Life history differences influence the impacts of drought on two pond-breeding salamanders

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Abstract. Drought is a strong density-independent environmental filter that contributes to population regulation and other ecological processes. Not all species respond similarly to drought, and the overall impacts can vary depending on life histories. Such differences can necessitate management strategies that incorporate information on individual species to maximize conservation success. We report the effects of a short-term drought on occupancy and reproductive success of two pond-breeding salamanders that differ in breeding phenology (fall vs. spring breeder) across an active military base landscape in Missouri, USA. We surveyed ~200 ponds for the presence of eggs, larvae, and metamorphs from 2011 to 2013. This period coincided with before, during, and after a severe drought that occurred in 2012. The two species showed contrasting responses to drought, where high reproductive failure (34% of ponds) was observed for the spring breeder during a single drought year. Alternatively, the fall breeder only showed a cumulative 8% failure over two years. The number of breeding ponds available for use in the fall decreased during the drought due to pond drying and/or a lack of re-filling. Estimates of occupancy probability declined for the fall-breeding salamander between 2012 and 2013, whereas occupancy probability estimates of the spring breeder increased post-drought. The presence of fish, hydroperiod, the amount of forest cover surrounding ponds, and canopy cover were all found to affect estimates of occupancy probabilities of each species. Pond clustering (distance to nearest pond and the number of ponds within close proximity), hydroperiod, forest cover, and canopy cover influenced both estimates of colonization and extinction probabilities. Our results show life history variation can be important in determining the relative susceptibility of a species to drought conditions, and that sympatric species experiencing the same environmental conditions can respond differently. Consideration of the spatial network and configuration of habitat patches that act as refuges under extreme environmental conditions will improve conservation efforts, such as the placement of permanent ponds for aquatic organisms. A better awareness of species-specific tolerances to environmental filters such as drought can lead to improved management recommendations to conserve and promote habitat for a greater diversity of species across landscapes of spatially connected populations.

Key words: Ambystoma annulatum; Ambystoma maculatum; amphibian; drought; hydroperiod; metapopulation; occupancy; phenology; pond.

INTRODUCTION

Environmental filters, or density-independent factors such as floods or droughts, may not influence all species equally within a given habitat, and their effects on population regulation may vary based on the timing of the event relative to the life history strategy or ontogeny of each species (Stark et al. 2004, Chase 2007). Consideration of species-specific responses to environmental thresholds is therefore critical to design effective management plans and perform mitigation actions. The use of a single surrogate species or functional grouping may not capture these fine-scale species differences, and limit the effectiveness of conservation strategies (Nicholson et al. 2013, Banks et al. 2014, Peterman et al. 2014). Furthermore, identifying key life history differences between closely related or functionally similar species that mediate population regulation would provide a framework for conservation actions that benefit multiple species (Stark et al. 2004, Banks et al. 2014).

Drought is a strong environmental constraint that negatively affects species that cannot adjust behaviorally or physiologically, which sometimes results in the elimination of populations or metapopulations that cannot tolerate persistent dry conditions (Engelbrecht et al. 2007, Bond et al. 2008, Debinski et al. 2013). A key determinant of the severity of these effects is the seasonal timing of drought in relation to ontogenetic

events of organisms, such as mating, reproduction, or critical periods of growth (Cavender-Bares and Bazzaz 2000, Willson et al. 2006, Miller-Rushing et al. 2010). Decreases in the viability of life stages that are highly susceptible to drought would likely result in altered population dynamics. Furthermore, in a community-level context, the relative effects of drought may vary between species that interact (i.e., competitors, predator–prey) due to drought conditions coinciding with critical ontogenetic stages in their respective life history strategies. These effects can then ultimately influence population dynamics, species interactions, and community assembly (Fotelli et al. 2001, Chase 2007, Debinski et al. 2013).
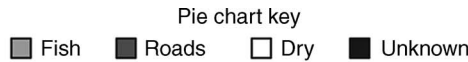
Organisms such as turtles (Gibbons et al. 1983), snakes (Willson et al. 2006), amphibians (Dodd 1993, Semlitsch et al. 1996, Werner et al. 2009, Walls et al. 2013a), and invertebrates (Jeffries 1994) that use lentic aquatic habitats or intermittent headwater streams are particularly susceptible to the detrimental effects of drought conditions due to the potential ephemerality of these ecosystems. Hydroperiod is well established as a critical abiotic factor that influences population and community dynamics of organisms inhabiting lentic waters (Schneider and Frost 1996, Wellborn et al. 1996, Chase 2007). The response of aquatic organisms to droughts and/or variable hydroperiod will differ based on their adaptability and life history strategy, as well as the intensity and timing of drought conditions. Increases in the frequency of drought-like conditions in some areas are expected to occur with climate change (predicted increases in temperature and stochastic precipitation), which will enhance the already severe negative consequences drought imposes on aquatic communities by further altering hydrological cycles (McMenamin et al. 2008, Brooks 2009). Therefore, our understanding of individual species' responses will be critical to mitigate the negative effects of increased drought due to climate change.

Pond-breeding amphibians are highly sensitive to drought conditions, as reproduction is dependent on pond habitats that fluctuate in hydroperiod in response to temperature and precipitation patterns (Walls et al. 2013a, Ryan et al. 2014). The most notable effect of drought on amphibians is catastrophic reproductive failure due to pond drying prior to completion of metamorphosis (Dodd 1993, Rowe and Dunson 1993, Semlitsch et al. 1996, Daszak et al. 2005). Drought conditions that alter hydroperiod regimes also influence breeding habitat availability, population growth rates, and amphibian occupancy (Scheele et al. 2012, Hossack et al. 2013, Walls et al. 2013b). In addition to affecting the survival of aquatic life stages, stochastic rainfall during droughts may alter breeding phenology, shifting breeding to earlier or later than usual (Todd et al. 2011, Walls et al. 2013a). Drought conditions can also affect permanent ponds by altering local physical condit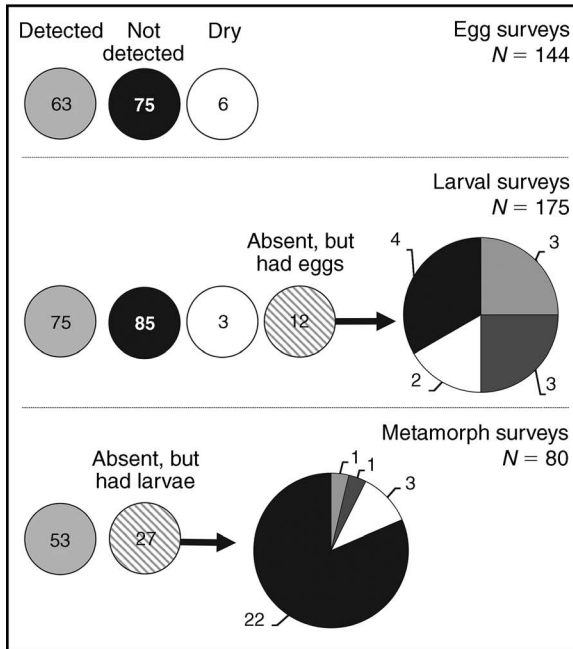ions such as reduced pond volume and depth that affect water temperature and/or increase densities of competitors and predators (Bond et al. 2008, Westervelt et al. 2013). Finally, drought may limit dispersal and/or colonization within spatially structured populations by increasing inter-pond distances as the landscape dries out, which similarly is expected to be exacerbated by climate change (Fortuna et al. 2006, Brooks 2009, Peterman et al. 2013).

To predict species-specific responses to drought, there must be a better understanding of the interaction between drought conditions and amphibian breeding phenology, which in turn can inform efforts to mitigate negative consequences such as reproductive failure. Early pond drying in the spring/summer and delayed inundation of pond basins in autumn are two predicted consequences of drought and/or climate change (Brooks 2009), and thus the time species breed is expected to influence their susceptibility to drought. A lack of recruitment to juvenile/adult stages may be the main consequence of drought for spring-breeding amphibians if individuals cannot metamorphose prior to pond drying (Semlitsch et al. 1996), or through mortality of terrestrial stages (especially juveniles) due to insufficient moisture in terrestrial habitats (Rothermel and Semlitsch 2006, Rittenhouse et al. 2009). Alternatively, amphibians that breed in the fall/winter may be more limited by the availability of breeding habitats when drought conditions persist beyond the summer months and ponds fail to fill (Werner et al. 2009). Additionally, adult migrations of fall-breeding species can be limited by the cumulative effect of low soil moisture (Westervelt et al. 2013). Complete reproductive failure due to pond drying is also a limiting factor in at least one fall-breeding salamander (Taylor et al. 2006). Thus, the timing and intensity of drought may variably affect amphibian species by influencing different points in ontogeny.
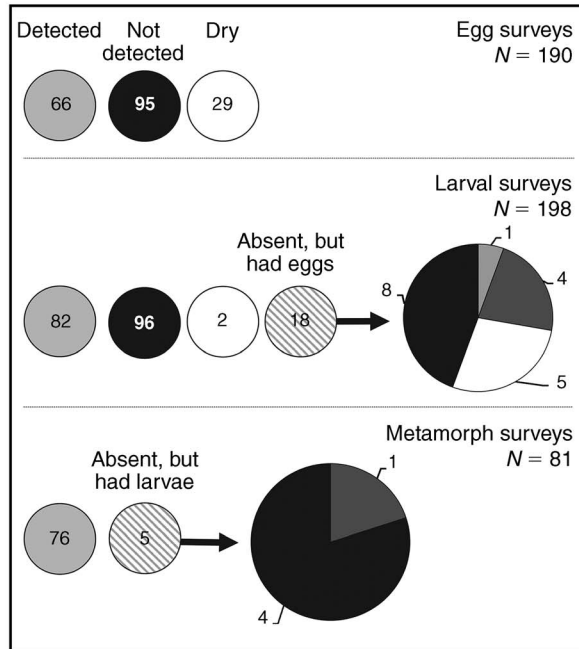
We conducted a comparative study of how drought conditions that lasted from spring to fall of 2012 affected the occupancy and survival of aquatic life stages (eggs, larvae, and metamorphs) of the fall-breeding ringed salamander (*Ambystoma annulatum*) and the spring-breeding spotted salamander (*A. maculatum*). We predicted that their difference in breeding phenology would influence the effects of drought. As the frequency of drought is predicted to increase across the range of *A. annulatum* (Strzepek et al. 2010), a species of conservation concern, developing a better understanding of how drought influences its population dynamics is critical to its management. To understand the level of recruitment failure (i.e., pond drying prior to metamorphosis), we examined whether the drought affected transitions between different life stages within a given year (eggs to larvae, larvae to metamorphs). We also examined whether different biotic and abiotic factors influenced initial occupancy patterns and transitions in occupancy (i.e., colonization and extinction) across the two years of the study. Given that spring-breeding species are often
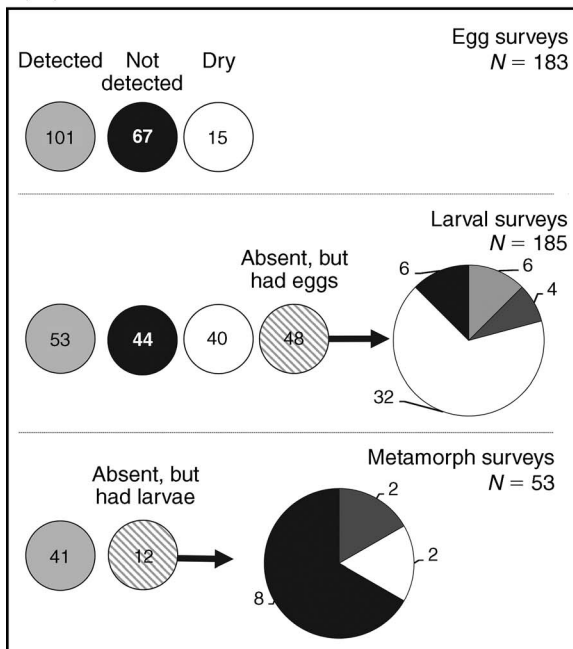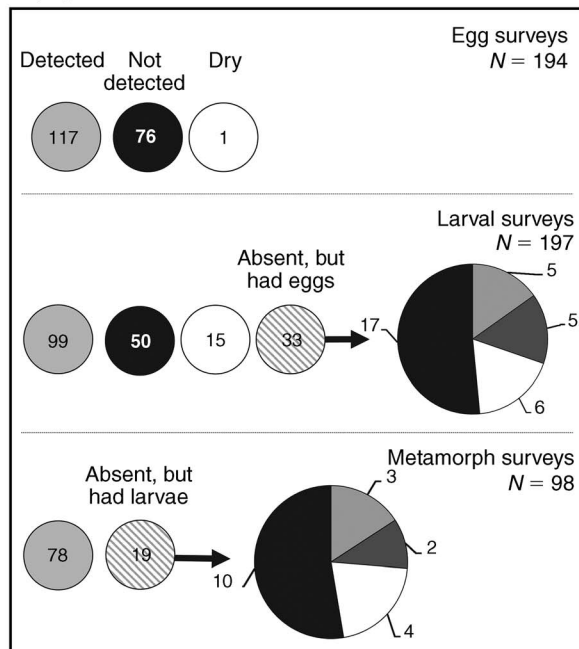
FIG. 1. Summary of surveys for eggs, larvae, and metamorphs of the (a, b) fall-breeding ringed salamander (*Ambystoma annulatum*) and the (c, d) spring-breeding spotted salamander (*A. maculatum*) in breeding ponds at Fort Leonard Wood, Missouri, USA. "*N*" is the total number of ponds sampled for each life stage. Gray circles indicate inundated ponds where that stage was detected, black circles represent ponds that held water but the stage was not detected, and open circles indicate dry ponds. Open circles with gray hash marks indicate ponds where the previous life stage was detected, but not current stage. Numbers within circles represent the number of ponds for each category. Pie charts represent the number of ponds (individual pieces of the pie) where either larvae or metamorphs were detected but not the previous life stage, and are color coded by possible explanatory factors. "Fish" indicates the presence of fish, "Roads" indicate ponds in active roadways, "Dry" indicates dry ponds, and

under selection to escape pond drying, we predicted reproductive failure to be higher for the spring-breeding *A. maculatum*. For both species, we predicted the spatial structure of ponds across the landscape to influence their likelihood of occupancy, with subsequent effects on colonization and extinction.

METHODS

Site description

We sampled breeding ponds at Fort Leonard Wood, Missouri, USA, an active military training facility in the Ozark Highlands. Fort Leonard Wood encompasses 24 686 ha that are primarily (~80%) forested. It has an extensive road system and hosts year-round military training. More than 500 constructed wildlife ponds and unintentional bodies of water (i.e., tire ruts and impact craters) occur at Fort Leonard Wood, and range in size from 1 m² to greater than 5 ha. For this study, we intensively sampled a subset of ponds ($n = 199$) in a 7140 ha area of the west–central portion of the base (hereafter, Focal Area).

Egg sampling

In October of 2011 and 2012, and March of 2012 and 2013, we searched ponds for egg masses of *A. annulatum* and *A. maculatum*, respectively (Fig. 1). The methods used to survey ponds also varied between sampling periods. In the fall 2011, two independent surveyors determined the presence/absence of *A. annulatum* eggs by visually searching ponds (see Fig. 1 for total numbers). Beginning in spring 2012 for *A. maculatum* egg surveys, randomized quadrat sampling (1 m²) was used to estimate egg density. The number of quadrats searched was scaled to pond surface area (one quadrat per 25 m²), and for each doubling of pond area, the number of quadrats increased by one (Shulse et al. 2010). A maximum of 20 quadrats were sampled at each pond. We searched quadrats both visually and by gently sifting through the water with an aquarium net when visibility was limited. Additional egg masses observed outside the quadrats were also tallied when observed. In the fall of 2012, during surveys for *A. annulatum* eggs, the sampling effort was doubled (i.e., two quadrats per 25 m²; Fig. 1). This sampling strategy was again used in the spring of 2013 to survey for eggs of *A. maculatum*. For *A. annulatum*, sampling occurred following rainfall events that would stimulate breeding migrations. We searched ponds on two separate days in both 2011 and 2012 (approximately two to three weeks apart within each year), as egg masses of this species deteriorate rapidly post-hatching. For *A. maculatum*, we visited ponds approximately two to three weeks after the primary pulse of breeding, and only once per pond as the structural integrity of this species' egg

masses allows them to be observed even after hatching occurs (Petranka 1998). We condensed our egg response metric into presence/absence for each pond–species–year combination, including non-quadrat observations, as our interest was in breeding attempts, but not effort.

Larval sampling

To determine larval occupancy, we sampled all known ponds within the Focal Area during the last third of the larval period for each species using repeated sampling to account for imperfect detection (Peterman et al. 2014). Each year, sampling occurred over five weeks in February–March for *A. annulatum* and three weeks in May/June for *A. maculatum* (Fig. 1). We surveyed ponds for three consecutive days with dip net sweeps (40 × 35 cm, 3.2-mm mesh size, sweeps 1 m in length) and funnel traps (3-mm mesh size; 6-mm openings; 38 × 26 × 26 cm; Memphis Net and Twine, Memphis, Tennessee, USA). The number of dip net sweeps and traps were scaled based on pond area (Shulse et al. 2010). We tabulated daily counts of salamander larvae using each method separately, and released larvae following each survey. Daily totals for each method were calculated separately to analyze whether sampling method influenced our ability to detect larvae (see *Analysis*). Some ponds were only surveyed using dip net sweeps due to low water depth or other logistical constraints. We also determined the presence/absence of fish (Centrarchidae, *Gambusia* spp., and *Pimephales promelas*) based on captures during these sampling periods. No ponds had fish that we visually observed but never caught by one of the two methods, and the trap openings were sufficient to capture large fish up to 25 cm in total length, indicating it was highly unlikely we missed detecting fish presence.

Metamorph sampling

In late April for *A. annulatum* and June for *A. maculatum* of each year, we determined how many ponds where larvae had been detected during the previous sampling round were still occupied by salamanders (Fig. 1). These two time periods corresponded approximately to when each species undergoes metamorphosis (Hocking et al. 2008, Semlitsch et al. 2014), and late-stage larvae are present, although a low percentage of actual metamorphosed salamanders were captured during this survey round for each species. We refer to this sampling as metamorph surveys to differentiate it from the larval sampling. The number of dip net sweeps was again scaled to pond area, as with the larval sampling. After the area-scaled sweeps, each pond was exhaustively surveyed with dip net sweeps until 20 late-stage larvae or metamorphs, or 60 person-minutes of effort were attained. We condensed data on

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"Unknown" were ponds that lacked obvious factor(s) influencing detection. The total number of ponds changed between life stage surveys due to discovery of new ponds and because eggs were difficult to detect in some pond conditions (i.e., murky water), resulting in the discrepancy between numbers within circles and the total number of ponds surveyed.

metamorphs to presence/absence data, as our interest was primarily in their presence as an indication of whether pond drying had occurred; the presence of metamorphs would indicate pond drying had not occurred.

Analysis

Our primary metric to test whether the drought influenced transitions between life stages (eggs to larvae, larvae to metamorphs) was whether ponds held water long enough to allow for metamorphosis to occur. We first calculated the number of ponds that held water and had eggs present, ponds which held water but with no eggs, and dry basins during each species' breeding season (fall for *A. annulatum* and spring for *A. maculatum*). From this, we then calculated the proportion of ponds where salamanders of that species were detected in the subsequent larval and metamorph sampling periods, the number of ponds that held water but were apparently unoccupied by salamander larvae, and the number of dry ponds (see total pond numbers in Fig. 1). We also determined the number of ponds where no eggs were detected, but that larvae/metamorphs were captured.

While our specific focus was on pond drying, we also tested three factors of management interest that could influence transitions from egg to larval and larval to metamorph stages, respectively: pond area, the presence of fish, and whether the pond was in an active roadway. Fish are a well-known factor that limit amphibian recruitment (Semlitsch 1987, Werner et al. 2009), and we had the expectation that eggs and larvae in ponds that were in the middle of roads would be susceptible to repeated vehicle disturbance. We used four subsets of data for this analysis: Ponds where we detected eggs and ponds where we detected larvae for each species in each year (Fig. 1). Within each subset, we tested for the presence/absence of the next life stage (i.e., presence of larvae given egg detection, and the presence of metamorphs given larval detection) with generalized linear models using a Bernoulli distribution. In an additional model, we also tested for effects of hydroperiod category (ephemeral, defined as dries multiple times a year; summer, defined as dries once a year in the summer; semi-permanent, defined as dries in extreme drought years; and permanent). Hydroperiod status was determined based on repeated visits to all ponds, and information from Fort Leonard Wood natural resources staff (K. Lohraff, *personal communication*). While a dry pond basin where we had previously detected eggs provides clear evidence of reproductive failure, testing hydroperiod category allowed us to determine if subsequent ontogenetic stages were more susceptible to a lack of detection in ponds with different hydroperiods. We also initially tested pond area, which, if significant, would indicate our ability to detect whether presence of salamanders varied among ponds of different sizes.

However, area was not a significant predictor of presence of either species in each year, suggesting our sampling adequately surveyed ponds of all sizes, and we dropped this covariate from our analysis.

Because the larval sampling was comprised of multiple sampling visits, we used the dynamic multi-season occupancy model of MacKenzie et al. (2003) in package *unmarked* in R (MacKenzie et al. 2002, Fiske and Chandler 2011, R Development Core Team 2014). This model allowed us to determine how occupancy dynamics of the larval stage changed across years due to drought (i.e., colonization and extinction). We did not fit all life stages (eggs–larvae–metamorphs) to these models as we had variable survey methods and effort across the two years for eggs and metamorphs. We tested identical models for the larval stage of both species and included the occupancy covariates of presence/absence of fish, percentage of canopy closure over the pond, pond area (maximum basin size), hydroperiod category, percent forest cover within 300 m of the site, the number of ponds within a 300 m radius of the site, and the distance to nearest pond (Peterman et al. 2014). Colonization and extinction covariates included hydroperiod category, percent forest cover within 300 m, the number of ponds within 300 m, the distance to the nearest pond, and pond area. In this context, colonization and extinction probabilities do not likely represent new colonization events and true extinctions, but rather changes in reproductive attempts across years (i.e., site use due to drought-induced mortality or skipping of breeding). Colonization/extinction also only examines transitions in occupancy across years rather than within a year. Detection covariates included water temperature (°C) taken during the survey, capture method (dip net or trap), and year. The multi-season model had two primary periods (the two years of the study), with sampling method per day as the secondary period (three days of dip nets and three days of traps; total $n = 6$ surveys for each species). We examined trends in occupancy between years using smoothed occupancy estimates, which estimates the number of occupied ponds in a given year (Weir et al. 2009). All continuous variables were centered and scaled prior to analysis to allow for a direct comparison of coefficients of each covariate as they were measured on different scales.

The drought was characterized using the Palmer Hydrological Drought Index (PHDI; Division 05, National Climatic Data Center Climate Indices, *available online*).[3] We compared the PHDI for each month of the study against the previous 50 years to place the current drought within a historical context. The difference in

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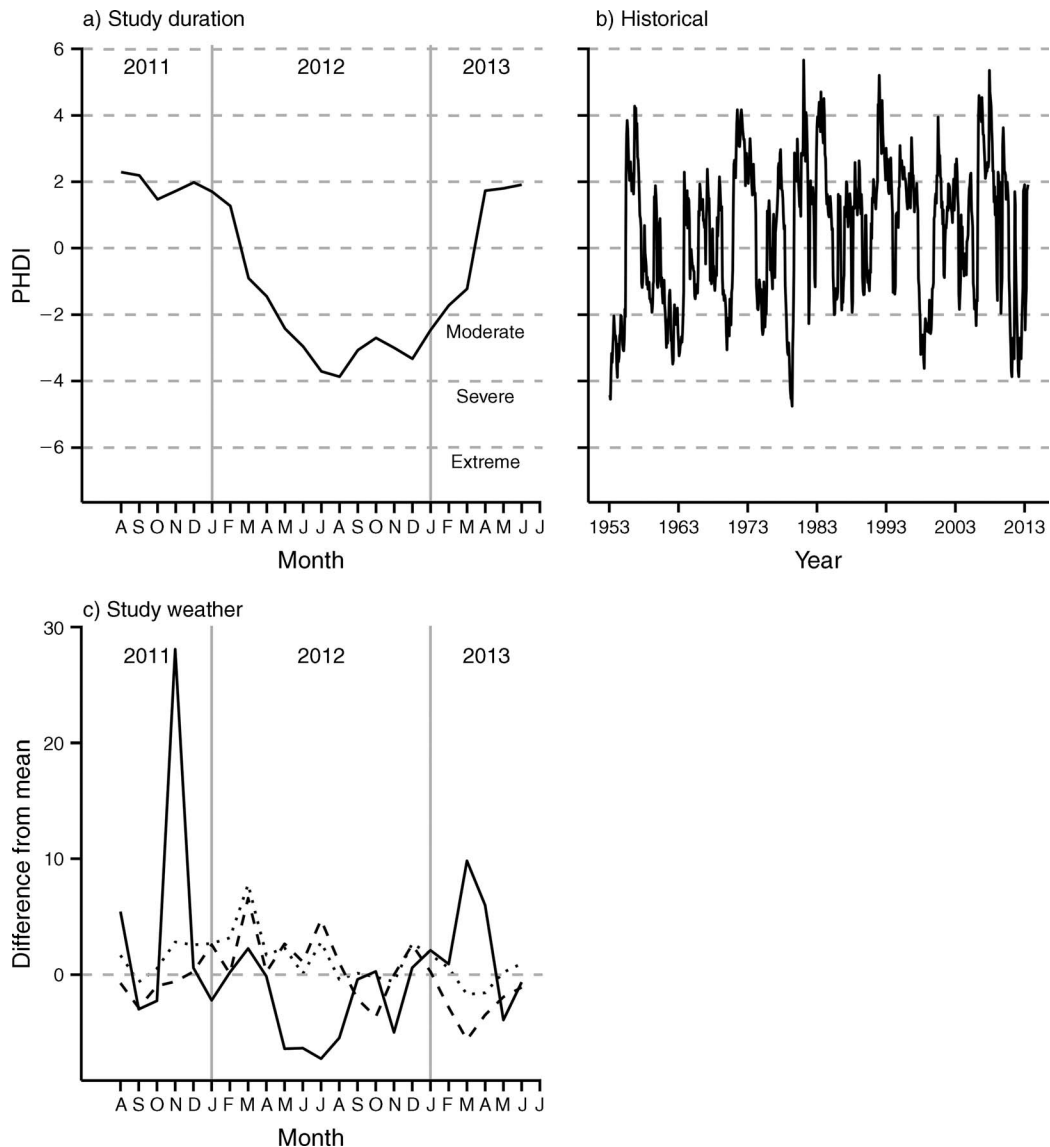[3] http://www1.ncdc.noaa.gov/pub/orders/CDODiv3152986715640.txt

FIG. 2.　Climate summary of the Palmer Hydrological Drought Index (PHDI) from the (a) duration of the study, (b) PHDI from the previous 50 years, and (c) departures from the historical mean value of monthly precipitation (solid line), maximum air temperature (dashed line), and minimum air temperature (dotted line) at Fort Leonard Wood, Missouri, USA, during the 24-month study period. In panel (c), the 70-year (1941–2011) monthly average in all three metrics is centered at zero, and each data line is departures from that mean. The units on the y-axis are in degrees C for temperature and centimeters for rainfall.

historical weather averages (maximum and minimum daily temperature and monthly rainfall from 1941 to 2011) were also compared against the observed data from the duration of the study. Historical data were obtained from the High Plains Regional Climate Center (*available online*)[4] station in Waynesville, Missouri, ~10 km north of the study area. Contemporary local weather data during the study were gathered from a NOAA weather station 6 km east of the Focal Area.

[4] http://www.hprcc.unl.edu/

RESULTS

Drought

The PHDI showed Fort Leonard Wood experienced a moderate to severe drought from March 2012 through January 2013 (Fig. 2a). The mean (±SD) PHDI value over this period was −2. 72 ± −0.9, where below −2.0 indicates a moderate drought, below −4.0 a severe drought, and below −6.0 an extreme drought. A drought of moderate magnitude occurs approximately every 20 years at this location (Fig. 2b). The PHDI of the remaining months throughout the study were all mid-

TABLE 1. Summary of ponds that were surveyed during egg, larval, and metamorphs sampling for the fall-breeding ringed (*Ambystoma annulatum*) and spring-breeding spotted salamander (*A. maculatum*) at Fort Leonard Wood, Missouri, USA.

Species, year, and life stage	Number surveyed	Number occupied	Dry ponds during survey	Occupied but dried
Ambystoma annulatum				
2011				
Egg	144	63	6	2
2012				
Larvae	175	75	3	3
Metamorph	80	53	3	0
Egg	190	66	29	6
2013				
Larvae	198	82	2	0
Metamorph	81	76	0	0
A. maculatum				
2012				
Egg	183	101	15	32
Larvae	185	53	72	2
Metamorph	53	41	0	0
2013				
Egg	194	117	1	6
Larvae	197	99	21	4
Metamorph	98	78	4	0

Notes: "Number occupied" indicates the number of ponds where that life stage was detected. "Occupied but dried" indicates ponds that were occupied by that stage, but experienced drying prior to the next survey round, indicative of reproductive failure.

range values, meaning neither exceptionally moist nor dry (mean ± SD = 1.26 ± 1.3; Fig. 2). The mean value of precipitation was at or below the historical monthly average from March through November 2012, and the max/min temperatures were also above average during approximately the same time period (Fig. 2c).

Ambystoma annulatum

In the fall of 2011, we recorded the presence of egg masses of *A. annulatum* in 44% of ponds surveyed (Table 1, Fig. 1a). Four percent of the ponds were dry in the fall of 2011, and no ponds dried between the two egg survey periods. The following spring, larvae of *A. annulatum* were captured at 43% of ponds surveyed, and at 81% of the ponds that had eggs the previous fall. Of the ponds that had *A. annulatum* eggs but did not yield any larval captures, 25% contained fish, 25% were in active roadways, and 17% had reproductive failure due to drying or freezing because of small shallow basins (Fig. 1). However, only the presence of fish was statistically significant for predicting larval presence given that we had found eggs ($\chi^2 = 6.46$, df = 1, $P = 0.01$; Fig. 3a.). Metamorphs of *A. annulatum* were captured at 71% of the ponds where larvae had been detected. Of the remaining ponds that had larvae but no metamorph captures, 4% were in roadways, 11% had dried, and 4% had fish. Hydroperiod category was the only significant factor that influenced whether we found metamorphs based on the presence of larvae ($\chi^2 = 16.31$, df = 3, $P < 0.001$), where metamorphs were less likely to be found in

ephemeral ponds (Fig. 3b). Overall reproductive failure from pond drying across the multiple surveys was 6% in 2011–2012.

In fall 2012, 15% of the ponds were dry when surveyed, and eggs of *A. annulatum* were found at 35% of the sites (Table 1, Fig. 1b). No ponds where eggs had been detected were dry when surveyed the following spring. However, hydroperiod monitoring using temperature dataloggers (Anderson et al., *in press*) indicated that 8% of the ponds where eggs had been detected had dried during the winter, likely due to the drought that extended through January 2013 (Fig. 2). Larvae were detected in 41% of ponds that were sampled in spring 2013, and in 74% of the ponds that had eggs the previous fall (Fig. 1b). Larvae were captured in five ponds that were dry the previous fall, indicating breeding occurred after our last survey on 28 October at these locations. Of the ponds that contained eggs in fall 2012 but did not produce any larval captures, 28% had dried, 22% were in roadways, and 6% had fish (Fig. 3c), but no factors were statistically significant. In general, ephemeral ponds were less likely to contain larvae where we previously detected eggs (Fig. 3c). Metamorph sampling resulted in captures of *A. annulatum* at 94% of ponds surveyed, and no ponds had dried since the larval sampling (Fig. 3d). No covariates significantly explained the few ponds where we did not capture metamorphs. Overall reproductive failure due to drying for this species was 7% in 2012–2013.
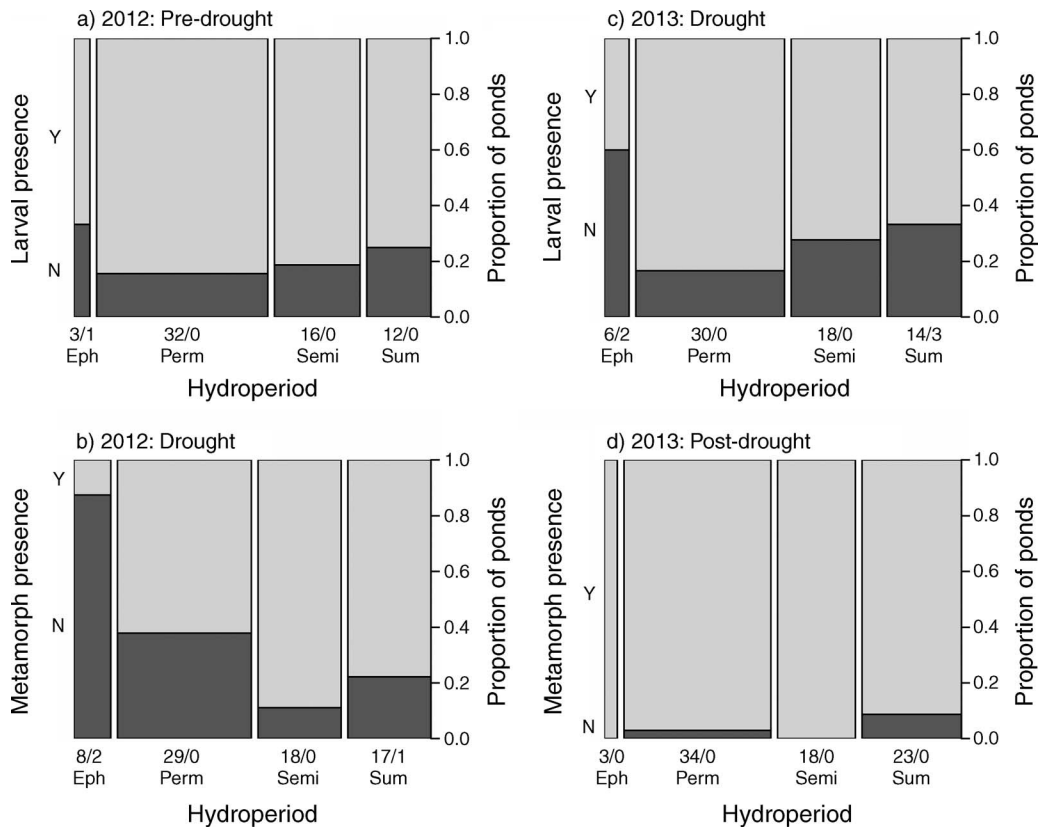
FIG. 3. (a, c) Presence ("Y") and absence ("N") of larvae where eggs had previously been detected, and (b, d) presence/absence of metamorphs where larvae had previously been detected of the fall-breeding ringed salamander (*Ambystoma annulatum*) in 2012–2013. The dark gray bars indicate unoccupied ponds and light gray occupied ponds, and the width of the bars is indicative of the sample size. The right *y*-axis indicates the proportion of ponds within the "Y" and "N" categories. Hydroperiod categories include ephemeral ("Eph"), summer ("Sum"), semi-permanent ("Semi"), and permanent ("Perm") ponds. The numbers underneath each bar show the total sample size and the number of ponds that were dry that contributed to the "N" category (total/dry).

Ambystoma maculatum

In March 2012, 8% of the ponds were dry at the time they were surveyed for eggs, and 55% of ponds were observed to have egg masses of *A. maculatum* (Table 1, Fig. 1c). Larvae of *A. maculatum* were detected in 29% of ponds surveyed in May 2012. Of the remaining ponds where larvae were not detected, 39% were dry. Larvae were captured in only 53% of ponds where eggs had been observed that spring. Of the ponds where eggs were observed but no larvae were caught, 13% contained fish ($\chi^2 = 13.81$, df = 1, $P = 0.05$) and 8% were in active roadways (not significant; Fig. 1c). Thirty-two percent of ponds had dried between the egg and larval surveys, and both the ephemeral and summer hydroperiod categories were less likely to contain larvae ($\chi^2 = 28.08$, df = 3, $P = 0.05$; Fig. 4a). Of the ponds that had larvae, 77% still contained larvae/metamorphs of *A. maculatum* when visited in June for metamorph sampling. The remaining ponds that did not result in any metamorph captures but had larvae previously were in active roadways (14%) or dried in the intervening time

and refilled (14%; Fig. 4b). Overall, pond drying resulted in 34% recruitment failure of ponds in 2012.

In April 2013, eggs of *A. maculatum* were found in 60% of ponds surveyed; only one pond was dry when it was visited (Table 1, Fig. 1d). Larval *A. maculatum* were captured in 50% of ponds surveyed in May–June of 2013, and in 72% of the ponds that had eggs. Of the ponds that had eggs but no larvae were captured in them, 18% were dry, 15% were in roadways, and 15% contained fish (no factors statistically significant; Figs. 1d and 4c). In late June, metamorphs were captured in 80% of ponds that larvae had been detected in previously. Of the ponds that had larvae and no metamorphs, 16% contained fish ($\chi^2 = 3.01$, df = 1, $P = 0.08$), 11% were in active roadways (not significant), and 21% had dried ($\chi^2 = 9.38$, df = 3, $P = 0.02$; Figs. 1d and 4d). Overall, reproductive failure due to drying occurred in 8% of ponds in 2013 for *A. maculatum*.

Larval occupancy

Given our sampling strategy, the probability of detecting larval *A. annulatum* and *A. maculatum* at least once was extremely high (>99%), indicating that larvae
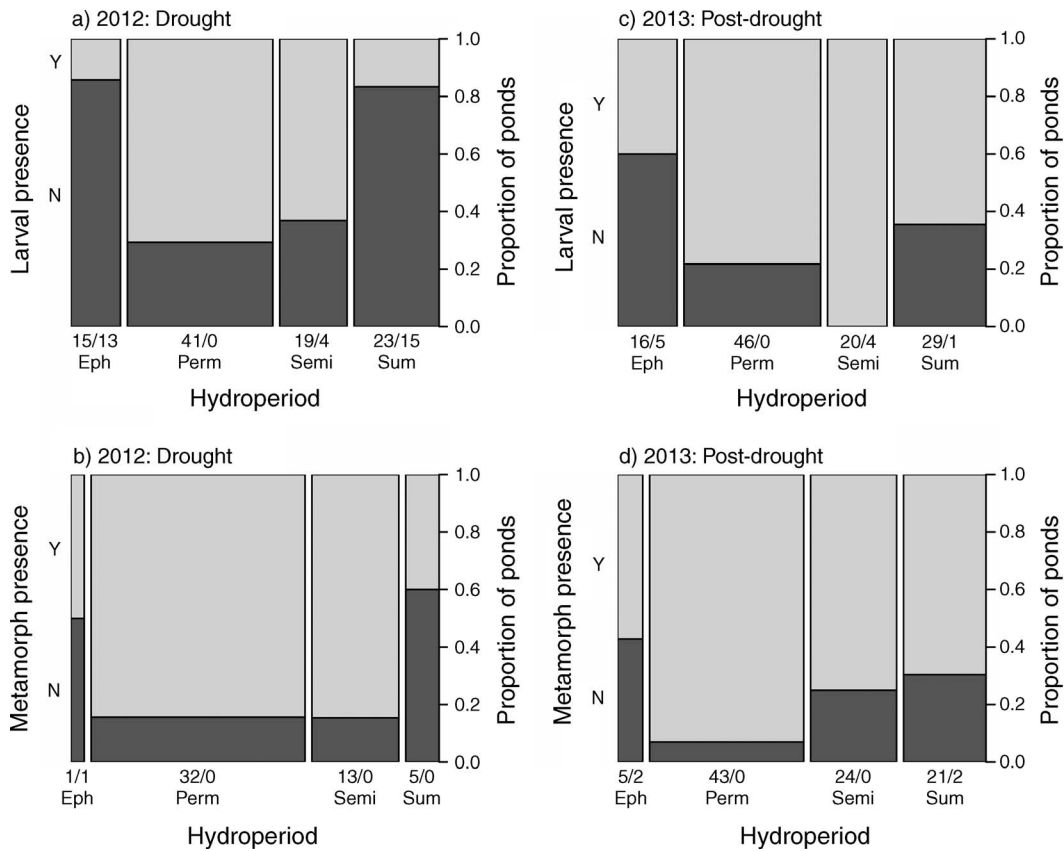
Fig. 4. (a, c)Presence ("Y") and absence ("N") of larvae where eggs had previously been detected, and (b, d) metamorphs where larvae had previously been detected of the spring-breeding spotted salamander (*Ambystoma maculatum*) in 2012–2013. The dark gray bars indicate occupied ponds and light gray unoccupied ponds, and the width of the bars is indicative of the sample size. The right *y*-axis indicates the proportion of ponds within the "Y" and "N" categories. The numbers underneath each bar represent the total sample size and the number of ponds that were dry that contributed to the "N" category (total/dry).

were unlikely to have been missed in ponds when they were present, and an observation of no larval captures indicated an unoccupied site or an event occurred that eliminated larvae. Water temperature affected detection in *A. annulatum*, where detection significantly increased at higher water temperatures (Fig. 5). No factors affected detection for *A. maculatum*.

Larval occupancy showed contrasting relationships across years for both species; smoothed occupancy estimates decreased for the fall-breeding *A. annulatum* ($\psi = 0.44$ to 0.35) between 2012 and 2013, and increased for the spring-breeding *A. maculatum* ($\psi = 0.33$ to 0.54) over the same time span. The significant factors affecting occupancy, colonization, and extinction also varied between species (Table 2).

For the fall-breeding *A. annulatum*, fish presence negatively affected larval occupancy (Fig. 5, Table 2). Occupancy was positively associated with increasing amounts of forest surrounding ponds. Hydroperiod also affected occupancy probability, which was higher in more permanent ponds (Fig. 5, Table 2). Colonization probability decreased as canopy cover, the number of ponds within 300 m and the distance to the nearest pond

increased (Fig. 5). Extinction probability decreased as the distance to the nearest pond increased. Permanent ponds had the lowest probability of extinction, and ephemeral ponds the highest probability of extinction (Fig. 5, Table 2).

For the spring-breeding *A. maculatum*, the presence of fish also negatively affected occupancy (Fig. 6, Table 2). Greater canopy closure and a greater amount of forest within 300 m both increased occupancy probability (Fig. 6). The percentage of forest within 300 m was positively related to colonization probability (Fig. 6, Table 2). No factors affected detection or extinction probability for *A. maculatum*.

DISCUSSION

Drought has strong negative consequences on aquatic community structure (Wellborn et al. 1996, Lake 2003, Bond et al. 2008). These impacts are exacerbated when drought conditions coincide with critical ontogenetic stages, imposing severe constraints such as reduced survival of immature or adult stages (Shoop 1974, Cavender-Bares and Bazzaz 2000). Our study indicates that the synchrony of drought with susceptible ontoge-
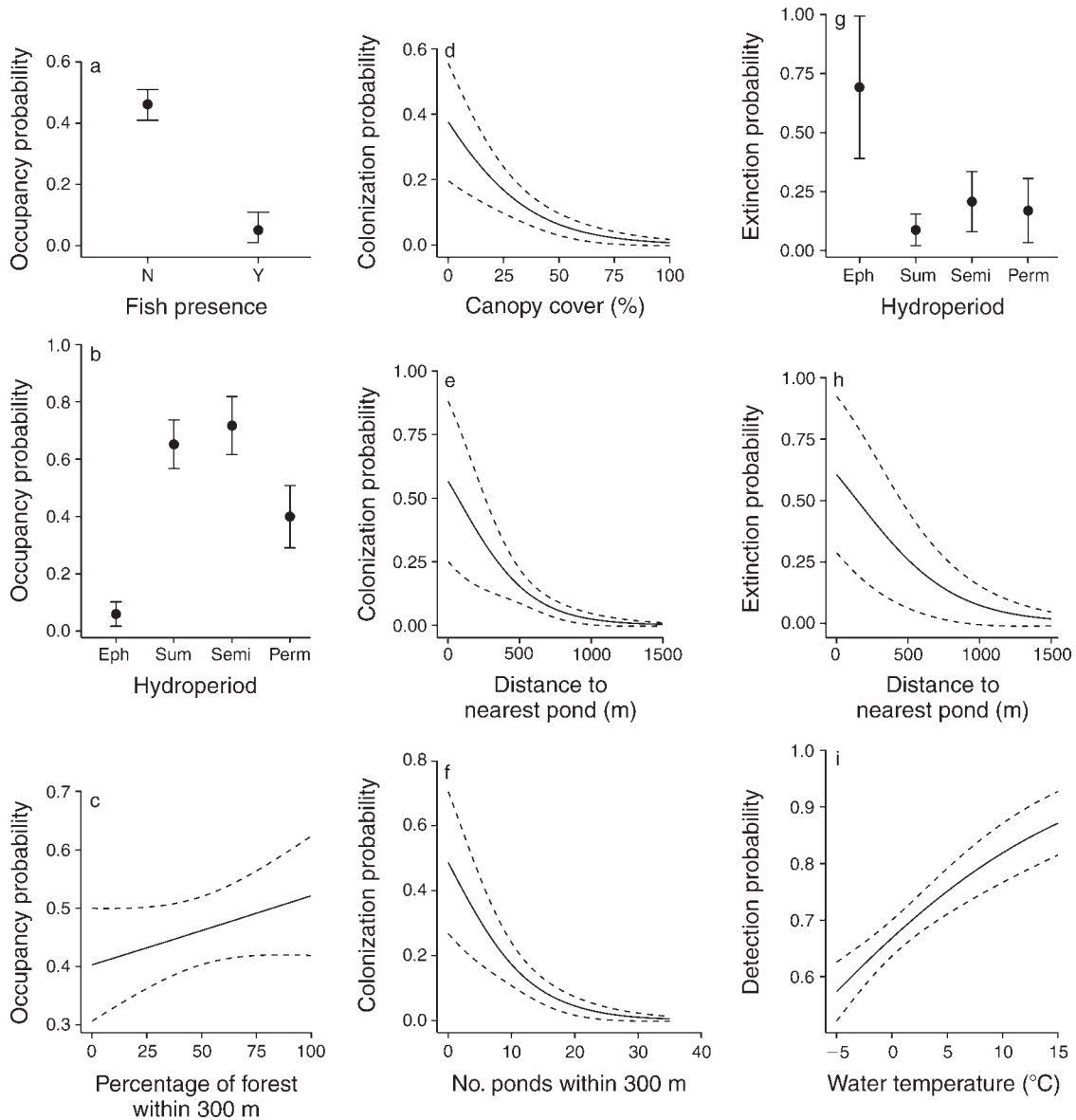
FIG. 5. Predicted relationships of significant covariates on occupancy, colonization, extinction, and detection probability of ringed salamanders (*Ambystoma annulatum*). Solid lines or points indicate model predictions, and the dashed lines and error bars indicate standard error estimates.

netic stages can impart differential effects on co-occurring species within a landscape, and that the relative magnitude of these effects can depend on factors such as life history strategy. While the long-term population consequences of the drought cannot be directly evaluated for the two salamanders based on two years, this study highlights that different implications should be expected for species that vary in history strategy (e.g., breeding phenology). Long-term changes in population structure may result if drought frequency increases, as is expected with climate change (Brooks 2009, Todd et al. 2011). Our study also highlights that variable management strategies may be warranted to

increase regional population viability that capture species-specific variation in life history parameters and in their responses to stressful environments (Stark et al. 2004, Willson et al. 2006).

Ambystoma annulatum

Reproductive failure was relatively rare in the fall-breeding *A. annulatum*, at least in terms of the number of reproductive failures due to pond drying (6% of ponds with eggs in this species vs. 17% of ponds for *A. maculatum* over two years). Pond drying during the larval period of *A. annulatum* is less likely to occur because of reduced evapotranspiration over the winter

TABLE 2. Significant parameter estimates for occupancy, colonization, extinction, and detection for the fall-breeding ringed salamander (*A. annulatum*) and the spring-breeding spotted (*A. maculatum*) salamander.

State variable and covariate	Estimate	SE	Lower	Upper
Ambystoma annulatum				
Occupancy				
Intercept	−2.78	0.75	−4.24	−1.27
Fish presence	−3.05	1.15	−5.28	−0.79
%Forest	0.68	0.26	0.17	1.17
Permanent H$_2$O	3.41	0.88	1.64	5.13
Semi-perm H$_2$O	3.72	0.92	1.87	5.51
Summer H$_2$O	2.44	0.77	0.84	3.87
Colonization				
Intercept	−3.71	1.36	−6.38	−0.96
Nearest pond	−2.81	1.25	−5.27	−0.33
Canopy	−1.75	0.68	−3.08	−0.42
Ponds within 300 m	−3.70	1.75	−7.20	−0.12
Extinction				
Intercept	0.81	1.42	−1.97	3.59
Nearest pond	−1.42	0.71	−2.82	−0.03
Permanent H$_2$O	−3.16	1.36	−5.83	−0.48
Detection				
Intercept	1.09	0.22	0.67	1.51
Temp	0.41	0.19	0.16	0.88
Ambystoma maculatum				
Occupancy				
Intercept	−3.24	1.79	−6.95	0.25
Fish presence	−2.93	1.10	−6.85	−1.19
Canopy	1.01	0.38	0.23	1.73
%Forest	1.43	0.48	0.48	2.35
Colonization				
Intercept	−1.21	0.75	−2.65	0.32
%Forest	0.60	0.25	0.10	1.07
Extinction				
Intercept	−5.97	6.77	−19.23	7.29
Detection				
Intercept	1.26	0.31	0.65	1.86

Notes: "Fish presence" is presence/absence of fish, "Canopy" is percent canopy closure over a pond, "%Forest" is the percentage of forest within 300 m of a pond, "Nearest pond" is the distance (m) to the nearest pond in the Focal Area, "Temp" is water temperature (°C). For hydroperiod ("Permanent H$_2$O" or "Semi-perm H$_2$O"), "ephemeral" ponds were the reference level. Parameter estimates are on the logit scale. Upper and Lower are the 95% confidence interval.

months in temperate climates compared to spring and summer months. However, compared to a non-drought year, we found that the number of ponds that were dry in the fall during the onset of breeding was higher following a summer of drought (in 2011, 4%; in 2012, 15% of surveyed ponds). Larval occupancy of *A. annulatum* also decreased the year following drought conditions, which indicates either delayed effects of the drought or was a byproduct of the fewer available ponds to breed in the previous fall. Taylor et al. (2006) reported reproductive failure in the fall-breeding marbled salamander (*A. opacum*) in 6 of 22 years at a single pond in South Carolina. Westervelt et al. (2013) and Palis et al. (2006) also reported that declining popula-

tions of the fall-breeding flatwoods salamander (*A. cingulatum*) in the southeastern United States were linked to climate patterns (increasing drought conditions). Fall-breeding species also contend with overwintering in ponds, potentially experiencing pond freezing or anoxic conditions under the ice. Urban (2007) reported reproductive failure for *A. opacum* due to pond freezing at several locations in Connecticut. Pond freezing may be especially problematic in drought years when water levels are low.

The absence of fish, increasingly permanent hydroperiod, and the amount of forest within 300 m of a pond all increased occupancy of *A. annulatum*, which matches patterns of larval abundance with these covariates (Peterman et al. 2014). Because larval *A. annulatum* overwinter in ponds, they require longer hydroperiods to complete their life cycle, thus explaining their increased occupancy in permanent ponds and higher probability of extinction in ephemeral ponds. We also found that as the number of ponds within 300 m and the distance to the nearest pond increased, colonization probability decreased. Occupancy was also reduced in 2013 compared to 2012 for *A. annulatum*, and the distance to the nearest pond and hydroperiod both influenced the probability of extinction. Based on this evidence, we hypothesize that *A. annulatum* may switch breeding ponds in response to drought when there is another pond within close proximity that has a more permanent hydroperiod or is otherwise more suitable. As the distance between ponds increased, access to alternative sites decreased and the only option was to breed in the same location. However, when ponds were clustered, the probability of any one pond being occupied and/or colonized decreased due to a dilution of pond habitats for breeding. Pond habitat quality, such as lower canopy cover (increased occupancy), and hydroperiod length (permanent ponds have higher occupancy, ephemeral ponds have increased extinction) could be the mechanism that would explain these patterns of occupancy and/or colonization. While most ambystomatids show high levels of philopatry to their natal pond (Gamble et al. 2007), the degree to which philopatry occurs in landscapes of highly clustered ponds is not known, though great crested newts (*Triturus vulgaris*) showed high levels of movement between tightly grouped ponds (Griffiths et al. 2010). Whether adult ambystomatids sample potential breeding sites needs further investigation to support our hypotheses.

Ambystoma maculatum

The spring-breeding *A. maculatum* suffered high regional reproductive failure during the drought period in 2012 (34% of ponds dried prior to metamorphosis), and higher mortality than *A. annulatum* due to pond drying even in a non-drought year. Despite the drought persisting through January 2013, we saw an increase in the number of sites containing eggs and predicted larval occupancy in spring 2013 for *A. maculatum*. From this
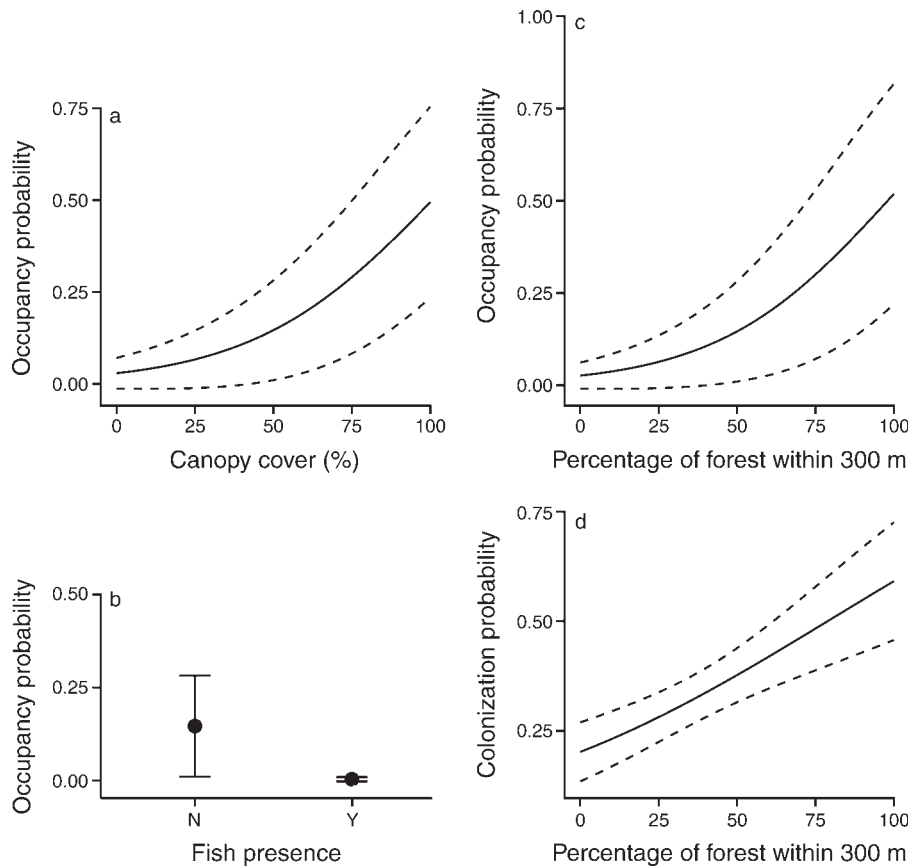
FIG. 6. Predicted relationships of significant covariates on occupancy and colonization probability of spotted salamanders (*Ambystoma maculatum*). Solid lines indicate model predictions, and the dashed lines indicate standard error estimates.

result, we suggest that adult persistence was high during the drought conditions, and breeding was not hindered the following year. Gaps in age structure at individual ponds may become apparent in future years, however, if the drought killed juvenile salamanders or affected actual reproductive effort (clutch size). Changes in regional population structure because of the lack of juvenile recruitment from the ponds that dried is a consequence that has been observed in other amphibians (Werner et al. 2009).

Colonization probability increased from 2012 to 2013 for *A. maculatum* when ponds were surrounded by a greater amount of forested habitat, indicating that adults were more likely to return to breed in ponds with more forest surrounding them. This response does not represent true colonization (i.e., ponds were previously unoccupied by *A. maculatum*). Rather, as the percentage of forest increased, larvae were more likely to be present in 2013 in ponds where they were absent in 2012, indicating adults were more likely to have laid eggs in these areas relative to areas with less forest. The mechanisms that affected occupancy of *A. maculatum* were similar to those previously identified in an assessment of larval abundance (Peterman et al. 2014), where increasing forest cover, canopy closure,

and the lack of fish all increased their likelihood of occurrence. As colonization and occupancy were both tied to forest attributes, ponds surrounded by forest likely represent high-quality habitat for adults (Harper et al. 2008), as well as increased likelihood of sustaining terrestrial populations of *A. maculatum* through drought conditions.

Other aquatic organisms

While the focus of our study was on two pond-breeding salamanders, the results can be applied to pond communities in general, including both vertebrates and invertebrates. Once the drought cycle began in March 2012, the potential number of breeding sites was reduced by nearly half for all amphibians and pond invertebrates that breed after approximately 15 May. Complete reproductive failure likely occurred in all other uni-voltine organisms as well, at least for those that have longer larval stages (i.e., Aeshnidae dragonflies and Ranidae anurans) and for species that cannot aestivate. Multivoltine species may recolonize ponds if they are re-inundated by water, a potential strategy to limit annual reproductive failure in stochastic aquatic environments. None of the ponds that dried had contained fish, which can promote colonization by amphibians and other

aquatic organisms after refilling (Wellborn et al. 1996, Petranka and Holbrook 2006, Werner et al. 2009). Species-specific responses to drought are also prevalent in other pond-associated organisms, such as water snakes, suggesting that management of both the pond attributes and the surrounding habitat matrix is necessary (Willson et al. 2006). Placement of ponds with varying hydroperiod regimes across a landscape such that permanent ponds are within known dispersal distances of aquatic organisms may permit re-colonization during drought years, and promote long-term persistence while maintaining regional diversity (i.e., species that need shorter hydroperiods; Semlitsch 2000).

Conservation implications and recommendations

In the short term, the spatial network of ponds at this location appears robust to severe temporary drought conditions, with the larger, fishless, permanent ponds acting as refuges (i.e., source habitat) for amphibians (Fortuna et al. 2006). Despite 34% reproductive failure due to pond drying alone in 2012, 53% of the ponds that *A. maculatum* bred in still had the potential to contribute individuals to the regional terrestrial population. Post-drought, ponds able to contribute to the terrestrial population increased to 67%, lending support for the hypothesis that short-term losses in reproduction can be tolerated by long-lived species such as ambystomatid salamanders (Taylor et al. 2006), and terrestrial stages act as a reservoir to regulate population growth rates (Vonesh and De la Cruz 2002, Harper et al. 2008). However, increased frequency of early drying or reduced refilling rates of ponds, both of which are expected with climate change for this specific region and many other areas (Brooks 2009, Strzepek et al. 2010), could limit both local and regional persistence of amphibians, increase inter-pond distances, and reduce the potential for re-colonization (Fortuna et al. 2006, Palis et al. 2006, Scheele et al. 2012, Peterman et al. 2013). The majority of ponds that dried during the drought were relatively small in area and were the consequence of human disturbance (i.e., impact craters from military activities, tire ruts), indicating the presence of permanent ponds on a landscape may be necessary for refuge or source populations. As many of the small ponds were re-colonized by *A. maculatum* in 2013, they likely represent high-risk/high-reward breeding habitats for this species. Failure occurs in most years when these habitats dry, but when water levels are replenished, predators are reduced from the drying and recruitment can occur (Wellborn et al. 1996, Werner et al. 2009). These ponds may connect metapopulations during boom years, and allow for re-colonization and the exchange of new genetic material (Peterman et al. 2013, 2015). What constitutes marginal habitat (e.g., road ditches, pot-holes) for amphibian breeding should be reconsidered based on our findings; monitoring of these sites may advance our understanding of the habitats animals use within fragmented or managed landscapes. Importantly,

whether organisms are successful at such sites under varying environmental conditions (e.g., drought vs. wet years) is important to differentiate from breeding attempts. While our study area may have a high density of breeding sites due to military activities and active pond construction, it is likely similar to other managed landscapes such as national forests or wildlife preserves that pursue similar management approaches (i.e., constructed wildlife ponds, tire ruts or skid trails used to build ponds, or tire ruts in unused roads; Cromer et al. 2002).

Variation in response to drought conditions between ecologically similar species (i.e., shared niche space) occur in many taxonomic groups, such as trees, stream organisms, and butterflies (Lake 2003, Engelbrecht et al. 2007, Debinski et al. 2013). As climate change increases drought frequency (Brooks 2009), adaptability of species will be important for local and regional persistence. When examined in isolation, a single pond that dries results in complete reproductive failure for aquatic organisms that cannot disperse or complete their life cycle (Semlitsch et al. 1996). At a regional scale, the consequences of losing individual habitat patches, given a mosaic of hydroperiod regimes, can influence aquatic diversity across small landscapes (Chase 2007, Werner et al. 2009). Multi-species studies examining the long-term effects of drought on population dynamics across large spatial scales are limited (Gould et al. 2012), especially for spatially structured populations or when drought occurs for periods longer than adult life spans (Scheele et al. 2012). Thus, continued long-term monitoring of all known populations in a landscape is needed to disentangle the many spatial and temporal factors influencing amphibian population dynamics (Pechmann et al. 1991, Blaustein et al. 2010). For species pairs that interact but vary in their susceptibility to these environmental constraints, such as larval *A. annulatum* and *A. maculatum* (Anderson and Semlitsch 2014), community-level monitoring will be essential to understand changes in species interactions as a result of their differential responses to environmental conditions.

Determining the environmental thresholds under which population crashes occur and whether rebounding from such crashes is possible are important conservation goals for many organisms, especially for endemic species or those of conservation concern such as *A. annulatum* or *A. cingulatum* (Westervelt et al. 2013). To improve habitat availability and successful reproduction of fall-breeding species such as *A. annulatum*, we suggest the creation and maintenance of long-hydroperiod ponds without predatory fish, which can act as refuges during periods of unsuitable conditions (i.e., drought). Sustaining a regional heterogeneity of pond hydroperiods (ephemeral to permanent) within clustered groups of ponds is also key to safeguard against continued regional reproductive failure in drought years, and to promote species with different life history strategies (e.g., breeding phenology; Semlitsch 2000). Hydroperiod

and clustering have been found to promote positive population growth rates, higher larval abundances, and re-colonization (Hossack et al. 2013, Peterman et al. 2013, 2014, Walls et al. 2013b, Ryan et al. 2014). Monitoring strategies should also target multiple species with different phenology patterns and across different ontogenetic stages to reveal the relative susceptibilities of each life stage to environmental constraints (Banks et al. 2014). Understanding and incorporating variability between species within management plans will ultimately advance and refine our ability to manage populations that face critical threats such as habitat loss or climate change, and improve our knowledge of when using surrogate species may be ineffective at conserving similar co-occurring species (Banks et al. 2014).

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