studies concern amphibians (reviewed by Maxwell et al. 2019). Among terrestrial vertebrates, amphibians may be most vulnerable to altered weather patterns due to their reliance on water for reproduction (Walls et al. 2013). Many species are opportunistic breeders that capitalize on extreme rainfall or temporary flooding to reproduce. Therefore, increases in the frequency of intense storms may influence their reproductive success (Walls et al. 2013, 2019), but effects will vary depending on life-history traits, habitat preference, geographic location, and life stage (Suazo-Ortuño

et al. 2018a,b). Amphibians that oviposit in lentic systems may benefit from greater rainfall if it prevents eggs from desiccating or provides additional breeding sites (e.g., Meshaka 1993; Smith 2013). However, stream-breeding species may be negatively affected if strong currents due to rain prevent breeding or wash eggs and larvae to suboptimal habitats (Lowe 2012). Moreover, the specific threats to each species will vary according to geographic location: species occupying coastal regions may be most vulnerable to storm surge or physical damage from windblown debris (Smith 2013; Walls et al. 2019) while inland populations may be affected by increased precipitation (Wojnowski 2000; Dorcas et al. 2006). Effects will also be species-specific at the local scale. For example, reduction in canopy cover due to tree fall may benefit species that prefer relatively warm, dry conditions but be detrimental to species that prefer cool, moist environments (Stewart 1995). Finally, in some cases, hurricanes have different effects according to life stage and life-history traits (Woolbright 1991). Clearly, no single trend describes the effects of hurricanes on amphibians.

Due to the unpredictability of hurricanes, much of what we know about their effects on amphibians comes from researchers opportunistically documenting effects while conducting long-term population studies (e.g., Stewart 1995; Woolbright 1996; but see Klawinski et al. 2014 for an experimental study).

As such, the diversity of amphibian taxa for which we have data is limited. For example, nearly all the most rigorous studies have been conducted using frogs from the genus *Eleutherodactylus* (Woolbright 1991, 1996; Stewart 1995; Klawinski et al. 2014). Moreover, due to the opportunistic nature of studies, most researchers report data on species diversity and abundance before and after a hurricane, leaving the mechanisms that drive these changes unknown. Given that many aspects of tropical storms can influence amphibians, studying the effects of all these changes on even a single species is challenging. This is further complicated given their biphasic life history: alterations in the terrestrial environment might have positive effects on adults, while changes in aquatic habitats negatively influence eggs or larvae (or *vice versa*). Because the effects of hurricanes on amphibians are species-specific (Woolbright 1991; Suazo-Ortuño et al. 2018a,b), no single species will serve as a representative model. Therefore, it is necessary to document the influence of specific hurricane-induced habitat alterations on various species to understand the effect of increased hurricane frequency or intensity.

In September of 2020, I began a study of the nesting behavior of Marbled Salamanders (*Ambystoma opacum*; Fig. 1) in Tuskegee National Forest, Alabama, USA. My goals were to quantify nest temperatures and perform a concomitant laboratory

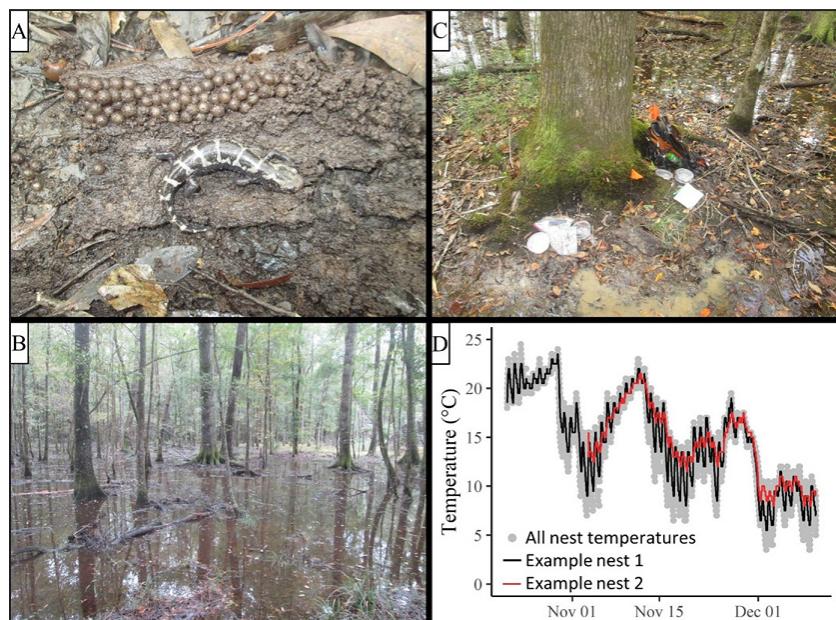


FIGURE 1. Photographs from the field site in Tuskegee National Forest, Alabama, USA. (A) Female Marbled Salamander (*Ambystoma opacum*) with eggs. (B) The field site after heavy rains caused premature flooding of nests. (C) An example of an island at the study site. The orange flag denotes the location of a nest. (D) Nest temperatures from 17 iButtons (gray dots). Two nests are shown (black and red lines) to illustrate differences in thermal variation among nests. (Photographed by Joshua M. Hall).

incubation study to understand the effects of variable temperatures on embryo development. Unfortunately, 2020 brought a record number of hurricanes ($n = 11$) to the Gulf Coast of the U.S., and three storms (Hurricanes Sally, Delta, and Zeta) came through the study site over six weeks, inundating the nesting grounds with rain. Therefore, I changed objectives and performed laboratory incubation experiments to understand the effects of premature nest inundation on embryo development and egg survival, and I monitored nests to quantify nest success in response to rainfall. Although opportunistic studies have shortcomings (described above), the laboratory experiments afford a unique opportunity to develop a mechanistic understanding of how hurricanes affect nest success. Finally, I conducted a systematic review of studies concerning hurricanes and amphibians to give the herpetological community a resource for future work. Few studies have rigorously assessed the effects of hurricanes on amphibian reproduction generally, and on salamanders specifically. Therefore, this study helps fill an important knowledge gap in our understanding of how amphibians may respond to variable precipitation regimes due to climate change.

MATERIALS AND METHODS

Study species and site.—Marbled Salamanders are atypical among mole salamanders (genus *Ambystoma*) because females lay eggs on land. In autumn (September to December), adults migrate to low elevation areas that will eventually flood. Females construct shallow nests in the mud, deposit eggs, and guard them while the embryos develop (Croshaw and Scott 2005). Nests are usually constructed beneath cover objects like leaves, fallen logs, or even human-made objects (reviewed by Hall et al. 2021). Eventually, females abandon their eggs when heavy rains flood the nest: adult Marbled Salamanders are poor swimmers and drown if unable to escape the water (Noble and Brady 1933; but see Newman 2017). Importantly, embryos can develop into larvae and remain unhatched until the nest floods. After the nest is submerged, low oxygen levels prompt hatching (Petraska et al. 1982) and the larvae live an aquatic life until metamorphosis. Because eggs must be submerged to hatch, nest-site selection is important for fitness: nests placed too far from ephemeral pools or too high in the future water column may never flood (100% egg mortality). Alternatively, nests placed at very low elevations may flood too soon, causing the larvae to hatch into small pools that subsequently dry (100% larval mortality; Petraska and Petraska 1981a). Importantly, no study has robustly assessed the consequences of premature

flooding on eggs and embryo development.

The study population was in Tuskegee National Forest, Alabama, USA ($32^{\circ}29'13.6''\text{N}$ $85^{\circ}36'11.2''\text{W}$). This population was approximately 250 km straight-line distance from the Gulf Coast. Soils in this area are mostly sandy loam and the study site is part of an expanse of hardwood bottomland that drains into Choctafaula Creek. At this site, Marbled Salamanders and their nests are found in abundance from September to November (pers. obs.). Other salamanders that co-occur at this site are Mole Salamanders (*A. talpoideum*), Spotted Salamanders (*A. maculatum*), Four-toed Salamanders (*Hemidactylium scutatum*), Northern Slimy Salamanders (*Plethodon glutinosus*), Hill's Dwarf Salamanders (*Eurycea hillisi*), and Southern Two-lined Salamanders (*E. cirrigera*).

Embryo staging.—To determine the relative age of embryos at the time nests were discovered and to calculate developmental rates during incubation studies, I staged embryos according to the Harrison Staging series for salamanders (using Duellman and Trueb 1994). Eggs can hatch across a wide range of stages, and some authors report that hatching occurs as early as stage 38 (Noble and Brady 1933; Graham 1971), although others have observed hatching at later stages (e.g., stage 42; King 1935). I used Harrison stage 40 as the stage at which hatching occurs.

Effect of temperature.—In line with initial study goals, I located as many nests as possible, placed Thermochron temperature loggers (OnSolution Pty Ltd., Baulkham Hills, New South Wales, Australia) into 27 nests, and collected 10 clutches for a lab incubation study relating temperature to egg survival and embryo development. After the second hurricane (Delta; 9–11 October), the purpose of the following assay became to measure developmental rates across temperatures to predict the developmental stages of embryos at the time nests were flooded in the field. I incubated eggs from two clutches collected 21 and 22 October ($n = 54, 122$ eggs, respectively) at four constant temperatures ($5^{\circ}, 10^{\circ}, 20^{\circ}, 25^{\circ}\text{ C}$). I chose these clutches because they were the youngest of all clutches discovered on the first day of intense searching for nests (Harrison stages 2–7; first cell division to early blastula). This minimized effects of field conditions before collection and incubation. I rinsed all eggs with deionized (DI) water, cleaned them of dirt and debris using a moist paper towel, and placed them in 60 mm petri dishes (five eggs per dish). Each petri dish had a substrate of paper towel moistened with 2 mL of DI water and was sealed with parafilm to prevent desiccation. I incubated eggs in a split-clutch design. One clutch was selected

to calculate developmental rates: five eggs from each temperature were periodically placed under a dissecting microscope to record the Harrison stage. On a per treatment basis, when eggs were at Harrison stage 44–46 (final stages), I removed all eggs from the incubator, placed them individually under a dissecting microscope, and I scored them as alive or dead based on the presence or absence of body movement, heartbeat, or blood flow.

To determine egg survival across temperature, I performed a Generalized Linear Model with a binomial distribution. I included temperature and clutch identity (ID) as categorical fixed effects. I did not include dish ID as a random effect because egg mortality was consistent across dishes. To estimate developmental rates, I fit asymptotic regressions to Harrison stage versus time (in days) using the SSasymp() and nls() functions in R and used these models to estimate the number of days required to reach stage 40 at each temperature. I fit the total days required to reach stage 40 versus temperature to an exponential decay function to allow for estimates of the number of days to complete development at other temperatures. To increase accuracy, I included an additional estimate for 15° C from Hale et al. (2016). Finally, I calculated retrospective development rates (Taylor et al. 2021) by taking the inverse of the estimated days required to reach stage 40, multiplying by 100 and then dividing by 24 (i.e., percentage development completed per h). I fit a simple Linear Regression to these data so that I could use nest temperatures to estimate the total time required to reach the hatching stage in each nest found during the field study.

Effect of inundation duration.—On 20 October, I collected three clutches with eggs ranging from Harrison Stage 8–12 (i.e., late blastula to late gastrula stage) and incubated them in petri dishes as described above. I divided dishes in a split-clutch design among two incubators set to 10° and 20° C. On 24 October, the nests in the field were flooded by seasonal rains (see below). Therefore, to opportunistically understand the effects of premature flooding on egg development, I removed eight petri dishes per clutch (120 total eggs) from the incubators and placed them in one of four treatments that varied in the amount of time the eggs were submerged in water. I placed eggs in glass jars filled with DI water (five eggs per jar) for 6, 24, 96, or 240 h. I kept the jars in total darkness at room temperature. When eggs had completed their time in the water, I returned them to petri dishes (as above) and continued incubating them at room temperature. I then placed all eggs in a 20° C incubator on the same day to finish developing. When

most eggs reached Harrison stage 40, I observed all eggs under a dissecting microscope and scored them as alive or dead (as described above). To observe how early inundation influenced developmental rate, I scored eggs from the two extreme treatments (6- and 240-h treatments) according to their Harrison stage.

Only one egg died during this experiment; therefore, I did not perform an analysis on egg survival. To analyze the Harrison stages (i.e., a proxy for developmental rate), I performed a Linear Mixed Model with initial incubation temperature (10° versus 20° C), treatment as a factor variable (6 versus 240 h), and their interaction as fixed effects. I included a random effect of dish ID nested in clutch ID. I removed the interaction term due to a lack of statistical significance ($P > 0.05$). I performed the mixed model using the lme4 package (Bates et al. 2014) and generated P values using the Satterthwaite approximation for degrees of freedom using the car package (Fox et al. 2012). Harrison stage was log transformed before analysis to normalize residuals and reduce heteroscedasticity.

Effect of early inundation.—To better understand the effects of premature inundation on egg survival under more natural conditions, I performed an additional laboratory experiment using a single clutch of eggs. I discovered these eggs 4 November, and they ranged from Harrison stages 11–13 (i.e., yolk plug to gastrula stage). I initially incubated eggs at 10° C for 1 d and on 5 November, I divided the eggs into two treatments: incubation in air and incubation in water (38 eggs per treatment). I placed eggs in the air treatment in petri dishes as described above, and I submerged eggs in the water treatment in glass jars filled with water collected from the field site. I first ran this water through a coffee filter to remove any macroinvertebrates that might harm the eggs. I incubated five or six eggs per dish/jar and placed them in an incubator at 20° C. When the eggs in the air treatment reached Harrison stage 44–46 (final stages), I placed them in water and scored hatching success. I monitored eggs incubated in the water treatment daily when they reached stage 40 and then I scored hatching success. Periodically, I scored five of these eggs according to Harrison stage to monitor developmental rate over time.

To compare hatching success between treatments, I performed a Generalized Linear Model with a binomial distribution (1 = hatched, 0 = did not hatch) using the base statistics package in R using the glm() function. Treatment (incubation in water versus air) was the fixed effect. I did not include a random effect of petri-dish/jar ID because mortality was evenly spread across containers: only two eggs died in the air

treatment and 2–3 eggs died in each jar of the water treatment. I recorded Harrison stage only for eggs in the water treatment; therefore, I did not perform an analysis to compare stages between treatments.

I used R (R Development Core Team 2020) to conduct all analyses and used $\alpha = 0.05$. I made graphs with the ggplot2 package (Wickham 2011). For parametric analyses, I visually inspected model residuals to assess statistical assumptions.

Field study.—The initial goals for the field study were to find as many nests as possible, place temperature loggers in each nest, and obtain eggs of the earliest developmental stage possible. Thus, I set up two 60-m transects on 5 September 2020: one transect was situated at a relatively low elevation where nests are found in abundance and seasonal rains result in flooding (pers. obs.). I placed the other transect approximately 6 m north, in an area that does not flood (pers. obs.). I used two transects, one outside and one inside the nesting grounds, because individuals typically migrate from the surrounding high elevation area into the low elevation sites for nesting. Therefore, I used these transects to determine the relative timing of salamander movements to the nesting grounds. Starting 5 September, I walked each transect once weekly, searching beneath every cover object (e.g., logs, slabs of bark, rocks) within 3 m on either side of the transect line. I recorded the number of Marbled Salamanders I encountered. I did not mark individuals but did measure body mass and snout-to vent length (SVL) on site and then returned them to their location of capture.

When I discovered the first nest, I looked beneath every terrestrial cover object within the 5,000 m² study site; however, most of this area was not searchable because it was under water (due to rains from hurricanes). I also opportunistically searched through piles of leaves to find additional nests. For 10 nests, I measured the attending female SVL and body mass, removed and counted the eggs, recorded the clutch mass, and measured the length and width of the nest. I took these eggs to the laboratory for the incubation studies described previously. To reduce negative impacts on the population, I did not measure the remaining females nor did I count eggs in the other nests. When disturbed, females will abandon the nest, reducing egg survival (Croshaw and Scott 2005). I marked every nest with a flag and returned to the site weekly until 10 December 2020. During most of this time, nests were below water so I measured the distance from the nest to the top of the water column (to 1 mm). After the initial flooding of the nest, which came long before eggs were fully developed, I counted all eggs remaining in each nest and determined if they

were alive by looking for a heartbeat or blood flow under a dissecting microscope.

I placed iButton temperature loggers in most nests (19 iButtons) on the day after they were discovered. I dipped each iButton in liquid parafilm for waterproofing and set to record temperature hourly. If multiple nests were under the same log, I only deployed one iButton to represent them all. The one nest discovered far from the nesting grounds was not provided with an iButton and two iButtons failed during the experiment; therefore, I have temperatures for 25 of 28 nests. I collected rainfall data from the National Weather Service website (www.weather.gov). These field data were observational rather than experimental; therefore, I performed no statistical tests.

Historical effect of hurricanes on amphibians.—I conducted a systematic literature review using Web of Science and Google Scholar, searching for all combinations of the terms hurricane or cyclone AND amphibian, frog, toad, Anuran, salamander, Caudate, Gymnophiona, or caecilian. I reviewed titles and abstracts in Web of Science and titles in Google Scholar and retained studies that reported any effect of a hurricane or cyclone on an amphibian. To be as inclusive as possible, I used no other criteria. I also included studies cited in a recent review (Maxwell et al. 2019) and a publicly available dissertation (Marroquín-Páramo 2021). I did not retain meta-analytic data (e.g., total number of hits in Web of Science, number of studies excluded per various criteria) because I did not exclude any studies that reported effects of hurricanes on amphibians. For each study, I recorded the name of the storm, the group(s) studied (Anura, Caudata, Gymnophiona), the species studied, the type of study (opportunistic versus experimental), the aspect of the storm considered (e.g., storm surge, flooding, canopy disturbance, etc.), a brief description of the methods and results, and an assessment of the overall effect on the population (positive, negative, neutral, ambiguous, or species-dependent). I calculated the percentage of studies related to each of the above categories.

RESULTS

Effect of temperature.—Temperature ($X^2 = 99.85$, df = 3, $P < 0.001$) and clutch ($X^2 = 6.15$, df = 1, $P = 0.013$) significantly influenced egg survival. Eggs in one clutch were 1.49 times (± 0.64 standard error) as likely to survive than those in the other clutch. Moreover, eggs were 4.76 times (± 0.87), 4.75 times (± 0.88), and 4.25 times (± 0.74) as likely to survive at 10°, 20°, and 25° C, respectively, than at 5° C (Fig.

2). It took 121, 39, 14, and 11 d to reach stage 40 at 5°, 10°, 20°, and 25° C, respectively. Per Hale et al. (2016), it takes 19 d to reach stage 40 at 15° C, so I included this value in the exponential decay regression (red dot; Fig. 2).

Effect of inundation duration.—Only one egg died prior to stage 40; therefore, the number of hours spent incubating under water did not influence survival to stage 40 (Fig. 3). Both the initial incubation temperature ($X^2 = 40.1$, df = 1, $P < 0.001$) and treatment ($X^2 = 13.5$, df = 1, $P < 0.001$) significantly influenced the final Harrison stage: eggs initially incubated at 10° C were less advanced (mean = 39.73 ± 0.64 standard deviation) than those initially incubated at 20° C (mean = 41.33 ± 1.06). Moreover, eggs submerged for only 6 h were more advanced (mean = 41.0 ± 1.26) than those submerged for 240 h (mean = 40.07 ± 0.91 ; Fig. 3).

Effect of early inundation.—Eggs submerged in water from the field site reached Harrison stage 40 after approximately 14 d; however, no eggs hatched at this stage but all kept developing until reaching the terminal stage of 46 (Fig. 3). At this time, 18

eggs (47.4%) hatched and 20 embryos (52.6%) died inside the egg. Of the eggs that were incubated in air and then placed in water, only two eggs (5.3%) failed to hatch. Thus, there was a significant difference in hatching success between the incubation treatments ($X^2 = 23.2$, df = 1, $P < 0.001$; Fig. 3).

Field study.—I found no salamanders on 5 September (Fig. 4), indicating they had not yet emerged from their underground refugia or were low in abundance. On 16 September, Hurricane Sally dropped 13.4 cm of rain onto the site, which likely triggered the salamanders to migrate to the breeding grounds because I found 10 individuals 18 September (Fig. 4). Over the following weeks, the salamanders moved into the nesting area, and by 8 October, most salamanders had likely moved into the nesting area because I detected salamanders in the transect inside the nesting grounds, but not in the transect outside the nesting grounds (Fig. 4). From 9–11 October, Hurricane Delta dropped about 10 cm of rain, flooding the nesting area. On 12 October, I found no salamanders inside the nesting area, which was under water, but I did find 25 salamanders in the dry transect (Fig. 4). Over the next two weeks, the salamanders

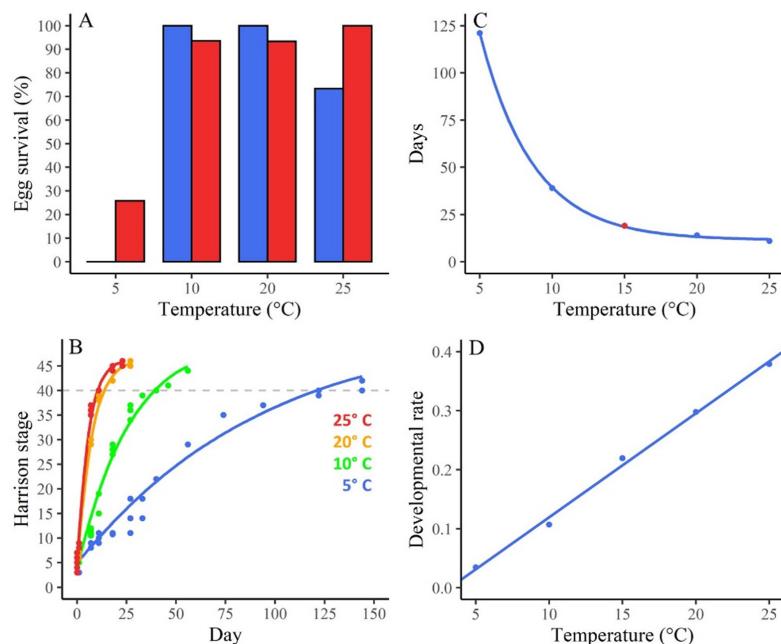


FIGURE 2. Survival and developmental rates of eggs of Marbled Salamanders (*Ambystoma opacum*) from Tuskegee National Forest, Alabama, USA, across constant temperatures. (A) Egg survival (%) for two clutches of eggs (red and blue). (B) Changes in the Harrison stage of embryos over time at four incubation temperatures. Dots show raw data and the lines are from fitting asymptotic functions to the data. (C) Relationship between temperature and days to complete development. Blue dots show an estimated number of days for embryos to reach Harrison stage 40 (i.e., hatching stage). The red dot was taken from the literature (Hale et al. 2016) and the equation of the relationship is Days = $11.461 + 430.467 \times e^{(-e^{(-1.295)} \times \text{Temperature})}$. (D) Developmental rate (percentage development completed per h) across temperature and the equation of the relationship is Developmental rate = $0.0176 \times \text{Temperature} - 0.056$.

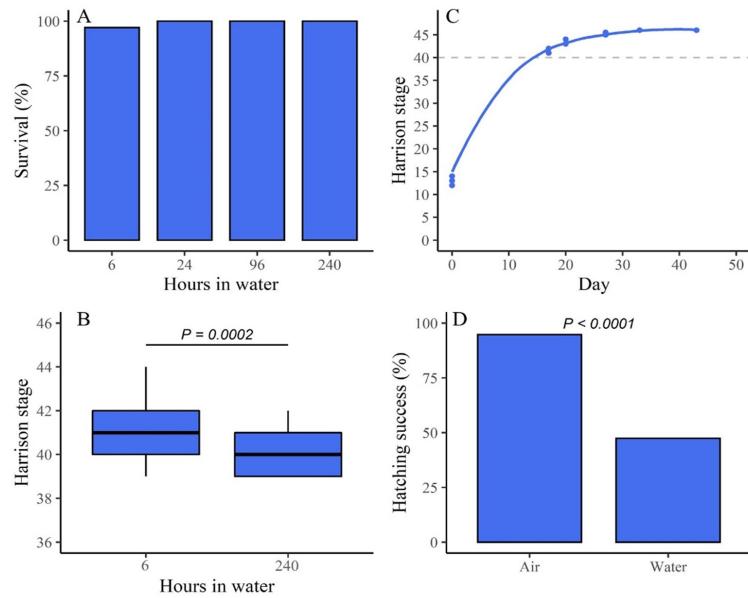


FIGURE 3. Survival and developmental rate of eggs of Marbled Salamanders (*Ambystoma opacum*) from Tuskegee National Forest, Alabama, USA, incubated under water. (A) Survival to stage 40 of eggs incubated in deionized (DI) water for various amounts of time. (B) Final Harrison stage of embryos incubated in DI water for 6 and 240 h. (C) Relationship between Harrison stage and time for eggs incubated in water from the study site. Blue dots show the raw data and the equation of the relationship is Harrison stage = $46.539 - 33.55 e^{(-e^{-2.167} \times \text{Day})}$. (D) Hatching success of eggs incubated in air and water from the study site.

returned to the nesting site, although much of the area was still under water. On 20 October, I found the first nests and over a 3-d period I located 24 nests (Fig. 4); however, most of the typical nesting area was still under water. On 24 October, about 5 cm of rain not associated with a hurricane fell, causing the water levels to rise and 22 nests were submerged (mean depth = 9.8 cm ± 3.0 SD, Fig. 4). These eggs were at early stages when discovered (Harrison Stage 2–19). Thus, nests were inundated only 2–4 d after

oviposition. Two nests were still dry, but these nests never flooded because one was too far from the nesting grounds (about 6 m) and the other was constructed at too high an elevation, but within the nesting area.

On 28 October, Hurricane Zeta released about 5 cm of rain, keeping water levels above the nests (mean depth = 4.1 cm ± 1.8). Twenty-one nests were completely submerged for 10–24 d (mean = 17.3 ± 5.2). One nest was only submerged for three d, but all eggs were gone after the waters receded. I discovered

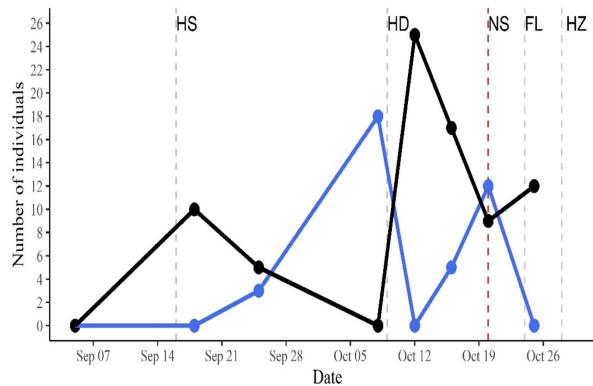


FIGURE 4. Results of transect searches and a timeline for important events during the field study of Marbled Salamanders (*Ambystoma opacum*) in Tuskegee National Forest, Alabama, USA. The black and blue dots and lines denote the number of salamanders found in transects outside and inside the nesting area, respectively. The vertical dotted lines denote important events during the field study: HS = rains from Hurricane Sally; HD = rains from Hurricane Delta; NS = nesting starts (24 nests found); FL = nest sites are flooded due to heavy rains; HZ = rains from Hurricane Zeta.

TABLE 1. Number of dead and living eggs of Marbled Salamanders (*Ambystoma opacum*) from four nests that had been prematurely inundated with water in Tuskegee National Forest, Alabama, USA. Minimum mortality is a conservative estimate of mortality assuming that all nests had the mean number of eggs (see Table 3) and that all missing eggs survived.

Dead	Alive	Mortality	Minimum mortality
20	0	100%	18.5%
37	0	100%	34.3%
54	0	100%	50.0%
27	49	35.5 %	25.0%

two additional nests 30 October, both of which were successful.

By 3 November, many of the initially flooded nests ($n = 11$) were no longer under water. The remaining nests were at a mean depth of only 0.7 ± 0.3 cm. At this time, I searched all nests for eggs. Most nests had no eggs remaining, but I recovered eggs from seven nests. Three nests contained fewer than 10 eggs (all dead); however, four nests contained 20–76 eggs and varied from 100% to 35.5% mortality (Table 1). I discovered two additional nests on 10 and 13 November, but due to cold temperatures, one nest likely did not have sufficient time to complete development before inundation. At this time, all nests were free of standing water until rains fell on 1 December, at which time all nests were submerged in water except for the two nests that were never submerged.

Of 28 total nests, I considered 25 (89.3 %) failed nesting attempts because they were either inundated with water long before the embryos could reach Harrison stage 40 ($n = 23$) or because they were never inundated with water ($n = 2$) (Table 2). Nests that were inundated early had a mean of 3.7 ± 3.0 d to develop before inundation. All nests but one were flooded after only 2–4 d. One nest, however, was free of water for 17 d, but nest temperatures were relatively cool (mean = 13.9°C). Thus, I estimate it would have taken these eggs 25 d to reach stage 40. Two of the successful nests had mean temperatures

of 15.9° and 15.2° C . For these, I estimated 18 d to reach stage 40, and eggs spent 31 d developing before inundation. The iButton failed for the third successful nest; however, these eggs were already at stages 34–37 when discovered and had 20 d to develop before inundation. Therefore, they had plenty of time to complete development. Nests exhibited substantial spatiotemporal variation in temperature. Hourly nest temperatures ranged from 3.5° – 24.5° C , and average daily temperatures ranged from 7° – 21° C due to temporal changes in ambient conditions. Additionally, on any given day, two nests differed by as much as 7° C (Fig. 1; Supplemental Information Table S1). Body size of nesting females and nest characteristics were typical for the species (Table 3).

Historical effect of hurricanes on amphibians.—I found 22 studies concerning the effects of hurricanes on amphibians (Supplemental Information Table S2). Twelve studies (55%) concerned only Anura, two (9%) only Caudata, and eight reported results for both (36%). Of the latter, the number of Anuran species studied was always greater than the number of Caudata. No studies concerned Gymnophiona. Three studies (14%) focused on flooding, three focused on canopy disturbance (14%), three focused on storm surge (14%), while 13 (59%) had no particular focus, but reported data collected before and after a hurricane. Twenty-one studies were opportunistic and only one was experimental (5%). For five studies reporting data on a single species, three demonstrated negative effects of hurricanes and two demonstrated positive effects. For 17 studies concerning multiple species, 10 (59%) reported species-dependent effects, one (6%) reported overall negative effects, one (6%) reported overall positive effects, and five (29%) reported neutral or ambiguous effects.

DISCUSSION

Increased severity of extreme weather may threaten species, communities, and ecosystems.

TABLE 2. Location, microhabitat, and success of nests ($n = \text{sample size}$) of Marbled Salamanders (*Ambystoma opacum*) in Tuskegee National Forest, Alabama, USA.

General location	n	Microhabitat	Result
Within the flood plain	17	beneath log/bark	Prematurely submerged
Within the flood plain	3	inside log	Prematurely submerged
Within the flood plain	1	beneath leaf mold	Prematurely submerged
Island in the flood plain	2	beneath log/bark	Prematurely submerged
Island in the flood plain	1	beneath leaf mold, between buttress roots of a tree	Never submerged
Outside of flood plain	1	under a log, 6 m from the edge of the flood plain	Never submerged
Edge of flood plain	3	beneath log	Sufficient time to develop prior to submergence

TABLE 3. Sample size (n), geometric mean, standard deviation (SD), minimum (Min), and maximum (Max) of seven variables of Marbled Salamanders (*Ambystoma opacum*) and their nests from Tuskegee National Forest, Alabama, USA. Five eggs from each nest were used for embryo staging. Body mass was not recorded for four females due to equipment failure and nest width and length were not measured for two nests. The abbreviation SVL = snout-vent length. The symbol † = one nest is not included in the summary statistics because eggs were much more advanced than the other nests (Harrison stage 34–36).

Variable	n	Mean	SD	Min	Max
SVL (mm)	10	68.5	3.6	64	75
Body mass (g)	6	7.89	0.92	6.52	8.99
Nest width (cm)	8	6.08	1.49	4.2	9.0
Nest length (cm)	8	9.53	2.6	7.2	15.5
Clutch size	10	107.8	24	54	136
Clutch mass (g)	10	9.96	3.6	3.39	15.3
Harrison stage†	40	9.9	3.8	2	19

Because amphibians rely on aquatic environments for reproduction, increases in extreme rainfall due to tropical storms may have negative effects on populations (Walls et al. 2013). Nesting success, in particular, may be adversely affected, but studies relating hurricanes to nest success typically focus on sea turtles (e.g., Milton et al. 1994; Ross 2005) or coastal birds (e.g., Walter et al. 2013; Schulte and Simons 2016). There is, however, potential for storms to adversely affect other taxa (Ernst 1974; Wojnowski 2000; Walls et al. 2019). Nest success of Marbled Salamanders was low during a year with successive hurricanes, with premature flooding of nests as a likely cause. My laboratory studies demonstrate that embryos can fully develop underwater, but hatching success is reduced by at least 50%. Therefore, increased frequency of extreme rainfall may lower egg survival of Marbled Salamanders in the future.

Effects of temperature.—Nest temperatures and developmental rates in response to temperature were needed to predict incubation periods in the field, and few studies report these data for Marbled Salamanders. Nest temperatures vary across previous studies from 0° to 25° C (7°–12° C, Lantz 1930; 16°–18° C, Moore 1939; 0°–25° C, Graham 1971; 11.4°–13° C, Anderson and Williamson 1973; 0°–14° C, Jackson et al. 1989; 6.8°–13.5° C, Watkins 1999); however, no consistent methodology has been applied and, to my knowledge, this study is the first to extensively monitor and report nest temperatures for Marbled Salamanders. Importantly, because temperatures change markedly through the nesting season, the timing of oviposition results in relatively large thermal variation for important developmental events (e.g., gastrulation versus gill formation) both within and across nests. More research is warranted

to understand the importance of this thermal variation for embryo development and survival.

My results are congruent with existing studies of nest temperatures and the effects of temperature on survival: embryos can develop successfully from 5°–25° C (King 1935; Anderson 1972). Additionally, I incubated eggs at 28°, 30°, and 32° C (data not reported here): all surviving embryos at 28° C had noticeable morphological abnormalities and all eggs died at 30° and 32° C. Although rising nest temperatures are a conservation concern for many reptiles, increased temperatures will not likely threaten egg survival of Marbled Salamanders because nest temperatures are not near the upper thermal limit for development. Therefore, the greatest climatic threat for nest success of Marbled Salamanders, and perhaps other terrestrially nesting salamanders, may be changes in precipitation. Additionally, the timing of nesting may interact with rainfall to influence nest success. Eggs that are laid relatively early in the season will experience the warmest temperatures and fastest development, while late-constructed nests experience cooler temperatures. Nesting early could be advantageous if pools flood early in the season; however, if inundation is delayed, this would result in fully developed embryos remaining unhatched for lengthy periods, potentially exposed to desiccation and depredation. Future studies should consider the interactions between patterns of rainfall and nest temperature to understand how both rising global temperatures and increased variation in rainfall influence nest success.

Development under water.—Hatching success is high under ideal conditions (i.e., appropriate time to develop before inundation), ranging from 80–99% (Graham 1971; Petranka and Petranka 1981b; Jackson et al. 1989; Croshaw and Scott 2005; Hale et al. 2016). Marbled Salamander embryos can fully develop underwater but hatching success is low. This finding is not wholly novel: Noble and Brady (1933) performed similar experiments and conclude that egg mortality is caused by a failure to hatch rather than a failure to develop. Moreover, King (1935) and Lantz (1930) report that early inundation results in low hatching success but do not provide data. To my knowledge, no previous study has rigorously determined the effects of early inundation on egg survival and development of Marbled Salamanders, but my results align with the anecdotal observations of past studies.

There are at least three reasons to assume that premature flooding of nests results in low egg survival at the field site. First, egg survival is higher when females guard nests compared to when they abandon

their eggs (King 1935; Jackson et al. 1989; Croshaw and Scott 2005). Thus, early inundation may expose eggs to predation and disease without maternal protection. Second, anecdotal data indicate that egg mortality is high in the field. Most nests contain only dead eggs after the initial flood waters recede. Three nests had a substantial number of dead eggs (20–54), and only one nest contained live eggs. Finally, despite completing development to Harrison Stage 46, more than half the eggs in my laboratory study died before hatching, indicating that any eggs that survived early inundation in the field were unlikely to hatch.

The reason why embryos fail to hatch is not obvious. Hatching is triggered by a reduction in oxygen levels when the nest is covered with water (Petraska et al. 1982). Indeed, for eggs of many amphibians and fishes, hypoxia late in development cues the release of hatching enzymes (e.g., chorionases), which dissolve the egg membranes. There is, however, potentially wide variation in hatching mechanisms across species. For example, some fish hatch in response to elevated rather than reduced oxygen levels (Martin et al. 2011). Moreover, among amphibians, the timing and rate of enzyme release can vary across species (Cohen et al. 2016). Without knowing the proximate causes of enzyme release and subsequent cascade of events specific to Marbled Salamanders, it is difficult to determine why early-inundation reduces hatching success. Development under water may interfere with the release of enzymes, their functionality, or both. Regardless, both fish and amphibians hatch in response to specific cues, and hatching is inhibited when these cues are absent. Aquatic development is likely the ancestral state for *Ambystoma*, and Marbled Salamanders have probably undergone multiple changes in embryo physiology to enable terrestrial nesting (Hale et al. 2016). We should, therefore, expect low hatching success in response to early inundation. Ultimately, premature flooding of nests may significantly reduce hatching success in the wild. When combined with other stressors (e.g., habitat loss, pollution, novel pathogens), this may contribute to population declines in the future.

Nest success.—Nest success in Marbled Salamanders can range from 0 to 100% depending on population and local conditions (Stenhouse 1987; Graham 1971; Doody 1996; Trauth et al. 1989; Glorioso et al. 2015). High mortality is usually due to nests that are never inundated. For example, Jackson et al. (1989) found that 44% of nests were never inundated during an unusually dry year, and Graham (1971) found that eggs die due to freezing temperature if nests are not inundated before winter. In Louisiana, USA, a drought prevented the filling of

ponds resulting in 100% nest failure (Glorioso et al. 2015). Over a 22-y study, reproductive success was poor in 10 y and total reproductive failure occurred in 6 y primarily due to a short hydroperiod (Taylor et al. 2006). Thus, most instances of nest failure are due to insufficient rainfall.

To my knowledge, no study has reported large proportions of nests prematurely inundated, and the effects of early flooding on egg survival have received little attention. One exception is that Dorcas et al. (2006) opportunistically monitored populations following two subsequent hurricanes in South Carolina, USA. They did not monitor nests but found no Marbled Salamander larvae during the following spring, indicating total reproductive failure due to the hurricanes. Most likely, the succession of hurricanes Sally, Zeta, and Delta resulted in reduced reproductive success; however, without nest data from previous years, it is impossible to know how my results differ from typical rates of nest success at this site. Additionally, Graham (1971) found that the breeding congress was reduced in flood years; thus, relatively few females may have been affected by these hurricanes. Complete reproductive failure is common for many amphibians and Marbled Salamanders in particular. Taylor et al. (2006) demonstrated that adult and juvenile survival must be relatively high for populations to persist in the face of catastrophic reproductive failure. Their models, however, only considered reproductive failure due to years with short hydroperiods and not the effects of extreme rainfall. Thus, future increases in the variance of precipitation could increase the number of years with low reproductive success due to short hydroperiods in some years and extreme flooding in others. Unlike during drought years, I did not observe complete nest failure due to hurricanes. An important caveat then is that larval survival and recruitment following hurricane-induced flooding may have been high enough to compensate for the observed reductions in nesting success. Such population-level effects deserve research attention.

Petraska and Petraska (1981a) proposed that selection favors individuals that nest at intermediate depths concerning the future water column (but see Jackson et al. 1989; Croshaw and Scott 2006). My data, however, indicate that a more complex model is required to explain the evolution of nesting behavior. For example, the timing of oviposition may have important effects on nest temperatures and thus developmental rates, influencing the timing of hatching for conspecifics (which affects larval survival; Boone et al. 2002). Moreover, the timing of oviposition may interact with patterns of rainfall to influence the evolution of nesting behavior. A

more complete model should include the timing of migration to the nesting grounds, resultant nest temperatures, and patterns of rainfall. Of course, future changes in precipitation, particularly due to extreme weather, may impose novel selection forces.

Additional costs of hurricanes.—Anecdotal data indicate there are costs of increased hurricane frequency other than egg mortality. Marbled Salamanders are not proficient swimmers and may drown if unable to find refuge while swimming (Noble and Brady 1933). After the nesting grounds were prematurely flooded, I found several adults and three nests located on islands (Fig. 1) within the nesting area. These islands were high elevation points, usually around the base of trees, that remained above the water level. Likely, individuals migrated to the nesting grounds and during heavy rains sought higher elevations and were trapped. This could have several costs. These individuals may become isolated from the rest of the population, reducing their chances of mating success, inducing physiological stress, or resulting in resource limitation. This is particularly true for males because they reach the breeding grounds before females (Noble and Brady 1933). Moreover, if rains cause water levels to rise further, drowning may occur. Given that high adult survival is critical to compensate for low reproductive success (Taylor et al. 2006), extreme weather may induce a combination of reproductive failure and adult mortality that increases the probability of population extinction.

Because the effects of extreme weather are species-specific, community structure could shift after a storm (Sergio et al. 2018). For example, Hurricane Hugo reduced the number of predatory spiders, which benefited frog populations (Woolbright 1991). Marbled Salamander larvae are aggressive predators of *A. maculatum* and *A. talpoideum*, which also inhabit the study site (Walls 1995). These species reproduce later in the season (winter and early spring) and lay eggs in water rather than on land. Thus, additional water from these hurricanes may have little negative effect on their reproductive success. High egg mortality of Marbled Salamanders may allow for increased recruitment of the other species. Additionally, because the earliest clutches were most adversely affected by the hurricanes, Marbled Salamander larvae may have less time to grow before the hatching of *A. maculatum* and *A. talpoideum*. Thus, these species may benefit from the potentially smaller-than-usual size of Marbled Salamander larvae, which are gape-limited predators (Urban 2007). Such downstream effects of extreme weather events on community structure warrant

further investigation.

My study adds to the body of knowledge concerning hurricanes and amphibians by: (1) focusing on salamanders, which are less studied than frogs; (2) experimentally assessing a hurricane-induced mechanism (premature flooding) rather than using opportunistic monitoring; and (3) focusing on reproduction rather than population demography and adult survival. Although hurricane effects have been documented for a diversity of salamander genera of North America (*Ambystoma*, *Amphiuma*, *Desmognathus*, *Eurycea*, *Notophthalmus*, *Plethodon*, *Pseudotriton*, *Siren*; Greenberg 2001; Enge 2005; Schriever et al. 2009; Gunzburger et al. 2010; Nicoletto 2013), Central America (*Bolitoglossa*; Gray and Strine 2017), and Europe (*Lissotriton*, *Triturus*; Lorrain-Soligon et al. 2021), only two studies have focused on salamanders (Wojnowski 2000; Walls et al. 2019). Unfortunately, these have both used terrestrial nesting, pond-breeding *Ambystoma* (Marbled Salamanders, Wojnowski 2000; Frosted Flatwoods Salamanders, *A. cingulatum*, Walls et al. 2019); therefore, my study does not increase taxonomic breadth. Regardless, all studies demonstrate either neutral or negative effects on salamanders (i.e., no positive effects), and the three studies specific to salamanders, including mine, demonstrate negative effects. Conversely, many frog populations experience positive effects after hurricanes (e.g., Woolbright 1996; Vilella and Fogarty 2005; Suazo-Ortuño et al. 2018a,b). Thus, salamanders may be more susceptible to increased hurricane frequency or severity than frogs. Studies focused on species outside of terrestrially nesting *Ambystoma* would be helpful, particularly if they use stream-breeding (e.g., *Eurycea*) or terrestrial species with direct development (e.g., *Plethodon*) because these are poorly represented by existing studies and may be susceptible to altered rainfall (e.g., Lowe 2012).

Most studies do not relate results to a specific aspect of the hurricane (e.g., storm surge, flooding, canopy disturbance) but only measure changes in species richness, evenness, or population size/density before and after the storm. Conversely, my study pinpoints a specific mechanism (premature flooding of nests) and assesses its effect in the lab and field. Moreover, very little experimental work has been conducted and most studies utilize opportunistic population monitoring. The exception is that Klawinski et al. (2014) experimentally reduced canopy cover and increased leaf litter in a factorial design to determine how changes in forest structure following a hurricane influence populations of Coqui Frogs (*Eleutherodactylus coqui*). Because many hurricane-induced habitat changes correlate with one

another (e.g., increased water depth and salinity due to storm surge; increased canopy openness and warmer ground temperatures), we need more controlled, factorial studies to isolate specific effects of habitat changes on amphibians. Although my study was not wholly experimental, it could serve as a model for future work, combining opportunistic field studies with controlled studies that mimic hurricane-induced environmental changes. This would greatly enhance our understanding of the specific ways that hurricanes alter population densities and species richness.

Finally, only four studies have considered the effects of hurricanes on amphibian reproduction, which includes nest success. Dorcas et al. (2006) reported a notable reduction in the number of anuran egg masses after two subsequent hurricanes. Importantly, they also found no Marbled Salamander larvae, indicating total nest failure. Wojnowski (2000) studied a population of Marbled Salamanders after a hurricane: pre-mature flooding of the study site resulted in all females ovipositing in areas that were too high in elevation (100% nest failure). Walls et al. (2019) found that juvenile recruitment of the Frosted Flatwoods Salamander was unusually low following hurricane storm surge. They suggest embryo and larval sensitivity to salinity was the cause. The only study reporting a positive effect of hurricanes on amphibian reproduction is Meshaka (1993): Hurricane Andrew induced breeding in three species of frogs, which benefited from an increase in the number of breeding sites due to the storm. Such positive effects on frog reproduction may be relatively common following storms (e.g., tornadoes; Smith 2013). Frogs may benefit from extreme storms because they can coordinate movement to newly created habitat via calling and quickly traverse long distances by jumping. Without such abilities, salamanders may be more susceptible to reproductive failure. Of course, this conclusion is based on only these few anecdotes. For the reasons stated previously, we need much more data to understand which amphibians may suffer most from increased frequency or severity of storms in the future.

Conclusions.—Amphibians are in decline worldwide, but little is known about the role that altered weather patterns play. This is particularly important given the reliance of these species on water and that altered patterns of precipitation may exacerbate existing stressors related to global change (e.g., pollution, disease). Few studies have rigorously considered the effects of hurricanes on amphibians and the vast majority have only studied effects on a few species of frogs. Here, I demonstrated that early inundation of nests can reduce hatching success for Marbled Salamanders using a combination of opportunistic field observations and experimental laboratory studies. The Southeastern U.S.

is a biodiversity hotspot for salamanders and this region experiences a high frequency of tropical storms. Thus, we need more studies to enhance our understanding of how an increased frequency of storms will influence salamanders in the future.

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