Environmental Drivers of Surface Activity in a Population of the Eastern Red-backed Salamander (*Plethodon cinereus*)

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Abstract.—Understanding the influence of spatiotemporal variation in environmental factors on phenology is crucial for determining the effects of climate change on amphibian populations. Here we quantify the relative influence of temperature and precipitation on surface activity of a terrestrial salamander, the Eastern Red-Backed Salamander (*Plethodon cinereus*) in Richmond, Virginia, USA. Specifically, we used spatial capture-recapture methods to test the influence of different metrics for temperature and precipitation on baseline detection probability. We found that soil temperature, particularly at 30 cm below the surface, is a better predictor of detection than air temperature or cumulative precipitation; however, greater cumulative precipitation resulted in a higher detection probability. We also show that a quadratic effect was favored in all scenarios suggesting this species has an optimal soil temperature and cumulative precipitation for surface activity during a particular year. The highest detection probability was associated with 12.6° C at 30-cm below the surface and 0.75 cm of cumulative precipitation during the 2-d period prior to the survey occasion. In addition to contributing knowledge on the specific environmental metrics that best predict surface activity for *P. cinereus*, this work illustrates the importance of incorporating soil temperature measurements in capture-mark-recapture studies of terrestrial salamanders. For projects with limited resources, our work indicates which fine-scale environmental measurements associated with terrestrial salamander activity in the southern portion of the range are best.

Key Words.—amphibians; baseline detection; cover boards; spatial capture-recapture; soil temperature; terrestrial salamander

INTRODUCTION

Climate change affects amphibian phenology through fluctuations in temperature and precipitation (Blaustein and Kiesecker 2002; Sheridan et al. 2017). Increased temperatures can be associated with shifts in reproductive timing, such as positive associations between warmer temperature and breeding time (Beebee 1995; Blaustein et al. 2001; Ficetola and Maiorano 2016). These changes in reproductive phenology may also alter predator-prey dynamics or competitive interactions and niche overlap (Boone et al. 2002; Todd et al. 2010). In some areas, climate change may also cause decrease precipitation, which can reduce seasonal surface activity and foraging opportunities for amphibians (Feder 1983). Decreased precipitation could have detrimental demographic consequences by reducing survival (Grafe et al. 2004) and breeding success (Banks et al. 1994). We lack an understanding of how spatiotemporal variation in both temperature and precipitation can predict phenological changes, however. Most studies make generalizations about the environmental influences on phenology based on average measurements at the surface (e.g., mean air temperature, mean precipitation), but the extensive use of subterranean habitat and complex life cycles of many amphibian species highlight the need to use quantitative approaches that account for the relevant speciesspecific cues across spatial and temporal gradients. This is especially important for terrestrial amphibians exhibiting high levels of philopatry that use behavioral adjustments to remain under appropriate environmental conditions (Muñoz et al. 2016a).

To advance our knowledge of the environmental drivers of amphibian population dynamics and phenology, recent studies have applied spatial capture-recapture methods to study *Plethodon cinereus*, the Eastern Red-backed Salamander (Muñoz et al. 2016a, b; Sutherland et al. 2016; Hernández-Pacheco et al. 2019). This species is a lungless terrestrial salamander that is

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noted for its sensitivity to environmental conditions and is widely distributed across eastern North America in temperate forests with high moisture levels and cool climates (Petranka 1998; Welsh and Droege 2001). During the more extreme temperatures of winter and summer, individual P. cinereus retreat underground where they decrease metabolism to conserve energy and avoid freezing or desiccation (Nagel 1977; Leclaire et al. 2008). Despite this well-established phenology, a study by Sutherland et al. (2016) failed to detect a relationship between detection probability at the surface and air temperature. In contrast, Muñoz et al. (2016b) used a multi-day average of air temperature and precipitation as covariate proxies for soil conditions, finding evidence that these two environmental factors can influence P. cinereus surface activity. Given the life history and behavior of P. cinereus, and the often limited environmental data available, it is not surprising to find contradictory results on the effects of environmental factors shaping surface activity in the wild. We suggest that air temperature may not be an appropriate cue for P. cinereus and that soil temperature and cumulative precipitation may be better predictors for modeling surface activity in this species.

With this study, we evaluated the relative influence of air temperature versus soil temperature and cumulative precipitation on surface activity patterns. We made use of spatial capture-recapture models to estimate the effects of these environmental parameters on baseline detection probability across depth and temporal gradients. Our models accounted for individual variability in detection, an important consideration when dealing with species that have cryptic and territorial behavior (Bailey et al. 2004; Mazerolle et. al 2007). We hypothesized that there would be an optimal depth-specific soil temperature and time-specific cumulative precipitation associated with the highest levels of salamander activity, which would define the conditions where individuals were more detectable. Thus, we predicted a non-linear relationship between salamander surface detection and environmental factors. Identifying these metrics contributes to maximizing monitoring efforts and increasing our knowledge on the spatiotemporal variation in environmental factors that influence surface activity for terrestrial salamanders.

MATERIALS AND METHODS

Study area.—We conducted our study in the James River Park System, Richmond, Virginia, USA (37°31'27N, 77°28'29W, elevation 45 m). The park was quarried for rocks in the early 1900s and is now characterized as Secondary Mixed Hardwood Deciduous Forest. The area is used primarily for recreation, but also contains established natural areas

dedicated to the conservation of native plants and animals. In addition to *P. cinereus*, amphibian species known to occur in this area include the American Toad (*Anaxyrus americanus*), Fowler's Toad (*A. fowleri*), Northern cricket frog (*Acris crepitans*), American Bullfrog (*Lithobates catesbeianus*), Southern Leopard Frog (*L. sphenocephalus*), and the Spotted Salamander (*Ambystoma maculatum*; Pullen et al. 2010).

collection.—In November Data 2015. we established an artificial cover board array at the study site following standard methods previously described (Hernández-Pacheco et al. 2019). In short, we removed natural cover objects (e.g., fallen trees, rocks) from a 10×5 m plot (approximately 85% canopy cover) and placed 50 cover boards $(30.5 \times 30.5 \times 2.1 \text{ cm})$ on the surface spaced 1 m apart in a rectangular grid. This design provided standard artificial habitat as the only cover objects where salamanders could seek refuge from surface exposure within the plot. We surveyed the cover board array six times between Fall 2016 (28 September, 19 October, 5 December) and Spring 2017 (1 February, 1 March, 29 March). Surveys entailed lifting individual cover boards, collecting all P. cinereus under the board, and transporting collected salamanders to nearby University of Richmond. At the laboratory, we identified and measured individuals. We gave new captures unique color identifications by injecting visible implantable elastomers (Northwest Marine Technologies, Inc., Shaw Island, Washington, USA) at up to four ventral locations on the abdomen adjacent to each limb, a method found to be safe and reliable for individual identification in amphibians, including this species specifically (Bailey 2004; Grant 2008). After marking, we released salamanders (within 24-48 h) under the same board from which they were collected. To minimize disturbance and ensure independence in capture rates, we separated surveys by at least three weeks (Marsh and Goicochea 2003; Hesed 2012).

We collected temperature using in-situ temperature data loggers and precipitation data from a weather station 12 km from the study area. Air temperature was collected hourly using an iButton (Model DS1921G-F5#, Maxim Integrated, California, San Jose, USA) located 2 m above ground at the center of the cover board array. We collected soil temperature data using a vertical arrangement of six iButtons separated 10 cm apart within a 1 m long, 1.9 cm diameter polyvinyl chloride (PVC) pipe inserted into the ground at the center of the cover board array (Appendix I). Thus, soil temperature readings were recorded at depths of 0 cm, 10 cm, 20 cm, 30 cm, 40 cm, 50 cm with a portion of the pipe above ground for finding and retrieving the data loggers. The iButtons recorded temperature every 4 h. Due to iButton failure at the greater depths, we focus our

analyses on air temperature and 10 cm, 20 cm, and 30 cm soil temperatures, i.e., the depths for which we had complete data spanning all six occasions. We acquired precipitation data through the Richmond International Airport database (about 12 km from study site), which records the amount of rainfall on an hourly basis (https://www.ncdc.noaa.gov/cdo-web/datasets/LCD/stations/WBAN:13740/detail). For our analysis, precipitation values recorded as trace or snow were set to zero.

Data analysis.—Our capture-mark-recapture protocol generated spatial encounter histories for all detected individuals. We analyzed these data using spatial capture-recapture (SCR) methods that allowed us to estimate the parameters of a spatial detection function and population density (Royle et al. 2013). Specifically, the spatial encounter model used describes the detectability, p[x,s], of an individual as a function of the distance between trap locations (x) and the individual's activity center (s):

$$y_{ijk} | s_i \sim \text{Bernoulli}(p[x_j, s_i])$$
$$p[x_j, s_i] = p_0 \times exp\left(\frac{d(x_j, s_i)^2}{2\sigma^2}\right)$$

where y_{ijk} indicates whether an individual *i* was detected under board *j* in occasion *k*, *s_i* is the estimated activity centers of individual *i*, *x_j* is the location of trap *j*, *p₀* is the baseline detection probability, or the probability of detecting an individual at its activity center, and *d*(*x*,*s*) is the Euclidean distance between trap *j* and activity center *s_i*. The parameter σ is the spatial scale parameter that characterizes the decline in detectability with distance from an activity center. To account for seasonal variation in detectability, which we attribute to variation in surface activity, *p₀* was modeled using standard logit-linear models, as a function of temporally varying covariates:

$$logit(p_{0k}) = \alpha_0 + \alpha_1 \times X_k$$

where X_k is a covariate that can vary across occasions (*k*, e.g., temperature), and α_0 and α_1 are the intercept and slope describing the relationship between detectability and the covariate of interest. For *P. cinereus*, quadratic effects of Julian day (a proxy for temperature), or air temperature directly, have successfully been used to characterize surface activity, and in particular to identify maximum activity periods (Sutherland et al. 2016; Muñoz et al. 2016b; Hernández-Pacheco et al. 2019).

We employed the simplest density model, which assumes that activity centers are uniformly distributed within a prescribed area of interest, or state-space S. The state-space S represents an area sufficiently large to contain the activity center of all individuals exposed

to capture. In our case, *S* was defined as a 4 m buffer around a convex hull of the coverboard array. As is standard for maximum likelihood SCR methods, this area is represented as a uniform grid of points, each of which represents the center point of equally sized pixels, which in this case were 0.5×0.5 m (total area = 189.25 m²). We selected the 4 m buffer based on a previous study of the same population where a sensitivity analysis was conducted (Hernández-Pacheco et al. 2019). The inference objective is to estimate the per-pixel (or point) density, and therefore the total density in the state-space *S* (Sutherland et al. 2016).

Our main interest was to expand the understanding of drivers of surface activity by fitting two sets of competing models representing alternative hypotheses. The first set was used to investigate which temperature measure best explains variation in detectability. These models included a linear and quadratic effect of daily mean temperature (24 h prior survey date) for all soil depths and air temperature and a linear and quadratic effect Day of Survey as covariates on detectability. We defined Day of Survey as a Julian day. A second set of models was used to investigate which precipitation measure best explains variation in detectability and included a linear and quadratic effect for 1-d, 2-d, and 3-d cumulative precipitation (24, 48, and 72 h prior to survey date, respectively) as covariates on detectability. Because time, temperature, and precipitation are highly correlated, we did not consider models in which both effects were present (Sutherland et al. 2016). All covariates were scaled to have a mean of 0 and a 1-unit standard deviation (i.e., z-score standardization). Considering all combinations of these potential effects on surface activity resulted in 11 models for temperature and seven for precipitation. Based on previous analyses that found increases in capture probability for P. cinereus after initial capture (i.e., a positive behavioral response), we included estimation of a behavioral response parameter allowing capture probability to change after an initial capture (Hernández-Pacheco et al. 2019). We analyzed these models in R (R Development) using the package oSCR (Sutherland et al. 2019) and compared models using Akaike's Information Criterion (AIC; Arnold 2010).

RESULTS

We captured 362 individual *P. cinereus* over the six sampling periods (one capture, 28 September 2016; 64 captures, 19 October 2016; 84 captures, 5 December 2016; 28 captures, 1 February 2017; 93 captures, 1 March 2017; 84 captures, 29 March 2017). Of these, we captured 130 individuals more than once. For a given occasion, the maximum number of individuals we captured under one board was six. Mean soil temperature



FIGURE 1. Mean soil and air temperature during the 24 h prior to occasion date of salamander sampling in Richmond, Virginia, USA. Error bars represent ± standard error.

at the 10 cm depth across occasions ranged from 5.2° C to 20.0° C (mean \pm standard error = 12.8° \pm 0.85° C; Fig. 1). Mean soil temperature at the 20 cm depth across occasions ranged from 5.6° C and 20° C ($12.6^{\circ} \pm 0.80^{\circ}$ C), while mean soil temperature at the 30 cm depth exhibited the least variation across occasions ranging between 6.3° and 20.0° C ($12.6^{\circ} \pm 0.76^{\circ}$ C). Mean air temperature across occasions ranged from 5.3° C to 20.5° C (14.4° ± 0.55°C; Fig. 1). In the warmer months during surveys (occasions 1, 2, 5 and 6 in September, October, and March), soil temperature decreased with depth, and was lower than air temperature. During the cooler winter months (occasions 3 and 4 in December and February), soil temperature was either warmer or varied similarly to air temperature. Cumulative precipitation showed an accumulation of up to 1.4 cm across occasions 1 d prior to survey date and up to 1.8 cm for 2 and 3 d prior to survey date (Fig. 2). Rainfall occurred throughout the sampling period and occasion 1 (September) exhibited the most cumulative precipitation prior to the survey date among other months.

Temperature and surface activity.—We found support for temperature-specific differences in salamander baseline detection probability, where the model with soil temperature at 30 cm of depth best explained the observed variation in detection (cumulative model weight = 0.91; Table 1). We found support for a quadratic effect of temperature, where the highest detectability was estimated at 12.6° C; p_0 = 0.065 ± 0.013 (Fig. 3A). Our model predicted an increase in detection after initial capture (positive behavioral response: $\beta_{p(b)} = 2.18 \pm 0.277$; Table 2). This is likely related to the patterns of seasonal emergence from underground, such that once an individual emerges at the surface and is encountered under a cover board, it is more likely to be subsequently detected. In addition,

TABLE 1. Variability in baseline detection (p_0) of the Red-backed Salamander (*Plethodon cinereus*) as a function of temperature (at air temperature level and soil depths of 10 cm, 20 cm, and 30 cm) and cumulative precipitation (at 24, 48, and 72 h prior to each survey day). The ~1 notation represents null or an interceptonly model with no covariate effect. Subscripts for cumulative precipitation represent hours and the subscript for temperature represent depth (cm). The superscript 2 represents the quadratic effect. Acronyms are LogL = log likelihood, K = number of model parameters, AIC = Akaike's Information Criterion, and Ω = model weights.

Detection (p_0)	logL	K	AIC	ΔΑΙϹ	Ω
Temperature					
$\mathrm{temp}_{30} + \mathrm{temp}_{30}{}^2$	785	6	1583	0	0.91
$\mathrm{temp}_{20} + \mathrm{temp}_{20}{}^2$	788	6	1587	4.6	0.09
$\mathrm{temp}_{10} + \mathrm{temp}_{10}{}^2$	792	6	1597	13.8	0.00
$day + day^2$	834	6	1680	97.1	0.00
day	838	5	1687	103.9	0.00
$temp_{air} + temp_{air}^2$	839	6	1690	107.4	0.00
temp ₃₀	843	5	1697	114.1	0.00
temp ₂₀	844	5	1699	115.9	0.00
temp ₁₀	846	5	1701	118.7	0.00
~1	849	4	1705	122.2	0.00
temp _{air}	848	5	1705	122.6	0.00
Cumulative precipitation					
$\text{precip}_{48} + \text{precip}_{48}^2$	804	6	1621	0	1.00
$\operatorname{precip}_{72} + \operatorname{precip}_{72}^2$	827	6	1665	45	0.00
$\operatorname{precip}_{24} + \operatorname{precip}_{24}^2$	831	6	1675	54	0.00
precip ₇₂	839	5	1687	67	0.00
precip ₄₈	843	5	1696	76	0.00
~1	849	4	1706	86	0.00
precip ₂₄	849	5	1708	88	0.00



FIGURE 2. Cumulative precipitation 72 h prior to salamander sampling. The Richmond International Airport precipitation data were obtained from the National Oceanic and Atmospheric Administration (NOAA) precipitation database (https://www.ncdc. noaa.gov/cdo-web/datasets/LCD/stations/WBAN:13740/detail).

we found a relatively high density of salamanders (5.84 \pm 0.654 salamanders/m²), and a mean 95% home range size of 17.2 m² on this particular plot.

Precipitation and surface activity.-We found support for precipitation-specific differences in salamander baseline detection probability with 2-d cumulative precipitation best explaining the observed variation (cumulative weight = 1.0; Table 1). A quadratic effect of precipitation was supported by our model, indicating the highest detectability at 0.80 cm of 2-d cumulative precipitation; $p_0 = 0.088 \pm 0.020$ (Fig. 3B). Similarly, the model supported an increase in detection after initial capture (positive behavioral response: $\beta_{n(b)}$ = 2.14 ± 0.272 ; Table 2), a relatively high density of salamanders $(5.97 \pm 0.673 \text{ salamanders/m}^2)$, and a mean 95% home range size of 17.1 m². Overall, we found the quadratic effect to be favored in all scenarios (i.e., temperature, precipitation, and day of survey).

TABLE 2. Regression coefficients of the top models describing the variability in baseline detection (p_q) of the Red-backed Salamander (*Plethodon cinereus*) as a function of temperature and precipitation. The covariates were scaled to have a mean of 0 and a 1-unit standard deviation (i.e., z-score standardization).

Factors	Coefficient	Standard error	
<u>Temperature</u>			
Detection p_0			
$\beta_{p(\text{intercept})}$	-2.667	0.216	
$\beta_{p(b)}$	2.180	0.277	
$\beta_{p(\text{temp30})}$	-0.083	0.099	
$\beta_{p(\text{temp30}^2)}$	-1.071	0.115	
Movement σ			
β _σ	-0.044	0.079	
Density D			
B_D	0.379	0.112	
Cumulative precipitation			
Detection p_0			
$\beta_{p(\text{intercept})}$	-2.370	0.246	
$\beta_{p(b)}$	2.136	0.272	
$\beta_{p(48)}$	0.402	0.11	
$\beta_{p(48^2)}$	-1.357	0.166	
Movement σ			
β _σ	-0.048	0.079	
Density D			
ß _D	0.401	0.113	

DISCUSSION

The general dependency of terrestrial amphibians on temperature and moisture to survive and reproduce is well established (e.g., Sexton et al. 1990; Sugalski and Claussen 1997; Peterman and Semlitsch 2013),



FIGURE 3. Baseline detection probability of the Red-backed Salamander (*Plethodon cinereus*) as a function of (A) mean soil temperature at 30 cm depth 24 h prior to occasion date and (B) cumulative precipitation 48 h prior occasion date. Lines and shaded areas represent model predictions and 95% confidence interval (CI), respectively.

but the specific spatiotemporal metrics associated with the greatest influence on salamander activity are less clear. In particular, the use of vertical space through subterranean habitat use and the often complex life cycle of salamanders highlights the need to understand relevant species-specific cues for surface phenology across spatial and temporal gradients. By implementing a robust spatial modeling approach, our study found that salamander surface detection was most strongly influenced by soil temperature at 30 cm of depth and 2 d cumulative precipitation prior to each survey. Specifically, we quantified a nonlinear relationship between salamander surface detection and these two environmental factors and accepted our hypothesis about the presence of an optimal depth-specific soil temperature and time-specific cumulative precipitation associated with the highest levels of salamander activity.

Salamander surface activity is limited by temperature on both ends of the thermal performance spectrum, which ranges from -1.5° to 32.5° C in P. cinereus (Markle 2015). For our study site, the greatest fluctuations in temperature occurred at the surface (i.e., air temperature), and variation in soil temperature decreased as depth increased, likely due to the low albedo and higher ability of soil to retain heat (Eltahir 1998). We found surface detection to be strongly associated with soil temperature. Specifically, when compared to air temperature or soil temperature at 10 cm and 20 cm of depth, soil temperature at 30 cm of depth explained most of the variation in surface activity with maximum detection occurring when mean temperature was 12.6° C. Similarly, quadratic effects of day of the year (a proxy for temperature) and direct effects of air temperature have been used in prior studies to characterize surface activity, and in particular to identify peak activity periods (Sutherland et al. 2016; Muñoz et al. 2016a; Hernández-Pacheco et al. 2019). For instance, a population located at a higher latitude than our study population showed maximum detection at approximately 9.5° C of air temperature using an 11-d average air temperature to roughly characterize surface soil temperature (Kang et al. 2000; Muñoz et. al 2016a). Although perhaps a good approximation in relatively stable environments, an 11-d average air temperature proxy for soil temperature may not be the most reliable metric when monitoring populations living in areas with highly fluctuating daily temperatures. If these previously observed patterns in higher latitudes than our study site are truly comparable to soil temperatures, then the warmer temperature for peak detection in our lower latitude population suggests the potential for a latitudinal gradient in underlying thermal performance traits (Novarro et al. 2018).

Moisture, as influenced by precipitation, is also critical to *P. cinereus* and we expected salamanders to change

surface activity patterns (e.g., movement, foraging, mating) in accordance with optimal moisture conditions by avoiding the surface during extremely dry conditions as well as at times of excessive moisture caused by heavy precipitation (Muñoz et al. 2016b). While we caution against direct comparisons between the studies because our precipitation measures differ, both our study and Muñoz et al. (2016b) show an optimal precipitation value (0.80 cm of 2-d cumulative precipitation and 4 cm of 3-d average precipitation, respectively) associated to maximum detection probability. Peak detection after a shorter period of time in our system could be attributed to potential population-specific adaptations to higher water evaporation rates associated to warmer sites across P. cinereus geographic range. Whereas a single day after substantial rainfall may not be enough to detect more salamanders at the surface, three days may be too much time for maximum availability. However, more explorations are needed given the relatively low variability in cumulative precipitation between 48 h and 72 h in our study.

Our study supports the general role of both surface and subsurface conditions on salamander detectability (i.e., surface activity) and highlights the stronger effect of subsurface thermal conditions. The ecoevolutionary dynamics explaining our findings may rely on P. cinereus life history, which includes strong intraspecific competition (Jaeger 1979), strong interspecific territoriality (Wrobell et al. 1980), and high susceptibility to surface environmental conditions such as extreme temperatures leading to freezing or desiccation (Spotila 1972; Caruso et al. 2014; Novarro et al. 2018). In combination, these traits may explain the advantage of underground refuge and the use of subsurface conditions as preferred cues for surface activity. Given the lower variability in soil temperature expected at even greater depths, it is likely that soil temperature at 40 and 50 cm are also relevant cues for surface activity; however, other variables at these depths may also play a role limiting the vertical distribution of P. cinereus, such as the density and distribution of other organisms who facilitate underground tunnels (e.g., earthworms; Cáceres-Charneco and Ransom 2010). Additionally, it is likely that soil moisture, like temperature, varies across a depth gradient and could be measured directly in a future study. Regardless, we expect temperature to be a relatively stronger driver of surface activity due to the surface phenology of our population, which exhibits predictable surface inactivity during summer months independently of precipitation (Hernández-Pacheco et al. 2019).

In this study, we aimed to quantify the relative effects of temperature and precipitation on baseline detection of *P. cinereus*, an indicator species of ecosystem health. Through spatial capture-recapture analysis, we

identified the spatiotemporal environmental metrics that best explain detectability and, correspondingly, surface activity. For projects with limited resources, our work provides important insights into the finescale environmental measurements that best predict salamander activity in the southern portion of the range of *P. cinereus*. Future work should focus on implementing standard robust analysis across the geographic range that collects optimal subsurface conditions for a range of populations to quantify latitude-driven differences. This knowledge would contribute to our understanding of species variability in behavior and surface activity for this widespread terrestrial amphibian species.

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LITERATURE CITED

- Arnold, T.W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. Journal of Wildlife Management 74:1175–1178.
- Bailey, L.L. 2004. Evaluating elastomer marking and photo identification methods for terrestrial salamanders: marking effects and observer bias. Herpetological Review 35:38–41.
- Bailey, L.L., T.R. Simons, and K.H. Pollock. 2004. Comparing population size estimators for Plethodontid salamanders. Journal of Herpetology 38:370–380.
- Banks, B., T.J.C. Beebee, and A.S. Cooke. 1994. Conservation of the Natterjack Toad *Bufo calamita* in Britain over the period 1970–1990 in relation to site protection and other factors. Biological Conservation 67:111–118.
- Beebee, T.J.C. 1995. Amphibian breeding and climate. Nature 374:219–220.
- Blaustein, A.R., and J.M. Kiesecker. 2002. Complexity in conservation: lessons from the global decline of amphibian populations. Ecology Letters 5:597–608.

- Blaustein, A.R., L.K. Belden, D.H. Olson, D.M. Green, T.L. Root, and J.M. Kiesecker. 2001. Amphibian breeding and climate change. Conservation Biology 15:1804–1809.
- Boone, M.D., D.E. Scott, and P.H. Niewiarowski. 2002. Effects of hatching time for larval Ambystomatid salamanders. Copeia 2002:511–517.
- Cáceres-Charneco, R.I., and T.S. Ransom. 2010. The influence of habitat provisioning: use of earthworm burrows by the terrestrial salamander, *Plethodon cinereus*. Population Ecology 52:517–526.
- Caruso, N.M., M. Sears, D.C. Adams, and K.R. Lips. 2014. Widespread rapid reductions in body size of adult salamanders in response to climate change. Global Change Biology 20:1751–1759.
- Eltahir, E.A. 1998. A soil moisture-rainfall feedback mechanism: 1. Theory and observations. Water Resources Research 34:765–776.
- Feder, M.E. 1983. Integrating the ecology and physiology of plethodontid salamanders. Herpetologica 39:291– 310.
- Ficetola, G.F., and L. Maiorano. 2016. Contrasting effects of temperature and precipitation change on amphibian phenology, abundance and performance. Oecologia 181:683–693.
- Grafe, T.U., S.K. Kaminsky, J.H. Bitz, H. Lüssow, and K.E. Linsenmair. 2004. Demographic dynamics of the Afro-tropical Pig-nosed Frog, *Hemisus marmoratus*: effects of climate and predation on survival and recruitment. Oecologia 141:40–46.
- Grant, E.H.C. 2008. Visual implant elastomer mark retention through metamorphosis in amphibian larvae. Journal of Wildlife Management 72:1247– 1252.
- Hernández-Pacheco, R., C. Sutherland, L.M. Thompson, and K.L. Grayson. 2019. Unexpected spatial population ecology of a widespread terrestrial salamander near its southern range edge. Royal Society Open Science 6:182–192.
- Hesed, K.M. 2012. Uncovering salamander ecology: a review of cover board design. Journal of Herpetology 46:442–450.
- Jaeger, R.G. 1979. Seasonal spatial distributions of the terrestrial salamander *Plethodon cinereus*. Herpetologica 35:90–93.
- Kang, S., S. Kim, S. Oh, and D. Lee. 2000. Predicting spatial and temporal patterns of soil temperature based on topography, surface cover and air temperature. Forest Ecology and Management 136:173–184.
- Leclaire, M.H., M. Levsseur, and R. Leclair, Jr. 2008. Activity and reproductive cycles in northern populations of the Red-backed Salamander, *Plethodon cinereus*. Journal of Herpetology 42:31– 38.
- Markle, T.M. 2015. Ecology and evolution of geographic

range size variation in North American plethodontid salamanders: perspectives from thermal physiology. Ph.D. Dissertation, University of Minnesota, St Paul, Minnesota, USA. 95 p.

- Marsh D.M., and M.A. Goicochea. 2003. Monitoring terrestrial salamanders: biases caused by intense sampling and choice of cover objects. Journal of Herpetology 37:460–466.
- Mazerolle, M.J., L.L. Bailey, W.L. Kendall, J.A. Royle, S.J. Converse, and J.D. Nichols. 2007. Making great leaps forward: accounting for detectability in herpetological field studies. Journal of Herpetology 41:672–689.
- Muñoz, D.J., K.M. Hesed, E.H.C. Grant, and D.A. Miller. 2016a. Evaluating within-population variability in behavior and demography for the adaptive potential of a dispersal-limited species to climate change. Ecology and Evolution 6:8740–8755.
- Muñoz, D.J., D.A. Miller, C. Sutherland, and E.H.C. Grant. 2016b. Using spatial capture–recapture to elucidate population processes and space-use in herpetological studies. Journal of Herpetology 50:570–581.
- Nagel, J.W. 1977. Life history of the Red-backed Salamander, *Plethodon cinereus*, in northeastern Tennessee. Herpetologica 33:13–18.
- Novarro, A.J., C.R. Gabor, C.B. Goff, T.D. Mezebish, L.M. Thompson, and K.L. Grayson. 2018. Physiological responses to elevated temperature across the geographic range of a terrestrial salamander. Journal of Experimental Biology 221:jeb178236. https://doi.org/10.1242/jeb.178236
- Peterman, W.E., and R.D. Semlitsch. 2013. Fine-scale habitat associations of a terrestrial salamander: the role of environmental gradients and implications for population dynamics. PLoS ONE 8:e62184. https:// doi.org/10.1371/journal.pone.0062184
- Petranka, J.W. 1998. Salamanders of the United States and Canada. Smithson Institution Press, Washington, D.C., USA.
- Pullen, K.D., A.M. Best, and J.L. Ware. 2010. Amphibian pathogen *Batrachochytrium dendrobatidis*

prevalence is correlated with season and not urbanization in central Virginia. Disease of Aquatic Organisms 91:9–16.

- Royle, J.A., R.B. Chandler, R. Sollmann, and B. Gardner. 2013. Spatial Capture-recapture. Elsevier, Amsterdam, The Netherlands.
- Sexton, O., C. Phillips, and J. Bramble. 1990. The effects of temperature and precipitation on the breeding migration of the Spotted Salamander (*Ambystoma maculatum*). Copeia 1990:871–787.
- Sheridan, J.A., N.M. Caruso, J.J. Apodaca, and L.J. Rissler. 2017. Shifts in frog size and phenology: testing predictions of climate change on a widespread anuran using data from prior to rapid climate warming. Ecology and Evolution 8:1316–1327.
- Spotila, J.R. 1972. Role of temperature and water in the ecology of lungless salamanders. Ecological Monographs 42:95–125.
- Sugalski, M., and D. Claussen. 1997. Preference for soil moisture, soil pH, and light intensity by the salamander, *Plethodon cinereus*. Journal of Herpetology 31:245–250.
- Sutherland, C., D.J. Muñoz, D.A. Miller, and E.H.C. Grant. 2016. Spatial capture-recapture: a promising method for analyzing data collected using artificial cover objects. Herpetologica 72:6–12.
- Sutherland, C., J.A. Royle, and D.W. Linden. 2019. oSCR: A spatial capture-recapture R Package for inference about spatial ecological processes. Ecography 42:1459–1469.
- Todd, B.D., D.E. Scott, J.H. Pechmann, and J.W. Gibbons. 2010. Climate change correlates with rapid delays and advancements in reproductive timing in an amphibia community. Proceedings of the Royal Society B: Biological Sciences 278:2191–2197.
- Welsh, H.H., Jr., and S. Droege. 2001. Using plethodontid salamanders for monitoring biodiversity and ecosystem integrity of North American forests. Conservation Biology 15:558–569.
- Wrobell, D.J., W.F. Gergits, and R.G. Jaeger. 1980. An experimental study of interference competition among terrestrial salamanders. Ecology 61:1034– 1039.



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APPENDIX. Description of soil temperature probe stake design.

Soil Temperature Probe Stake

1 m Length of 3/4 inch (1.91 cm) PVC 3/4 inch (1.91 cm) PVC cap (not threaded) PVC Cement 3/4 inch (1.91 cm) PVC couple with no thread on one side, male threaded on side two 3/4 inch PVC threaded cap Plumbing tape 3/4 inch (1.91 cm) Caulk saver/backing Permanent marker Knife

Construction:

6 iButtons6 lengths of 9.5cm pipe saver





- 1. Mark pipe at 50 cm (midpoint) with permanent marker
- 2. Cement non-threaded side of coupler to one end of 1 m PVC pipe
- 3. Wrap threaded end of coupler a few times with plumbing tape to create water-tight seal a. Screw threaded cap onto taped and coupler
- 4. Place first programmed iButton into PVC pipe
 - a. Insert a 9.5 cm length of caulk saver
 - b. Repeat inserting iButtons followed by piece of caulk saver, finishing with the 6th and final temperature. This probe is the ground surface probe and should approximately be at the 50 cm mark. No insulation should be on top of this surface iButton
- 5. Place non-threaded cap on top of stake (DO NOT CEMENT)

