

Life history plasticity does not confer resilience to environmental change in the mole salamander (*Ambystoma talpoideum*)

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Abstract Plasticity in life history strategies can be advantageous for species that occupy spatially or temporally variable environments. We examined how phenotypic plasticity influences responses of the mole salamander, *Ambystoma talpoideum*, to disturbance events at the St. Marks National Wildlife Refuge (SMNWR), FL, USA from 2009 to 2014. We observed periods of extensive drought early in the study, in contrast to high rainfall and expansive flooding events in later years. Flooding facilitated colonization of predatory fishes to isolated wetlands across the refuge. We employed multi-state occupancy models to determine how this natural experiment influenced the occurrence of aquatic larvae and paedomorphic adults and what implications this may have for the population. We found that, in terms of occurrence, responses

to environmental variation differed between larvae and paedomorphs, but plasticity (i.e. the ability to metamorphose rather than remain in aquatic environment) was not sufficient to buffer populations from declining as a result of environmental perturbations. Drought and fish presence negatively influenced occurrence dynamics of larval and paedomorphic mole salamanders and, consequently, contributed to observed short-term declines of this species. Overall occurrence of larval salamanders decreased from 0.611 in 2009 to 0.075 in 2014 and paedomorph occurrence decreased from 0.311 in 2009 to 0.121 in 2014. Although variation in selection pressures has likely maintained this polyphenism previously, our results suggest that continued changes in environmental variability and the persistence of fish in isolated wetlands could lead to a loss of paedomorphosis in the SMNWR population and, ultimately, impact regional persistence in the future.

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While the drivers of paedomorphosis have previously been examined, few studies have applied advanced quantitative methods to understand how those dynamics structure responses to environmental change.

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Introduction

Plasticity in life history characteristics is thought to provide an evolutionary advantage for species that inhabit variable environments (Moran 1992; Whiteman 1994). Polyphenism refers to the expression of two or more distinct phenotypes produced by a single genotype; expression depends on both genetic factors and environmental cues and, thus, is maintained to some degree by selection (Semlitsch and Gibbons 1985; Moran 1992; Jackson and Semlitsch 1993; Whiteman 1994; Doyle and Whiteman 2008). Specifically, discrete polyphenisms in life history strategies, where variation is limited to alternative morphs and not a continuous distribution of traits, are useful for understanding the processes that contribute to phenotypic

plasticity in response to changing environments (Whiteman 1994; Scott 1993). Several wetland breeding salamander species exhibit polyphenic life histories and provide an ideal opportunity to examine how different strategies are favored in differing environments (Patterson 1978; Semlitsch 1985a; Ryan and Semlitsch 2003; Ryan and Plague 2004).

Facultative paedomorphosis is the ability to retain larval characteristics as a reproductively viable adult (Jackson and Semlitsch 1993; Whiteman 1994; Doyle and Whiteman 2008; Denoël et al. 2009). For wetland breeding salamanders such as the mole salamander (*Ambystoma talpoideum*), facultative paedomorphosis results in two distinct phenotypes: metamorphic terrestrial adults and paedomorphic aquatic adults (Jackson and Semlitsch 1993; Whiteman 1994; Denoël et al. 2009). Paedomorphic adults are able to initiate breeding rapidly as conditions become favorable, whereas terrestrial adults require specific environmental conditions to initiate and complete migration to breeding wetlands (Ryan and Plague 2004; Doyle et al. 2010). As such, offspring of paedomorphic adults may gain a fitness advantage because they have more time to grow prior to wetland desiccation and are less likely to experience high intra- and interspecific competition early on in development (Semlitsch 1987; Whiteman 1994; Scott 1993; Ryan and Plague 2004; Doyle et al. 2010). In addition, this strategy may buffer populations against harsh terrestrial conditions and costs associated with breeding migrations that can decrease survival of adults post-metamorphosis (Semlitsch et al. 1990; Whiteman 1994; Church et al. 2007; Semlitsch 2008; Rittenhouse et al. 2009).

Typically, the mole salamander breeds in fishless wetlands of intermediate hydroperiod, where individuals can complete larval development prior to wetland desiccation and where pressure from fish predation is minimized (Ryan and Plague 2004; Walls et al. 2013a; Walls et al. 2013b). However, some populations take advantage of favorable conditions in semi-permanent and permanent wetlands and will remain in ponds as paedomorphic adults for more than a single season (Ryan and Semlitsch 2003; Walls et al. 2013a). Increasingly permanent ponds, though, are also more likely to harbor fish, which mesocosm experiments have demonstrated to decrease the frequency of the paedomorphic phenotype in mole salamander populations (Jackson and Semlitsch 1993).

We examine the dynamics of paedomorphosis in a metapopulation of mole salamanders on the St. Marks National Wildlife Refuge (SMNWR), FL, USA. The refuge is located near Apalachee Bay of Florida's northwest panhandle and contains approximately 27,500 ha of crucial habitat for several species of conservation concern (Walls et al. 2013b). Periods of extensive drought have occurred at the refuge over the past decade, most recently from spring 2010 to fall 2011. Additionally, two severe weather events in 2012 and 2013 led to extensive overland flooding that connected adjacent freshwater waterbodies and introduced

fishes to isolated wetlands across the refuge. The drying of waterbodies due to drought, along with novel introductions of fishes as a result of increased waterway connectivity, is likely to have had consequences for populations of many species on the refuge, including the mole salamander. We used this natural experiment to understand how responses to changing conditions are shaped by the mole salamander's highly variable life history.

Drawing on a six-year study, we fit multistate multiyear site occupancy models to test specific hypotheses about the environmental drivers of phenotypic plasticity in mole salamanders on the refuge, while accounting for imperfect detection in our observations. We predicted that paedomorph occupancy would decline in the presence of fishes and as a result of drought (and subsequent reductions in wetland hydroperiod). A decline in the occurrence of paedomorphic individuals would suggest that paedomorphic populations were being lost through metamorphosis, thereby resulting in an increase in metamorphic populations, or suffering mortality from fish predation. The presence of fishes and drought conditions could theoretically increase the likelihood that individuals metamorphosed to escape predation pressures and/or the risk of desiccation. Given this, we also predicted that, unless environmental conditions (e.g., fishes and drought) were sufficiently extreme to dramatically reduce larval survival, larval occupancy would either remain stable or increase relative to populations of paedomorphic individuals (Walls et al. 2013a).

Methods

Species life history

The mole salamander is a common species throughout most of its range in the Southeastern United States (Semlitsch and Gibbons 1985). Breeding typically occurs from November to January and the migration of terrestrial adults to breeding wetlands has been tightly linked to environmental cues, such as temperature and precipitation (Semlitsch 1985a, b). This species exhibits high site fidelity, with terrestrial adults returning to the same wetlands year after year to breed (Semlitsch 1985b; Semlitsch and Gibbons 1985). Larvae are capable of metamorphosing approximately 4–5 months after hatching, though plasticity in development time at the individual- and population-level has been observed in response to variable environments (Patterson 1978; Semlitsch 1985b; Ryan and Semlitsch 2003; Ryan and Plague 2004). Juvenile metamorphs typically leave wetlands in mid- to late-summer. However, delayed metamorphosis may occur, depending on wetland suitability and environmental variability at a given location (Semlitsch 1985b). In general, larvae that survive the

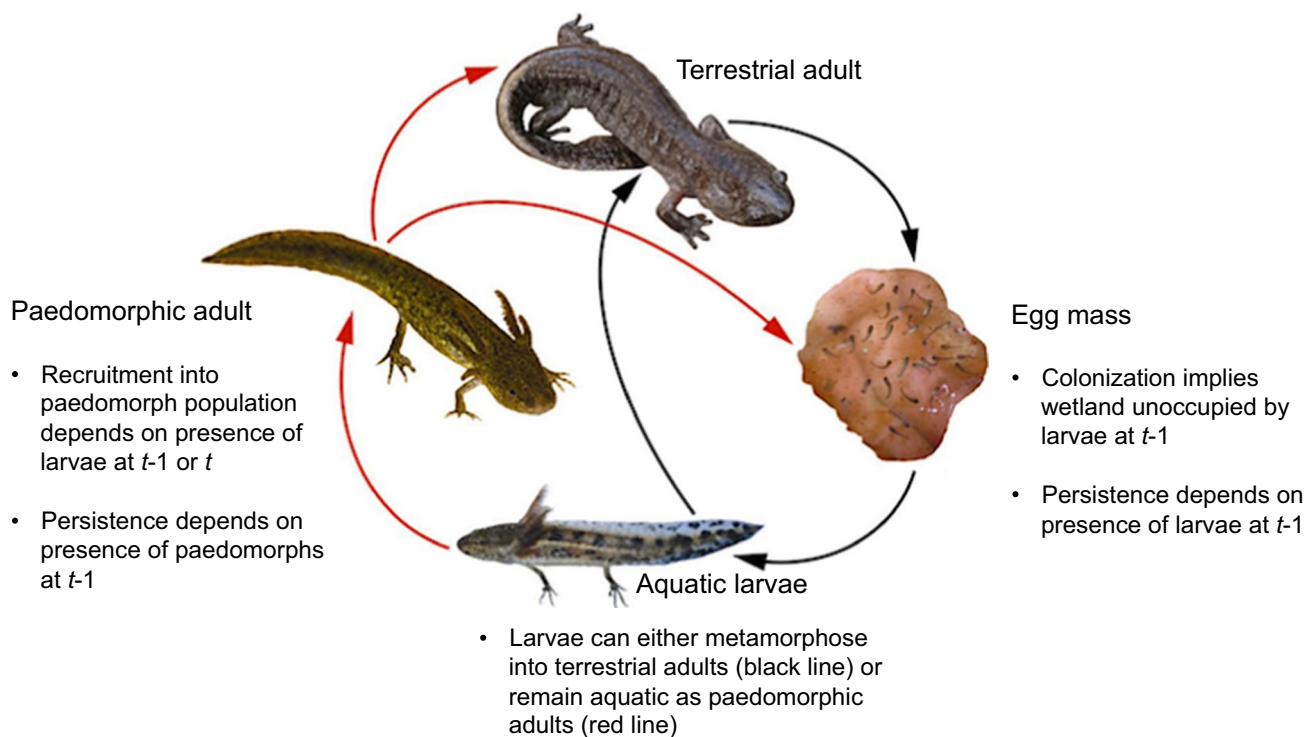


Fig. 1 Paedomorphic life history of the mole salamander (*Ambystoma talpoideum*) as it relates to estimated transition probabilities in our multistate occupancy model. *Dashed lines* relate to transitions

only observed in individuals that exhibit paedomorphosis. Modified from Walls et al. (2013a)

summer may either metamorphose and become terrestrial adults or remain aquatic as reproductively viable paedomorphic individuals until environmental conditions trigger metamorphosis (Fig. 1).

Data collection

We monitored 60 wetlands in the Panacea management unit of SMNWR during the spring (March–April) and fall (September–October) seasons from 2009 to 2014. We surveyed 45 wetlands from 2009 to 2011 and added an additional 15 wetlands in the spring of 2012. From 2012 to 2014, therefore, all 60 wetlands were surveyed in the spring and fall seasons. Originally, wetlands were categorized based on average time between drying events using a combination of instrumental records and observations on wetland depth during sampling (Riley et al. in review). This resulted in our 60 wetlands being split into short-duration wetlands that were observed to dry, on average, >1 time per year ($n = 25$) and long-duration wetlands that went on average >1 year between drying ($n = 35$). Mole salamanders were never observed in any of the short-duration wetlands over the course of the study (Davis et al. 2016). We restricted our analysis to focus solely on the 35 long-duration wetlands, which included ponds of semi-permanent and permanent nature that were presumably

more suitable for larvae as well as paedomorphic adults, but were also more likely to be colonized by, and subsequently maintain, predatory fishes (Walls et al. 2013b).

Modified commercial crayfish, aluminum screen funnel and minnow traps were deployed for 8-trap nights/site/season from 2009 to 2010, 16-trap nights/site/season in 2011 and 20-trap nights/site/season from 2012 to 2014 (Walls et al. 2013b). We checked traps daily and recorded and released all captured amphibian and fish species. For mole salamanders, we also recorded whether each individual was a larva or a paedomorphic adult at the time of capture. We used snout-to-vent length (SVL, in mm) measurements to verify life stage using a cut-off of >30 mm to assign individuals as paedomorphic adults for all individuals where visual characteristics were not diagnostic (a total of eight individuals; Jackson and Semlitsch 1993; Petranka 2010). Due to the breeding phenology of this species, we assumed that all larvae metamorphosed prior to fall sampling occasions and that all aquatic gilled mole salamanders captured in the fall were paedomorphic adults. While this may not be a valid assumption for all populations (Semlitsch 1985b), our measurements suggested this to be appropriate over the course of our study. Therefore, we restricted our analysis for larval salamanders to spring seasons when they could occur.

Table 1 List of estimated parameters for dynamic, multispecies-integrated habitat models

Parameter	Description
η	Probability a wetland remains suitable between seasons
ω	Probability a dry, unsuitable wetland becomes suitable
$\gamma^{A,d}$	Probability of mole salamanders colonizing a wetland that was dry the previous season
$\gamma^{A,f}$	Probability of mole salamanders colonizing a wetland that was unoccupied by fishes the previous season
$\gamma^{A,F}$	Probability of mole salamanders colonizing a wetland that was occupied by fishes the previous season
$\gamma^{F,d}$	Probability of fishes colonizing a wetland that was dry the previous season
$\gamma^{F,a}$	Probability of fishes colonizing a wetland that was unoccupied by mole salamanders the previous season
$\gamma^{F,A}$	Probability of fishes colonizing a wetland that was occupied by mole salamanders the previous season
$\phi^{A,f}$	Probability of mole salamanders persisting at a wetland in the absence of fishes
$\phi^{A,F}$	Probability of mole salamanders persisting at a wetland in the presence of fishes
$\phi^{F,a}$	Probability of fishes persisting at a wetland in the absence of mole salamanders
$\phi^{F,A}$	Probability of fishes persisting at a wetland in the presence of mole salamanders
$p^{A,f}$	Probability of detecting mole salamanders when fishes are not present
$p^{A,F}$	Probability of detecting mole salamanders when fishes are present
$p^{F,a}$	Probability of detecting fishes when mole salamanders are not present
$p^{F,A}$	Probability of detecting fishes when mole salamanders are present

Modeling framework

We extended the multi-season occupancy model of MacKenzie et al. (2003, 2011) and the integrated habitat, multi-state model of Miller et al. (2012) to analyze data. We assumed that each wetland belonged to one of five possible states during each season. A site was either: (1) unsuitable habitat (i.e., dry) and unoccupied; (2) suitable habitat but unoccupied; (3) suitable habitat, occupied by the mole salamander; (4) suitable habitat, occupied by fishes; or, (5) suitable habitat, occupied by both the mole salamander and fishes (Miller et al. 2012). We then used estimates of transitions among these states from season to season and their relationship to the dynamics of mole salamanders, fishes, and habitat to draw inferences about factors determining occurrence of the larval and paedomorphic life-stages in wetlands. Our dynamic model was Markovian, where the probability a site was in any of the five states in time $t + 1$ depended on which state it occurred in during time t (MacKenzie et al. 2009).

Transition probabilities were modeled via several sub-parameters, as presented in Table 1, representing seasonal colonization and persistence probabilities, habitat suitability and co-occurrence with fishes (MacKenzie et al. 2004; Miller et al. 2012). We were able to examine interactions in dynamics among salamanders, fishes, and wetland suitability by allowing transition parameters to be conditional on each other. For example, the probability a wetland transitioned from state 1 to state 4 ($\varphi^{1,4}$) was a function of the probability that (1) a previously dry wetland became suitable (ω), (2) fishes

colonized the wetland, which was previously unoccupied by amphibians ($\gamma^{F,a}$) and (3) the wetland was not colonized by amphibians during that season ($1 - \gamma^{A,f}$). Therefore, the full transition probability (Miller et al. 2012) is described by: $\varphi^{1,4} = \omega \times (\gamma^{F,a}) \times (1 - \gamma^{A,f})$. All analyses were independently conducted using separate datasets for larvae and paedomorph observations, allowing us to ask how the dynamics leading to occurrence of each of these life-stages differed.

We used the 2-month Standardized Precipitation Index for Northwest Florida (Division 01, National Climatic Data Center 2014) as a predictor of drought conditions. The Standardized Precipitation Index is a probability index based on long-term normalized precipitation values and, in our case, quantifies hydrologic inputs (i.e., precipitation) to wetlands (Guttman 1998; Cancelliere et al. 2007; Jenkins and Warren 2015). Previous work that examined a variety of climate variables found that the Standardized Precipitation Index calculated for a 2-month time interval best captures short-term effects of drought on wetland inundation during the periods of our observations (Davis et al. 2016). Values of the 2-month Standardized Precipitation Index were averaged across the months of March and April for spring sampling occasions and September and October for fall sampling occasions.

We accounted for variable and imperfect species detection within our modeling framework (MacKenzie et al. 2004; Miller et al. 2012). We were able to account for the possibility that detection of one species is often dependent on the presence of another. This is of particular relevance in studies of predator–prey interactions, where behavioral

changes due to the presence of predatory fishes are likely to alter observability of the mole salamander (Bailey et al. 2009; Falke et al. 2012; Miller et al. 2012). As such, we allowed the detection of larval and paedomorphic mole salamanders to be conditional on the presence of predatory fishes. Species detection for this analysis reflected the probability an individual was caught in a trap.

As part of predicting transitions among our five states, we estimated seasonal colonization and persistence probabilities by both mole salamanders and by fishes. Colonization of a wetland by larvae reflected the probability that an unoccupied site became occupied (i.e., successful breeding of adults occurred in that season). Recruitment of larvae into the paedomorph population (i.e., site colonization by paedomorphic adults), on the other hand, can be thought of as a function of: (1) the probability larvae colonized or occupied a wetland; and (2) the probability larvae became paedomorphic adults. We allowed these colonization probabilities of larval and paedomorphic mole salamanders to be conditional on whether fish were present, the habitat state in the previous season (i.e., whether the wetland was dry), and the 2-month Standardized Precipitation Index.

Persistence described the probability that a wetland remained occupied from time t to time $t + 1$ and was estimated for both mole salamanders and for fishes. Larval persistence was dependent on the successful breeding of adults in a wetland that was also successful in the previous spring and the probability a wetland remained suitable from one year to the next. Paedomorph persistence depended on the probability that this phenotype persisted at a wetland either through survival of existing individuals or recruitment of new larvae into this stage and was also conditional on the wetland remaining suitable between seasons. We also examined whether larval and paedomorph persistence was a function of fish presence and the 2-month Standardized Precipitation Index.

When fitting models, we used a sequential approach to select among alternative parameterizations, dealing, in order, with the parameters associated with: (1) species detection probabilities; (2) the initial state distribution (i.e., the proportion of sites initially in each of the 5 states); (3) habitat dynamics (i.e., the probabilities that individual wetlands transition between suitable and dry); (4) probabilities that mole salamanders and fishes persist at sites where they were present in the previous season; and (5) probabilities that sites that were previously unoccupied were colonized.

All models were fit in R (R Core Team 2014) using the maximum likelihood estimator derived by Mackenzie et al. (2009) (see Miller et al. 2012 and Davis et al. 2016 for the base code used to fit models). Using our sequential approach, we dealt with models related to each of the five component parameter types, so that models for our second

component (initial occupancy parameters) were fit using the best-supported parameterization for species detection, but were the most general parameterizations for the final three components. A complete list of candidate models is provided in Online Resource 1. We ranked models using AIC to select the best-fit parameterization for each component (Akaike 1973) and reported estimates and standard errors are from the overall best-fit model only.

Results

Species detection and initial state distribution

Estimates of detection probability indicated that neither salamanders nor fishes were captured during a substantial proportion of trap nights, even when they were present (Fig. 2a, b). Moreover, the presence of either salamanders or fishes altered the probability that the other taxon was observed. We observed dissimilar patterns in detection as a response to fish presence between the two salamander phenotypes. Larvae were more easily detected in wetlands where fishes were present (Fig. 2a), whereas paedomorphs were less likely to be detected when they co-occurred with fishes (Fig. 2b).

The initial state distribution (i.e., the proportion of wetlands in each of the five states at the start of the study) for both larval and paedomorphic salamanders varied according to fish presence. Both phenotypes were less likely to occur in wetlands where fish were present at the start of the study.

Estimated transition probabilities

Our best fitting model was one where larval colonization and recruitment into the paedomorph population depended on the presence of fishes and the state of the wetland (i.e., whether the wetland was dry) the previous season. Additionally, larval colonization varied according to the 2-month Standardized Precipitation Index (Table 2; Fig. 2c). Wetlands that were occupied by fishes in the previous season were ‘colonized’ by either salamander phenotype with a probability <0.03 throughout the entire study period. Given previous presence of larvae is a necessary condition for the recruitment of paedomorphic adults, wetlands that were dry in the previous season were rarely occupied by paedomorphs (Table 3; Fig. 2d).

Larval persistence at a wetland was best explained by the 2-month Standardized Precipitation Index and whether fishes were present. Overall, persistence was lower in wetlands occupied by fishes and decreased from 2010 to 2011, presumably as a result of drought (Table 2; Fig. 2e). Paedomorph persistence was also influenced by fish

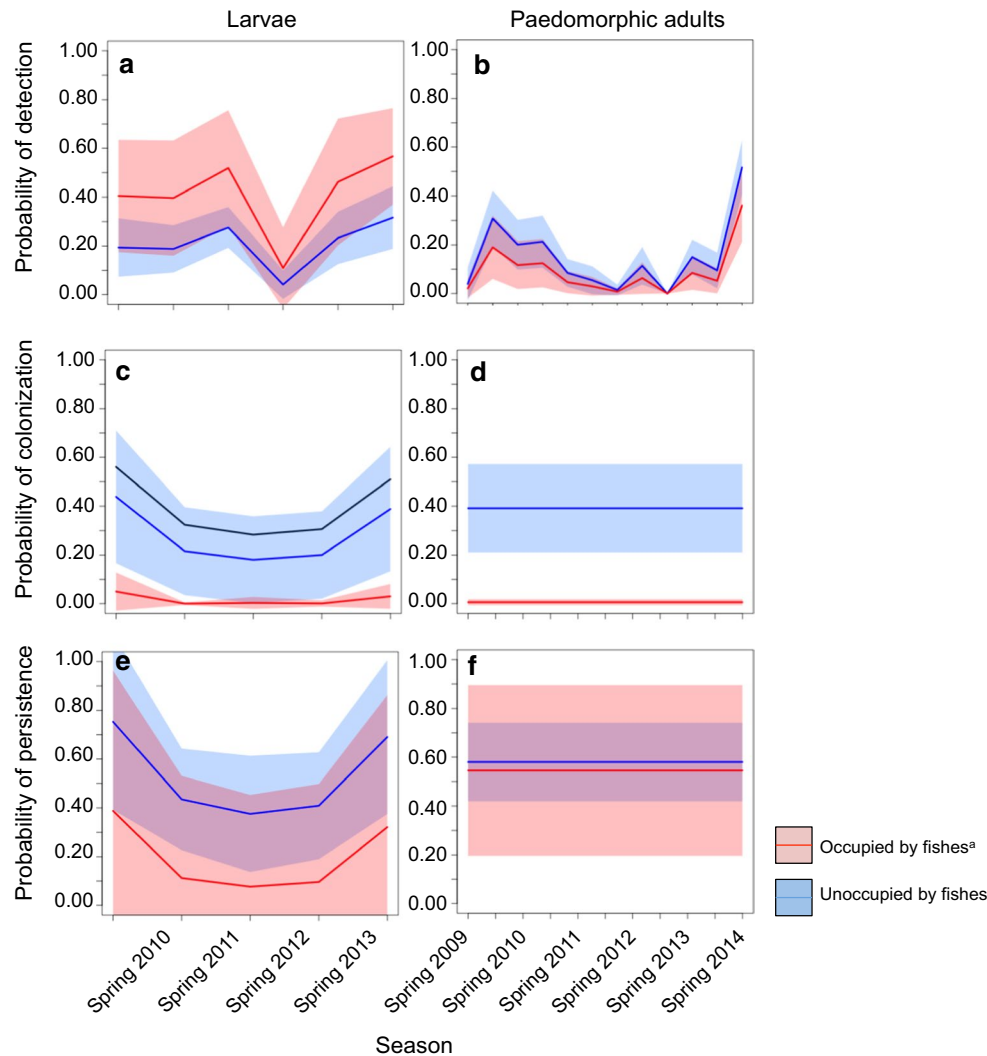


Fig. 2 Mean estimates of detection and occurrence dynamics of the mole salamander on the St. Marks National Wildlife Refuge 2009–2014 ($n = 35$) when wetlands are occupied (*dashed line*) or unoccupied (*solid line*) by fishes. Detection of the mole salamander was

influenced by conditions at time t ; colonization and persistence probabilities were influenced by conditions at time $t-1$. Bands represent 95% confidence intervals

presence, with the probability of this phenotype persisting in a wetland being slightly lower where fish were present (0.58 ± 0.08 vs. 0.55 ± 0.18) (Table 3; Fig. 2f).

Species occurrence

We estimated that overall occurrence of larval salamanders decreased from 0.39 in 2009 to 0.15 in 2014, with the greatest decline occurring between 2010 and 2011 (Fig. 3a). Co-occurrence of larvae with fishes also declined from 0.06 to 0.01 during 2010 to 2011, as a consequence of drought. Flooding events and the introduction of fishes to these isolated wetlands in 2012 and 2013 did not appear to heavily impact occurrence of larvae; the proportion of wetlands occupied by larvae remained relatively stable

following these flooding events and subsequent increases in fish occurrence (Table 4; Fig. 4a). Paedomorph occurrence also decreased from 0.42 in 2009 to 0.10 in 2014 (Fig. 3b). In contrast to larval occurrence, the proportion of wetlands occupied by paedomorphic adult mole salamanders declined more rapidly in response to increases in fish occurrence (Table 4; Fig. 4b). More information regarding the estimated occupancy of fishes detected throughout the study period can be found in Online Resource 2.

Discussion

Life history theory suggests that phenotypic plasticity in species such as the mole salamander is an adaptive response

Table 2 Estimated transition probabilities from the best-supported model for larval mole salamander occurrence

	Colonization		Persistence	
	Estimate ^a	SE ^a	Estimate	SE
Spring 2009–Spring 2010				
Dry ^b	–	–	NA	NA
No fish ^b	0.438	0.14	0.753	0.18
Fish ^b	0.050	0.04	0.388	0.29
Spring 2010–Spring 2011				
Dry	–	–	NA	NA
No fish	0.215	0.09	0.435	0.11
Fish	0.000	0.00	0.112	0.21
Spring 2011–Spring 2012				
Dry	–	–	NA	NA
No fish	0.180	0.09	0.375	0.12
Fish	0.004	0.01	0.077	0.19
Spring 2012–Spring 2013				
Dry	–	–	NA	NA
No fish	0.200	0.09	0.409	0.11
Fish	0.001	0.00	0.096	0.20
Spring 2013–Spring 2014				
Dry	–	–	NA	NA
No fish	0.388	0.13	0.691	0.16
Fish	0.030	0.03	0.321	0.27

^a Larvae were never observed in wetlands that were dry in the previous season. As such, parameter estimates for previously dry wetlands were unreliable and standard errors could not be estimated

^b State of the wetland in the previous year (i.e., wetland was dry, unoccupied by fish or occupied by fish)

Table 3 Estimated transition probabilities from the best-supported model for paedomorphic mole salamanders

	Colonization ^a		Persistence	
	Estimate ^b	SE ^b	Estimate	SE
Dry	–	–	NA	NA
No fish	0.609	0.09	0.580	0.08
Fish	0.006	0.01	0.545	0.18

^a Note that colonization, here, refers to the recruitment of larvae into the paedomorphic adult population

^b Paedomorphs were never observed in wetlands that were dry in the previous season. As such, parameter estimates for previously dry wetlands were unreliable and standard errors could not be estimated

to environmental stochasticity (Moran 1992; Whiteman 1994; Denoël et al. 2009). Thus, we predicted that, in the presence of predatory fishes and/or premature drying of wetlands because of drought, the occurrence of paedomorphic mole salamanders would decline as individuals metamorphosed to escape such environmental conditions. We also anticipated that, unless environmental conditions

were sufficiently extreme to preclude larval survival, occurrence of larvae would remain stable or even increase relative to populations of paedomorphic individuals because of paedomorphic populations transitioning to metamorphic ones (Walls et al. 2013a). In contrast to our predictions, both drought and the arrival of fishes negatively influenced the occurrence dynamics of both larval and paedomorphic mole salamanders, presumably through modifications to the frequency of paedomorphosis and through differential effects on the survival of the two stage classes. Consequently, mole salamander occurrence at SMNWR greatly decreased from 2009 to 2014, a period of time characterized by high environmental variability. Despite the phenotypic plasticity of mole salamanders, it did not confer resilience to environmental change under the conditions of our study.

Drought most noticeably reduced the persistence of larvae. The migration of adult salamanders to breeding wetlands requires specific environmental conditions, which were likely not met during severe drought conditions (Semlitsch 1985b; Whiteman 1994; Church et al. 2007; Semlitsch 2008; Rittenhouse et al. 2009). In addition, limited hydrologic inputs would shift mean hydroperiod, presumably making some long-duration wetlands unsuitable for successful larval development (Walls et al. 2013a). Larvae were also less likely to recruit into paedomorphic populations during this time. Drought could have impacted occurrence of paedomorphic adults by either (1) increasing the probability larvae metamorphosed in response to wetland drying, (2) increasing larval mortality, or (3) increasing mortality in the terrestrial environment and contributing to inhospitable conditions for terrestrial adult dispersal, thus resulting in reduced breeding effort and fewer larvae present in ponds to recruit into the paedomorphic population (Semlitsch and Wilbur 1988; Semlitsch et al. 1990; Denoël et al. 2009; Walls et al. 2013a). The persistence of paedomorphs did not vary in response to drought, which suggests either (1) paedomorphic adults were more likely to occupy permanent wetlands that were negligibly impacted by reduced precipitation, or (2) mean wetland hydroperiod, in general, was not affected by drought. If the latter, declines in the occurrence of larvae during this time were likely a result of insufficient cues to initiate adult migration to breeding sites (Semlitsch 1985b).

Our results also indicated that the presence of predatory fishes more severely impacted paedomorphic adult occurrence than did drought. This outcome could be a consequence of a reduced probability that larvae recruited into paedomorphic adult populations, rather than a reduced probability of paedomorph persistence once they are present. In fact, our results indicate that larvae never became paedomorphic adults if fishes were present. For many species of amphibians, the presence of aquatic predators may

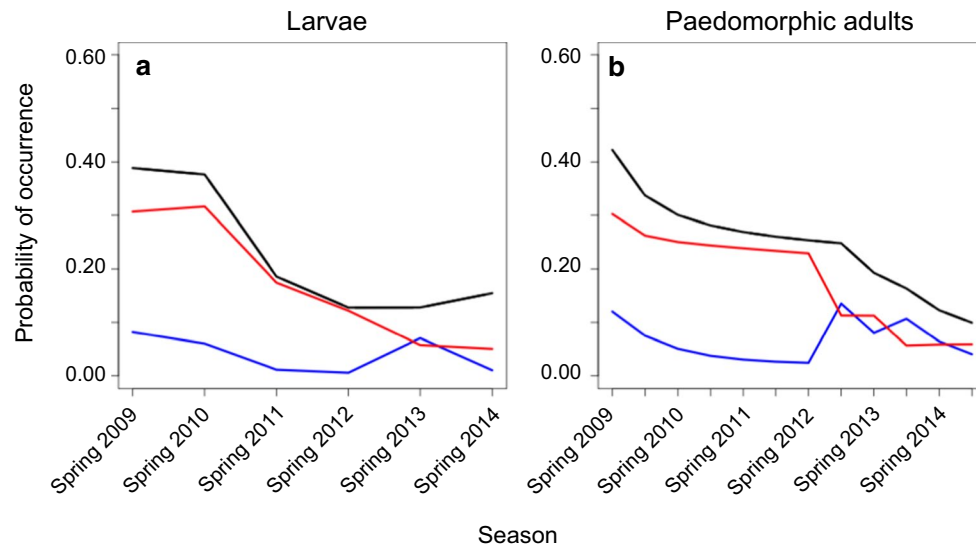


Fig. 3 Occupancy of **a** larval and **b** paedomorphic adult mole salamanders ($n = 35$). Total occurrence (solid black line) is the sum of (1) the probability a wetland was occupied only by the mole sala-

mander (dashed line) and (2) the probability a wetland is occupied by both the mole salamander and fishes (dotted line)

Table 4 Predicted species occurrence on St. Marks National Wildlife Refuge

	Fish ^a	Larvae ^b	Paedomorphic adults
Spring 2009	0.459	0.389	0.424
Fall 2009	0.469	–	0.336
Spring 2010	0.478	0.377	0.299
Fall 2010	0.487	–	0.280
Spring 2011	0.496	0.186	0.268
Fall 2011	0.504	–	0.260
Spring 2012	0.512	0.128	0.254
Fall 2012 ^c	0.755	–	0.249
Spring 2013	0.753	0.128	0.194
Fall 2013 ^c	0.870	–	0.165
Spring 2014	0.862	0.155	0.125
Fall 2014	0.854	–	0.105

^a The paedomorph database was used to calculate the presented estimates of fish occupancy; these estimates differed slightly between the datasets due to different model parameterizations (see Online Resource 2)

^b Larval occurrence was only estimated in spring seasons; it was assumed that metamorphosis occurred before fall sampling occasions

^c Flooding events occurred between the fall and spring seasons in 2012 and 2013

influence the timing of larval metamorphosis; increased levels of stress hormone in response to fishes could trigger metamorphosis, thereby decreasing the probability that individuals remain in a wetland as paedomorphic adults (Jackson and Semlitsch 1987; Ryan and Semlitsch 2003; White-man 1994; Denoël et al. 2009). In addition, fish presence

decreased larval persistence. Increased predation pressure either (1) decreased the probability that adult mole salamanders returned to breed in a wetland that was previously occupied by fishes or (2) decreased larval survival, thereby eliminating larvae from a portion of our sampled wetlands (Semlitsch 1987). Our results also suggest that fish presence did not influence paedomorph persistence; paedomorphic adults are larger in size than larvae and are therefore presumably less vulnerable to predation by fishes, some of which are naturally gape-limited predators (Caldwell et al. 1980; Semlitsch 1987; Jackson and Semlitsch 1993).

In addition to these differences in occurrence dynamics, our results also indicate differences in behavioral responses to predators. Larvae were more easily detected with aquatic traps in wetlands where they co-occurred with fishes (i.e., larval detection probabilities were lower in wetlands where fishes were not present than in wetlands where fishes were present). Paedomorphs, on the other hand, were more likely to be detected when fishes were not present. While behavioral adaptations, such as microhabitat selection, activity reduction or temporal restriction, and use of structurally complex habitats, are typical predator avoidance mechanisms, our results indicate that these adaptations differ based on phenotype (i.e., larvae vs. paedomorphic individuals) (Jackson and Semlitsch 1993; Babbitt et al. 2003; Miller et al. 2012). Larvae, in the presence of fishes, may be more likely to spend time closer to the wetland edge and are, given our trapping methods, therefore, more likely to be detected (Semlitsch 1987). Alternatively, larger larvae may be more active foragers to offset exploitative competition with fishes (Jackson and Semlitsch 1993).

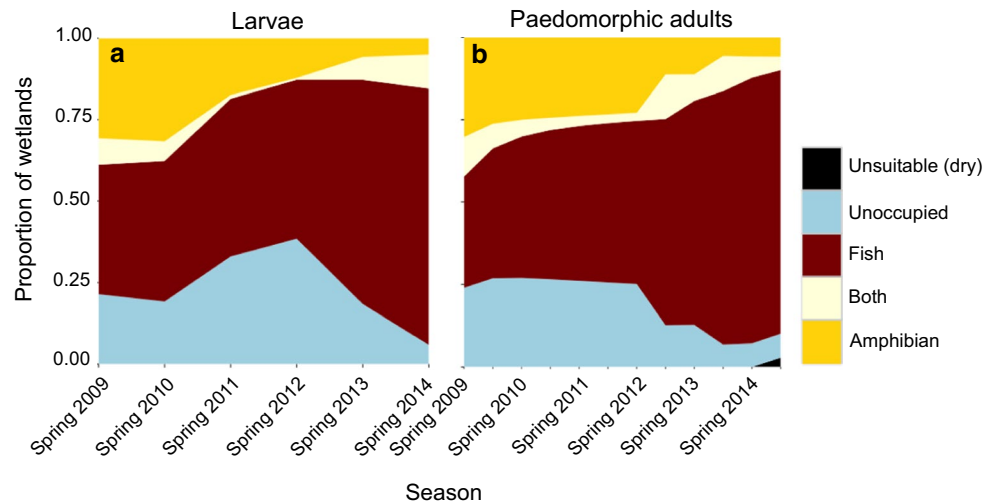


Fig. 4 Estimated proportion of wetlands in each of five possible states throughout the study period for **a** larval and **b** paedomorphic adult mole salamanders. A dramatic decrease in the proportion of wetlands occupied by larvae can be observed during 2010–2011,

corresponding to severe drought conditions that likely altered wetland hydrology and impacted adult migration to breeding sites. The proportion of wetlands occupied by paedomorphic adults, however, remained relatively stable during this time

Paedomorphic adults, on the other hand, may reduce overall activity when fishes are present or may be selecting microhabitats that were not well sampled using our methods. Changes in detectability could also suggest that paedomorphic adults persist in wetlands at much lower densities when fishes are present.

Our results indicate that this polyphenism proved insufficient to buffer mole salamander populations to observe short-term declines when environmental variation included multiple stressors (i.e., drought and introduction of predators). However, life-stage-specific responses suggest that such a plastic response still may be selected for in response to temporal variability. Our results suggest that both metamorphosis and paedomorphosis provide context-specific evolutionary advantages. Paedomorphs were much less affected by drought in the long-duration wetlands we monitored, as they were able to persist during periods of low water availability by avoiding harsh terrestrial conditions (i.e., desiccation risk and/or predators; Semlitsch 1987, 1988). However, in the presence of fishes, recruitment of new paedomorphs was essentially eliminated, reducing the viability of this strategy. In addition, during shifting environmental conditions, metamorphic individuals are more likely to disperse and colonize new wetlands, thereby contributing to species persistence across the landscape (Semlitsch and Wilbur 1988; Semlitsch et al. 1990). Colonization was especially important in our system, where high probabilities of local extinction necessitate frequent colonizations, rescue effects, and recolonizations to maintain the overall metapopulation persistence.

The simultaneous modeling of habitat and species annual dynamics can provide a robust framework for inferences

on how species will respond to environmental change or, more specific to wetland systems, changes in hydrologic dynamics. Using an integrated approach, we demonstrated that (1) we can use natural perturbations such as those that occurred on SMNWR to understand how species responses to changing conditions are shaped by their life histories, (2) we can detect life-stage specific differences in behavioral responses to predators, which can inform management or monitoring initiatives, and (3) it is important to account for changes through time in both habitat suitability and species interactions.

Our results suggest that, despite context-specific fitness advantages of both life history strategies, if increased environmental perturbations continue, mole salamanders may potentially be extirpated at SMNWR in the future. Changes in the frequency of disturbance events (i.e., drought and flooding) as a result of climate change could limit local and regional persistence of this species (Semlitsch and Gibbons 1985; Scott 1993; Denoël et al. 2009; Walls et al. 2013a; Anderson et al. 2015). In this system, drought and fish colonization have presumably impacted adult fitness by altering factors associated with larval growth (i.e., costs associated with competition and predation, as well as increased metabolic requirements to complete development on restricted time scales) and the propensity for paedomorphosis (Semlitsch et al. 1988; Semlitsch and Wilbur 1988). Environmental shifts could, in fact, favor a fixed response over a plastic one, thereby impacting persistence in variable environments over time (Semlitsch et al. 1990).

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Author contribution statement CLD and DAWM analyzed occurrence data and prepared the manuscript; SCW, WJB, and JWR designed the study and along with MEB led data collection in the field. All authors contributed input into the design and interpretation of the analysis and contributed to writing the final manuscript.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable institutional and/or national guidelines for the care and use of animals were followed.

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