

Modeling response of frosted flatwoods salamander populations to historic and predicted climate variables



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ABSTRACT

For many amphibian species, particularly those that rely on ephemeral ponds for reproduction, population persistence can be dependent on landscape hydrology with years of suboptimal rainfall resulting in reproductive failure. Therefore, in order to accurately predict population persistence under future climate scenarios, it is necessary to incorporate pond hydrology. The frosted flatwoods salamander (*Ambystoma cingulatum*), a federally threatened species, has experienced dramatic population declines at Fort Stewart, Georgia. Here we used spatially explicit agent-based modeling to quantify the effects of historic climate data, with an emphasis on associated ephemeral pond depth and water retention, on salamander egg and larval survival. We then use these models to make predictions about climate thresholds for population persistence. Our models indicated wide fluctuations in Fort Stewart salamander populations from 1960 to 2010. Similar to what was documented with field collected survey data, our models showed a sharp decrease in populations during a drought in the late 1990s. Even modest reductions in annual rainfall (5–10%) would result in further population declines and more moderate reductions (20–25%) would result in population extirpation. Although climate change models predict relatively minor increases in temperature and precipitation in the Fort Stewart area, our models demonstrate the sensitivity of this salamander population to climate fluctuations and provide climate thresholds, below which, this population would likely not be able to recover.

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1. Introduction

Global amphibian populations have been declining at an alarming rate (Stuart et al., 2004). A variety of mechanisms have been implicated in the declines including habitat loss, overexploitation, infectious disease, introduction of predators, and chemical contaminants (Alford and Richards, 1999; Collins and Storer, 2003). However, an emerging threat, climate change, has received extensive recent attention (Pounds, 2001; Carey and Alexander, 2003). Climate change is thought to be at least partially responsible for amphibian declines in some populations (Pounds et al., 1999), with climate-induced mechanisms including wetland desiccation (McMenamin et al., 2008), increased exposure to ultraviolet radiation, increased rates of infectious disease (Pounds et al., 2006; Bosch et al., 2007), or a combination of several climate-induced factors (Kiesecker et al., 2001).

Because many amphibian species depend on precipitation amount and timing for survival and reproduction, they are extremely sensitive to climatic variations. Particularly for species

that rely on ephemeral ponds for reproduction, population persistence can be dependent on landscape hydrology and hydroperiod (McMenamin et al., 2008). A single year of suboptimal precipitation can lead to reproductive failure (Pechmann et al., 1991) and multiple or successive years of suboptimal rainfall could, therefore, lead to regional extinctions. By including hydrology in species population models, we can make much more accurate predictions of species persistence. Here we use historical climate data to model hydrological effects on the population of frosted flatwoods salamanders (*Ambystoma cingulatum*) on Fort Stewart, located near the Atlantic coast in southeast Georgia (Fig. 1) and make predictions about climate thresholds for population persistence.

The flatwoods salamander is a federally threatened species with distribution limited to the Coastal Plain region of the southeastern United States. Flatwoods salamander reproduction is tightly linked to the timing and amount of precipitation, with the egg and larval stage occurring in ephemeral wetlands. Fall/winter rain events trigger adult migration to breeding sites (Means, 1972; Anderson and Williamson, 1976; Palis, 1997a) where mating occurs terrestrially. Eggs are laid on the ground prior to inundation of the breeding sites, and do not hatch until after immersion in water (Anderson and Williamson, 1976). The larval period then lasts 3 to 4.5 months (Means, 1986; Palis, 1995) with successful emergence

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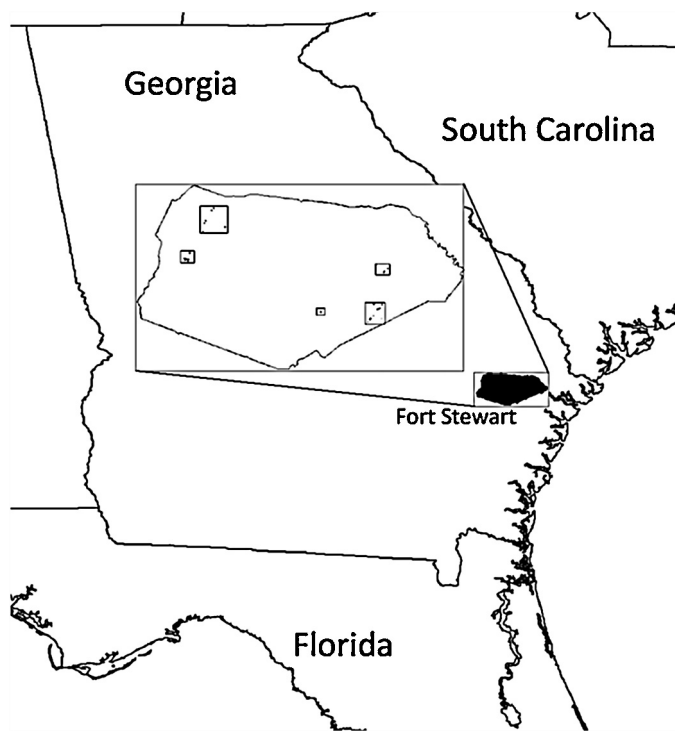


Fig. 1. Location of Fort Stewart in Southeast Georgia and, within Fort Stewart, the five rectangular study areas that contain the 13 ponds used in the hydrology model. All of the ponds included are known to have historically supported frosted flatwoods salamanders larvae (Macey, unpublished data). Details of pond characteristics are included in Table 2.

dependent on consistent water retention in wetlands throughout that time. Without suitable rainfall, breeding migration can be disrupted and/or wetlands can dry prior to larval emergence, thereby leading to reproductive failure (Palis et al., 2006).

At Fort Stewart, 22 wetlands were identified as confirmed salamander breeding sites and survey efforts in 1994 documented larvae at 18 of 19 sites sampled (Bevelhimer et al., 2008). Since that time, Fort Stewart biologists documented a steady decline in flatwoods salamander sightings, and surveys conducted in 2006 and 2007 resulted in only one pond with documented larvae (Bevelhimer et al., 2008). Insufficient rainfall was correlated with amphibian declines at a nearby site during the same time period (Daszak et al., 2005) and was implicated as a cause of the Fort Stewart salamander decline (Bevelhimer et al., 2008); however, no empirical research has been done to test this assumption. Here we use spatially explicit agent-based modeling to quantify the effects of climate warming, with an emphasis on associated ephemeral pond depth and water retention, on flatwoods salamander reproduction and egg/larval survival. Our objectives were to: (1) Determine whether recent drastic reductions in the salamander breeding population on Fort Stewart are likely due to hydrologic changes and (2) Identify temperature and precipitation thresholds likely to impact population viability on Fort Stewart.

2. Methods

2.1. Study site

The location for our modeling effort was Fort Stewart, GA, an 111,600-ha US Army installation in the Lower Coastal Plain of southeastern GA (32°N, 81°33'W, Fig. 1). The installation's active management of longleaf pine (*Pinus palustris*)–wiregrass (*Aristida stricta*) communities, as well as numerous ephemeral ponds,

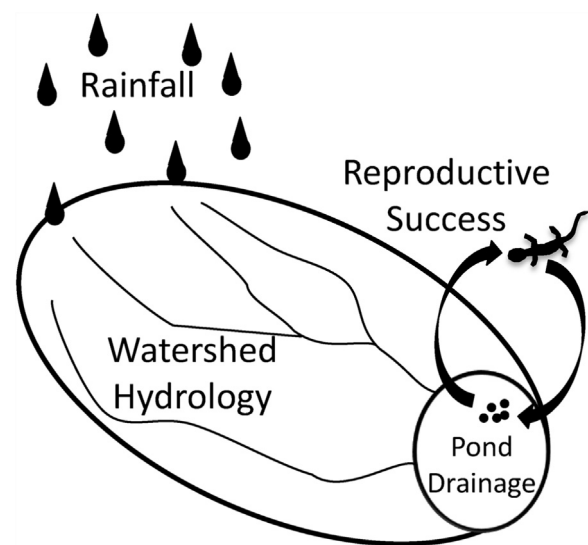


Fig. 2. Schematic of frosted flatwoods salamander agent-based model at Fort Stewart, GA incorporating weather, pond hydrology, and salamander reproduction. In this model, rainfall amounts (as determined through historic, 1950–2010, weather data) influence watershed hydrology which, in turn, influences ephemeral pond hydrology (duration of pond persistence), which, in turn, influences flatwoods salamander reproductive output.

provide several areas of preferred habitat for the flatwoods salamander (Palis, 1997b).

2.2. Model description

We implemented the model in NetLogo (Wilensky, 1999) and followed the overview, design concepts, details (ODD) protocol for describing individual-based models (Grimm et al., 2006, 2010).

2.3. Entities, state variables and scales

We incorporated two types of individual-based entities in our model: Fort Stewart ponds and flatwoods salamanders (Fig. 2). Ponds were defined by location, diameter, depth and watershed area; all of which were identified from 5-m resolution LIDAR images collected in 2009. Using GRASS processing software (Neteler and Mitasova, 2008), we imported the LIDAR data using the v.in.ascii GRASS program to create point-based vector maps and then generated 5-m resolution raster maps using v.surf.rst, a program that uses equations based on thin plate spline with tension to create a digital elevation model (DEM; Neteler and Mitasova, 2008). Depressions in the DEM were then identified with r.terraflow, which resulted in a large number of locations where rainfall would pool instead of reaching streams and rivers. These locations were clumped together to generate distinct ponds and lakes using r.clump. Clumps that were greater than 1.25 and less than 100 ha were selected as potential ephemeral ponds of interest, resulting in 8155 ponds on or near the installation. Each pond was then processed to calculate the size of the watershed that feeds the pond: The spill point for the pond was identified by finding the lowest elevation one grid cell away from the pond, and running the r.watershed program to identify the upstream watershed from that point. With that completed, a new vector map was created containing the outline of each of the LIDAR-based ponds, each associated with the average depth of the pond, the maximum depth, the area of the pond, and the area of the watershed upstream from the pond. This information provided the primary information for the hydrologic component of the model. Four study areas within Fort

Stewart were chosen based on historical presence of flatwoods salamanders and locations of field-collected pond depth data (**Error! Reference source not found.**) and, within those areas, all modeling efforts were focused on 13 ponds identified as known salamander breeding sites (Macey, Personal Communication; Bevelhimer et al., 2008).

Salamanders were modeled as agents defined by age, location, and association with specific breeding ponds. Only female salamanders were included in the model. Salamanders move according to season, rainfall and life history stage (see below). Salamanders moved on weekly time steps over 5-m resolution maps.

2.4. Initialization

Model initialization involved setting parameters, reading in maps that represent the study area, reading weather data for the desired timeframe, and initiating pond and salamander agents. Key parameters, identified in Table 1, capture a combination of values from the literature and/or subject matter expert opinion. Maps and weather data are discussed below. Ephemeral ponds used in the models were identified by field site surveys (Macey, unpublished data), but augmented with pond size and depth information derived from a LiDAR-based digital elevation model (DEM). The model was initialized with salamanders associated with every ephemeral pond within the study area, even though it is very unlikely that every pond could support a salamander population. This approach provides every chance that salamanders might currently persist in every pond that did not undergo a local extirpation during the simulation time. A total of 66 females were initialized per pond hectare (Palis, 1997a; Palis et al., 2006, Haas and Gorman, Personal Communication).

2.5. Input data

Locations and digitized outlines of ponds were determined through field surveys (Macey, unpublished data) and used to initialize the simulation model. Weather data was retrieved from the NOAA historic weather data archives for Fort Stewart, GA weather stations (IDs 091544 and 093538) from 1960 through 2010. Missing data were filled in from nearby weather stations. These data provided the model with daily temperature means, minimums, maximums, and rainfall.

The LiDAR-based DEM was processed with r.shaded.relief to generate a shaded relief image used as a background to the model. Fort Stewart supplied vector maps showing roads, streams, and boundaries, which were also used for spatial orientation during inspection of the model.

2.6. Submodels

2.6.1. Hydrology

The hydrology of ephemeral ponds determines the likelihood of salamander reproductive success. The ephemeral ponds that have been identified as salamander breeding ponds at our study area are typically less than a hectare in size and are fed by watersheds less than ten times larger. We chose to establish a very simple hydrology submodel that used the weekly weather data to update the water depth in the ponds. Each pond was modeled as an inverted cone with a representative fixed diameter and depth at its full point. We chose to model ponds with a very simple lumped parameter approach using two parameters. Individual ponds collected rainfall from their respective small watersheds and then lost water at a constant rate. The pond depth from the previous week was reduced by the pond drainage rate, establishing a new pond volume to which the new rainfall volume was added. A rainfall interception parameter (RI) established the amount of rainfall each week that did not

flow into ponds. This takes into account rain that is intercepted by vegetation, water that evaporates or is transpired out of the soil, and water that is lost to groundwater. The second parameter, pond drainage rate (PDR), is also a fixed value that accommodates the drop in water level from ponds each week due to evaporation, transpiration, and leakage. At each weekly time step the pond depth (D) is decreased by PDR (Eq. (1)), with the resulting depth converted to pond volume (V), assuming the inverted cone (Eq. (2)). The volume is then increased with rainfall (R) minus the rainfall intercept multiplied times the watershed area (WA) (Eq. (3)), with the resulting depth converted back to depth (Eq. (4)).

$$D = D - \text{PDR} \quad (1)$$

$$V = (D \times \text{TA})^3 / (3 \times \text{TA} / \pi) \quad (2)$$

$$V = V + (R - \text{RI}) \times \text{WA} \quad (3)$$

$$D = (3 \times V \times \text{TA} / \pi)^{1/3} / \text{TA} \quad (4)$$

The first simulation experiment, described below, sets the RI and PDR parameters for Fort Stewart as a whole. This assumes that these values are not significantly different across the installation due to differences in geology, soils, and vegetation. Future detailed geologic studies of the installation would allow each pond to be modeled with its own unique parameters.

2.6.2. Salamander movement

Adult salamander agents display several different types of movement in the model. First, adults are assumed to mostly remain near their natal ponds (Semlitsch, 1998). In this model, adults do not move if they are not in water, are outside of the breeding season, or if there is no weather trigger during the breeding season. Second, salamanders that do find themselves within ponds holding water scatter randomly until they find themselves in the surrounding upland. They can remain within the boundaries of dry ponds. Third, during or following autumn rains between October and January (Means, 1972; Anderson and Williamson, 1976; Palis, 1997a), adults migrate to breeding sites. Breeding migration appears to be triggered by passing cold fronts with movement often correlated with precipitation and decreased temperatures (Palis, 1997a). In the model, adults that have not laid eggs move downhill in an attempt to reach the nearest pond when maximum daily rainfall exceeds 1.8 cm (Palis, 1997a) after the 36th week of the year. Actual salamander movement is likely more incremental than demonstrated in our model; because most salamanders ultimately end up at a breeding site, we chose to simplify the movement pattern in this way.

Based on these movement parameters, salamanders in the model exhibit strong site fidelity (92.75% breed in their natal pond and 98.76% breed in the same pond they previously used). This is similar to what is seen in natural population in that individuals of most *Ambystoma* species return to natal breeding sites in successive years (Blackwell et al., 2004; Homan et al., 2007; Semlitsch et al., 1993) and breeding site fidelity was shown to exceed 90% in one well-studied species (Gamble et al., 2007).

2.6.3. Salamander reproduction and survival

Reproduction is captured in three stages: laying eggs, egg/embryo survival, and larval survival after wetland inundation. Following movement of adults to breeding areas, adults lay 97–222 eggs terrestrially (Anderson and Williamson, 1976). To capture the large variation in possible clutch sizes, we used an initial clutch size of 97 eggs/female plus a random number of 1–125. After deposition, eggs develop into embryos within egg capsules and attain hatching stage in approximately 3 weeks (Anderson and Williamson, 1976).

Table 1

Model parameterization variables, value at initialization, units and associated citations for frosted flatwoods salamander model of Fort Stewart, GA.

Model parameter	Value	Unit	Citation/assumption
Initial females	66	#/HA	Palis (1997a), Palis et al. (2006), Haas and Gorman, (Personal Communication)
Egg hatch rate	25	Percent	See text
Larvae survival	25	Percent	See text
Maximum age	9	Years	Scott (2005)
Pond drainage rate	2.50	cm/week	Derived via calibration
Rain interception rate	6.40	cm/week	Derived via calibration
Egg viability	8	weeks	Anderson and Williamson (1976), Petranka (1998)
Time as larvae	15	Weeks	Palis, 1995, 1997b
Adult survival	80	Percent/year	Taylor et al. (2005)
Earliest week for reproduction	39	Week of year	Means (1972), Anderson and Williamson (1976), Palis (1997a)
Trigger to move to ponds in fall	1.80	cm	Palis (1997a)
Minimum age at reproduction	104	Weeks	Palis (1997a), Scott (2005)

Embryos then remain in a state of arrested development for up to 8 weeks before which the pond must have standing water or the embryos will perish (Anderson and Williamson, 1976). Upon inundation, the embryos hatch from egg capsules into free swimming larvae (Anderson and Williamson, 1976; Petranka, 1998). The larval stage lasts approximately 11 to 18 weeks with metamorphosis occurring between March and April (Palis, 1995, 1997b), but sometimes as late as May (Bevelhimer et al., 2008). In the model, ponds that dry up prior to 18 weeks result in larvae mortality. Because eggs and larvae experience mortality from other factors, even in inundated ponds (e.g. predation), we used default survival rates for eggs and larvae. Although egg survival rates are not known for *A. cingulatum*, documented survival rates for *Ambystoma opacum*, a species with a similar life history, range from 0% to 85.2% (Graham, 1971; Stenhouse, 1987; Jackson et al., 1989). Given the wide range of observed egg survival, we used a median default value of 25.0% survival. Observed larval survival for *A. opacum* ranges from 0.00% to 84.0% (Stenhouse, 1987; Petranka, 1989; Scott, 1990) so we again used a median default value of 25.0%. Adult survival was capped at 9 years and age at first reproduction was set at 104 weeks (Palis, 1997a; Scott, 2005).

2.6.4. Model evaluation

Our model was evaluated through comparisons between model output and field collected data. Model hydrology parameter values and outputs were compared to field collected pond depth information (see details below) and salamander population outputs were compared to published larval survey results (Bevelhimer et al., 2008).

3. Simulation experiments

3.1. Hydrologic calibration

To calibrate the hydrologic parameters, rainfall interception rate and pond drainage rate, we used the pond extent data set described above and compared model-produced pond depths to field collected data. We incorporated a larger number of Fort Stewart ponds for the calibration to take advantage of the full field dataset. Ponds were visited in February 2009 and between December 2009 and April 2010 (83 ponds with 185 total observations) and visually assessed for pond depth. That data was entered in spreadsheets somewhat subjectively as empty, 0.25 to 0.5 full, and full. These were entered into the model tables as 0.0, 0.3, and 0.8, respectively. During model runs, each of the pond and date combinations associated with field collected information was captured in output files for post-model run analysis. The average squared difference between the field observations and the model calculations for pond size were calculated and tabulated.

The average squared difference between calculated and observed pond depths for various combinations of rainfall intercept

(4.8–6.6 cm/week) and pond drainage rates (0.03–0.13 cm/week) ranged from 0.079 to 0.352. A visual inspection of the test results identified the best fit for the two hydrologic parameters: 6.4 cm per week for rainfall interception and 2.5 cm per week for pond drainage. These parameters were used in all model runs.

3.2. Population response to climate change

Global Circulation Models (GCMs) for this area suggest very small increases (1.2–3.0 °C) in temperature through mid-century (Westervelt and Hargrove, 2011). Rainfall forecasts are varied, but GCMs predict a general increase (<25%) in rainfall (Westervelt and Hargrove, 2011).

To examine the effects of altered climates on salamander populations, we re-ran the model from 1960 through 2010 using the historic weather patterns, but varied the rainfall amounts from 20% less to 20% more to identify the impacts of such a change on salamander population viability. Because the predictions for future rainfall are so wide ranging, we did not feel that fine scale analyses, such as predictions of precise seasonal patterns of rainfall, would be feasible. Although timing of fall/winter rains have been shown to be important for reproductive migration, we focused on overall precipitation levels using historic weather seasonal patterns as a baseline. Our goal was to determine overall precipitation thresholds that would affect salamander populations.

4. Model results

4.1. Population response to historic weather

We modeled 13 ponds known to have supported flatwoods salamanders historically. Model runs incorporating weather data from 1960 through 2010 resulted in large fluctuations in flatwoods salamander populations at Fort Stewart. Our models showed population declines in the early 1960s, early 1980s and late 1990s–early 2000s (Figs. 3 and 4), concurrent with long periods of decreased rainfall. Eight of the ponds exhibited localized salamander extirpation, for at least a subset of the runs, during these dry periods.

The results for the time period 1990 through 2010 (Figs. 3 and 4) corroborate very well with the field salamander survey data taken during that time (Bevelhimer et al., 2008) in which the majority of ponds surveyed in 1994 had larvae but very few larvae were detected from 1998 through 2007. Our model documented similarly low population growth during this period with larval production occurring in only 4 of the 10 years (Figure) and drastic population declines (Fig. 4).

Two key pond physical properties, the maximum depth and watershed-area to pond-area ratio, appear to be associated with probabilities of local extirpation (Table 2). The six ponds that

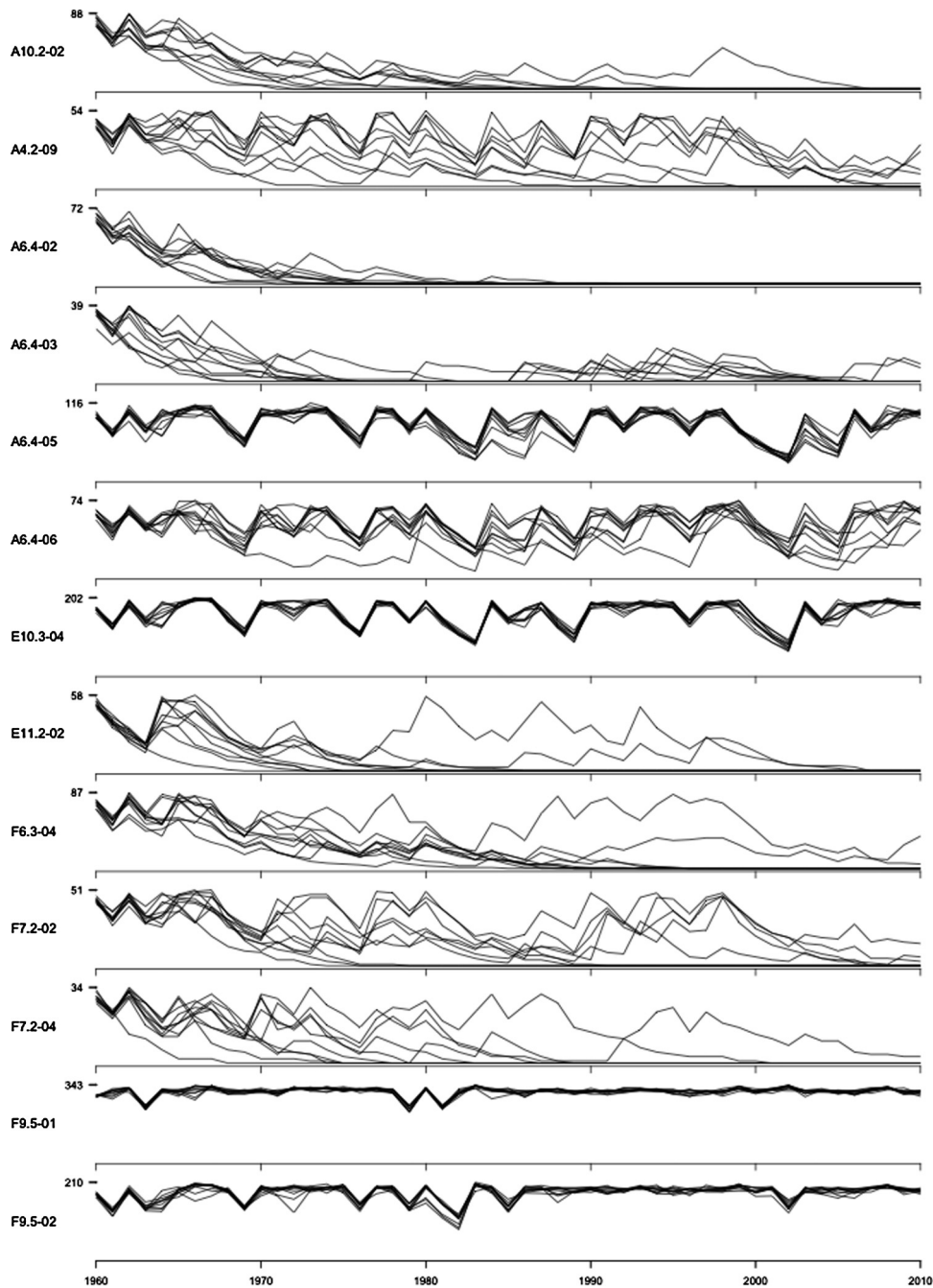


Fig. 3. Model output results of frosted flatwoods salamander populations in 13 individual ephemeral ponds at Fort Stewart, GA using historic (1960–2010) weather data. Each line represented. Parameters used in model are presented in [Table 1](#).

maintained the largest salamander populations had deeper depths and/or higher watershed to pond area ratios. Deeper ponds, once filled, would retain water longer and those with larger ratios would capture more rainwater.

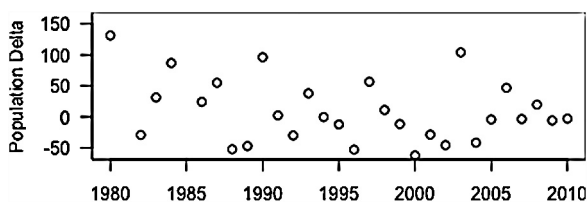


Fig. 4. Model output results of flatwoods salamander yearly population change at Fort Stewart, GA using historic (1960–2010) weather data.

4.2. Population response to climate change

According to our models, a 5% reduction in rainfall would result in a 5.6% reduction in population size, with 8 of the 13 ponds able to support a salamander population. A 10% reduction would result in an 11.9% reduction with 5 ponds still able to support populations. A 15% reduction would result in a 40.4% reduction in population size and only 2 ponds would support a salamander population. Local extinction would occur at rainfall levels 20–25% lower than historic with the two remaining ponds no longer able to sustain a substantial salamander population at that precipitation level. Conversely, a 5% or 10% increase in rainfall would result in 4.9% and 4.3% increases in population, respectively, with 9 and 10 of the ponds, respectively, supporting salamander populations.

Table 2

Pond physical characteristics including maximum depth (m) and the ratio of watershed area to pond area at Fort Stewart, GA. Salamander population persistence potential references the relative likelihood of salamander populations persisting in each pond, as indicated by model results in Fig. 4.

Pond ID	Maximum depth (m)	Watershed area to pond area ratio (m)	Salamander population persistence potential
1	0.548	2.62	Higher
2	0.497	4.63	Higher
3	0.498	1.85	Higher
4	0.482	1.61	Higher
5	0.477	3.73	Lower
6	0.501	4.13	Lower
7	0.524	4.20	Lower
8	0.439	5.57	Lower
9	0.608	2.11	Lower
10	0.465	3.62	Higher
11	0.542	2.07	Higher
12	1.346	1.92	Lower
13	0.867	1.95	Lower

5. Discussion

We were able to demonstrate, through spatially explicit models of pond hydrology and flatwoods salamanders, that historic rainfall likely contributed to the declines in populations documented in the late 1990s. Very similar to what was shown with larvae sampling efforts (Bevelhimer et al., 2008), our model showed steep declines in population sizes, primarily due to reproductive failure, during the drought years of 1999–2002.

Given our ability to model field-verified historic population trends, our next step was to determine climate thresholds that could be used to predict population response to future climate parameters. We found that even a slight decrease in rainfall (5%) would lead to decreases in population size and in the number of ponds that could support populations. For the most resilient pond, the rainfall threshold is between 20% and 25% reduction. Conversely, slight increases in rainfall would benefit salamander populations. Climate projections predict a slight increase in precipitation levels in the area of Fort Stewart (Westervelt and Hargrove, 2011). Given the results of this model, even a modest increase in rainfall would likely benefit the flatwoods salamander population. However, we did not incorporate climate induced increases in evaporation, which could offset any increases in overall precipitation (Brooks, 2009).

An important aspect of salamander reproductive biology that is not addressed in our predictive models is the potential for changes in the timing of precipitation. Adult salamander migration to breeding sites is triggered by fall/winter rainfall (Palis, 1997a). In our determination of precipitation thresholds, we did not take into account timing of rainfall but rather used historic seasonal patterns of rainfall as a baseline to which we added or decreased precipitation levels. Although changes in climate could affect timing of precipitation as well as overall amounts, we did not feel that climate predictions are precise enough to incorporate into our model. Instead, we used the relationships between historic weather and salamander populations to determine the relative effects of changes in rainfall on population size.

Our models incorporated a very simplistic representation of ephemeral pond hydrology that relies on pond watershed size, pond volume, a weekly rain intercept rate, and a pond level drop rate. In our hydrology calibration experiment, we were able to identify that a weekly rain intercept rate of 6.4 cm per week and pond drainage rate of 2.5 cm per week resulted in model predictions that varied from observed values by an average of 0.25 full. We consider this suitable based on the resolution of the observations (“puddles”, “1/4 to 1/2 full”, and “full”) and the fact that observations were on a daily basis, while the model predictions were on a weekly

basis. The calibration experiment assumed that each of the visited ponds had the same rain intercept and drainage rates. The former are partly based on the amount of vegetation that could intercept rain within a pond’s watershed and the ability of the watershed soil to absorb rain. The latter assumes that the geology-based pond leak rate and groundwater fill rate are similar across ponds. Because this is likely overly simplistic, our hydrology model could likely be greatly improved if detailed data on individual pond characteristics were available.

The salamander population model experiment results suggest that substantial increases and decreases in flatwoods salamander populations are common. Intermittent years of suboptimal rainfall resulted in recurring population declines, followed by rainfall mediated rebounds. According to the model, nearly all populations that might have existed during the 1970s probably experienced a substantial crash that continued to 1985. Consistent with larvae survey data, we found a general increase in populations through the early 1990s and then a population crash in the late 1990s, reaching a low point in 2002. Our models indicate that breeding would have been possible in several years between 2003 and 2009. However, field surveys indicate that populations may have remained low up until 2010 (Macey, unpublished data). This discrepancy may be due to a variety of factors. First, the population rebounds predicted by our models were based on isolated rain events that occurred in the fall months. However, precipitation amounts are localized and every watershed in our study area may not have received large influxes. In addition, our model, based on a 9-year salamander lifespan, indicates that populations could persist over the time frame of the drought. However, if the drought also affected adult survival (a variable that remained constant in our model) populations may have been reduced more than our model demonstrates. If so, the population may have been reduced to such a level that a rebound would not be possible.

Compared to many other taxa, including other amphibian species (e.g. Swanack et al., 2009; Pie et al., 2013), relatively few ecological models have been created for salamander populations. Although salamander populations have been evaluated using GIS and metapopulation approaches (e.g. Compton et al., 2007; Gustafson et al., 2001), we are not aware of any agent-based models that explicitly take into account behavior of individuals in response to landscape and weather. Because of the inherently cryptic nature of many salamander species and the associated difficulty involved in field surveys of populations, ecological models can provide a useful means of evaluating population response to both contemporary and predicted perturbations. This model may provide a foundation for models of any ephemeral-pond dependent species and interested parties are welcomed to contact the authors for a copy of the model.

6. Conclusions

Flatwoods salamanders have been associated with a small number of ephemeral ponds on Fort Stewart since 1970 but larvae population declines, in association with suboptimal rainfall, occurred throughout the late 1990s and early 2000s (Bevelhimer et al., 2008). Because the maximum lifespan of an adult is likely 8–10 years, consecutive years of drought and associated reproductive failure over that period could result in regional extirpation. This model suggests that populations did crash recently in association with a drought. Predictions of future increased precipitation in the area of Fort Stewart would likely have positive impacts on the remaining salamander population assuming biologically relevant timing of precipitation (i.e., fall and winter rainfall).

The probability that an ephemeral pond is associated with a population of flatwoods salamanders appears to be associated with

several key factors. For a salamander population to persist at any given pond, the combination of pond depth, pond watershed area, and pond drainage rates must result in water retention for at least 15 weeks between late fall and early winter and this must occur every nine or fewer years. Although a pond may receive immigrants from nearby ponds, this is likely a relatively rare event given the high site fidelity seen in *Ambystoma* species.

We used a relatively simple hydrology model that resulted in salamander population data similar to what was seen through larval survey data. However, this model could be improved with better field data including detailed flatwoods salamander life history data, pond depth records, pond hydrology and geology, and vegetation associated with the pond and its watershed.

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