

Capture Probability and Survivorship of the Southern Two-Lined Salamander (*Eurycea cirrigera*) in Drought and Non-Drought Conditions

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Droughts represent a major disturbance in lotic systems, and likely negatively influence stream-inhabiting amphibian populations. However, because of the inability to predict droughts, empirical investigations examining the response of stream amphibians to drought are uncommon. We conducted a capture–mark–recapture (CMR) study of a population of *Eurycea cirrigera* (Southern Two-lined Salamander) at one stream from 2005–2010; during this five-year period several drought events occurred. This stochasticity provided an opportunity to examine the effects of drought on survivorship and capture probability of *E. cirrigera*. We found that capture probability was influenced by season and drought conditions. We also found that salamander survival was influenced by drought; monthly survivorship decreased from 0.96 ± 0.03 during non-drought conditions to 0.79 ± 0.03 during drought conditions. Our results suggest that drought leads to decreased survivorship of *E. cirrigera* and the effects of drought on capture probability varies by season. Increased capture probability, especially during the reproductive season, may be a result of salamanders seeking refuge in the stream as opposed to seeking refuge in the adjacent terrestrial environment.

DROUGHTS can strongly influence animal populations in aquatic ecosystems. Droughts directly result in changes to hydroperiod and habitat connectivity, and these changes lead to deterioration of water quality, alteration of food resources, and changes in species interactions (Lake 2003; Rudolf, 2006; Walls et al., 2013a). For fully aquatic taxa (i.e., fishes), drought conditions can decrease survival (Labbe and Fausch, 2000; Hodges and Magoulick, 2011), ultimately resulting in population declines (Lake, 2003; Magoulick and Kobza, 2003; Matthews and Marsh-Matthews, 2003; Love et al., 2008). The effects of drought on semi-aquatic animal populations are less predictable and often dependent on the species-specific refugium-use strategies, which may include emigration to refuges in both the terrestrial and aquatic environments (Humphries and Baldwin, 2003; Boulton and Lake, 2008; Price et al., 2012). Because the occurrence of droughts, especially exceptional or non-seasonal droughts, is difficult to predict, relatively few empirical investigations on the response of semi-aquatic animal populations to drought have been conducted (but see Price et al., 2012; Walls et al., 2013b). Understanding the responses of semi-aquatic animals to drought is becoming increasingly important due to the increased likelihood of drought caused by climate change (Dai, 2011).

In eastern North America, lungless salamanders in the family Plethodontidae occur at high densities and represent the dominant vertebrates of low-order stream systems (Petranka and Murray, 2001; Davic and Welsh, 2004; Peterman et al., 2008). Flow and availability of freshwater in low-order streams is largely influenced by precipitation and air temperature (Vogel et al., 1997), which decrease and often increase, respectively, during droughts. Salamanders inhabiting low-order streams and adjacent terrestrial environments likely deal with drying in a variety of ways, including emigrating to in-stream refuges (Price et al., 2012) or moving from the terrestrial environment to the streambed (MacCulloch and Bider, 1975). Prolonged periods of insufficient water may ultimately lead to decreased breeding activity (Jansen et al., 2009), reproductive failure (Taylor

et al., 2006), decreased survival (Scheele et al., 2012), and changes in occupancy (Price et al., 2012).

Knowledge of population vital rates (i.e., survival) during drought and non-drought conditions is an important first step in assessing the effects of drought on stream salamander populations. In this study, capture–mark–recapture (CMR) data for the geographically widespread, semi-aquatic lungless salamander, *Eurycea cirrigera* (Southern Two-lined Salamander), were collected monthly at one stream in North Carolina, USA from October 2005 through November 2010. During this study, several periods of drought occurred, allowing for an in-depth investigation of the effects of drought on *E. cirrigera*. We had two specific objectives: 1) estimate capture probability of *E. cirrigera* over a five-year period to determine if drought influences capture probability, and 2) evaluate the effects of drought on survival of *E. cirrigera*. We predicted that capture probability during drought would increase, possibly as a result of temporary emigration from the terrestrial to the aquatic habitat (e.g., MacCulloch and Bider, 1975), and survivorship would decline during droughts.

MATERIALS AND METHODS

Study species.—*Eurycea cirrigera* is a salamander in the family Plethodontidae and is often the most abundant species in low-order streams in the southeastern U.S., where they can reach larval densities of 72 individuals/m² of stream (Nowakowski and Maerz, 2009). Breeding and egg deposition of *Eurycea cirrigera* occurs primarily in low-order streams, and larva spend up to two years in streams prior to metamorphosis (Noble and Brady, 1930; Richmond, 1945; Petranka, 1984; Green and Pauley, 1987). *Eurycea cirrigera* and closely related species (i.e., *E. bislineata* and *E. wilderae*) often inhabit the terrestrial environment (i.e., forest) during summer and fall months (MacCulloch and Bider, 1975; Petranka, 1998; Crawford and Semlitsch, 2007). MacCulloch and Bider (1975), studying the movements of *E. bislineata* in Quebec, documented movements of >100 m away from the stream, yet drought conditions caused salamanders to return to aquatic habitats independently of breeding

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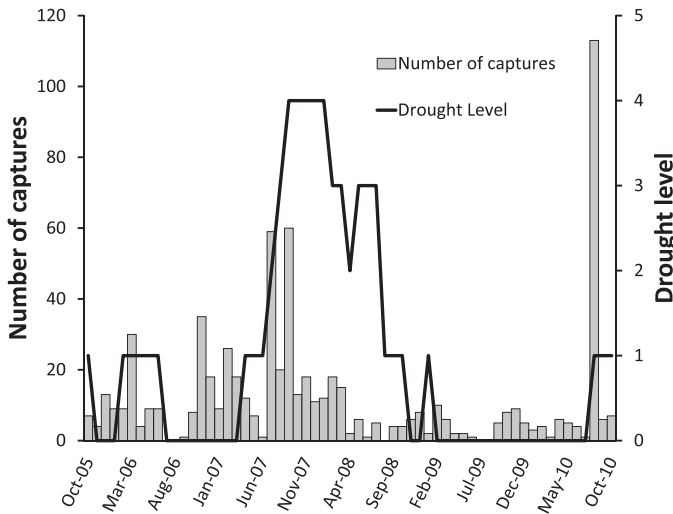


Fig. 1. Number of captures of *E. cirrigera* per month and corresponding drought index data for Mecklenburg County, NC, USA. Drought conditions include normal (N), abnormally dry (D0), moderate drought (D1), severe drought (D2), extreme drought (D3), and exceptional drought (D4); we show all conditions above abnormally dry (D0). Abundance of salamanders in the summer months of 2007 and 2010 was due to large numbers of recently transformed individuals.

behavior. No study has estimated survival of *E. cirrigera*, although MacCulloch and Bider (1975) report that only 25% of the closely related individuals of *E. bislineata* that migrate from the stream to the terrestrial environment return the following year.

Study site.—We conducted a CMR survey for post-metamorphic *E. cirrigera* along a 100 m reach of a first-order stream in the Piedmont region of North Carolina, USA (Universal Transverse Mercator coordinates E05 04913, N3917456, Zone 17; datum = NAD83). This stream had a catchment size of 35 ha, which was 92% forested. Stream substrate was dominated by cobblestone, sand, silt, and detritus with a few, scattered large boulders (see Price et al., 2012 for details on the study site). Salamander species detected within or directly adjacent to the stream included *Desmognathus fuscus*, *E. guttolineata*, *Gyrinophilus porphyriticus*, *Pseudotriton ruber*, *P. montanus*, and *Plethodon cylindraceus*.

We considered the stream to be semi-permanent and water flow was strongly influenced by season and precipitation. From October 2005 to July 2007, the sampling reach contained surface water during each of our visits to the stream. A significant drought began in August 2007; from October 2007 through August 2008 the drought was classified as either exceptional or extreme (see Methods; North Carolina Department of Environment and Natural Resources available at www.ncwater.org/Drought_Monitoring/dmhistory/; accessed online March 2011) and stream flows were at 110 yr low levels (Fig. 1). During the time of this significant drought, surface flow ceased, with only the first 10 and final 10 m of the sampling reach containing surface water. The surface flow resumed at low levels in late October 2007, yet ceased again once more in May 2008 until July 2008, with only the first 20 m and final 10 m of stream containing surface water. Moderate droughts also occurred through the sampling period (Fig. 1), although surface flow was maintained throughout the entire 100 m sampling reach during these periods.

Field methods.—Starting in October 2005, we conducted CMR surveys for 61 consecutive months with the 100 m stream transect. We sampled the stream twice each month (See Price et al., 2012); however, because of low captures of *E. cirrigera*, we combined the bi-monthly samples into monthly samples. We captured salamanders using a cover-controlled active search in which one person, moving upstream, searched all cover items (e.g., rocks, logs, etc.) within the stream and within 0.5 m of the stream edge. Cover-boards (73 cm × 73 cm section of 11 mm plywood) were placed every 5 m along the 100 m section of stream to provide additional capture opportunities. Salamanders were captured using a dip-net or by hand. All surveys were conducted during daylight hours. Post-metamorphic salamanders were brought back to the lab, individually marked by subcutaneous injection of visible implant elastomer (VIE, Northwest Marine Technologies, Shaw Island, Washington, USA) and released within 2 m from the point of capture prior to the next sampling session for that month.

Capture-mark-recapture modeling.—For CMR analyses, we combined capture data from each sampling session to generate salamander monthly encounter histories. Cormack-Jolly-Seber (CJS) open-population mark-recapture models (Lebreton et al., 1992) in Program MARK (version 7.0; White and Burnham, 1999) were used to determine estimates of apparent survival (Φ) and capture probability (p) of post-metamorphic salamanders. Apparent monthly survival probability is the probability that an animal alive at time t will be alive at time $t + 1$, whereas capture probability is the probability that a marked animal available for capture at time t is captured at time t .

Using a step-down approach (Lebreton et al., 1992; Muths et al., 2006), we first evaluated the effects of drought on capture probability of *E. cirrigera*. Holding survival constant over time (i.e., $\Phi(\cdot)$), we generated the following candidate models for capture probability: 1) constant capture probability ($p[\cdot]$), 2) drought-specific capture probability ($p[\text{drought}]$), 3) reproduction season specific capture probability ($p[\text{reproduction}]$), and 4) reproduction season and drought specific capture probability ($p[\text{reproduction} \times \text{drought}]$). Reproduction months were classified as December, January, February, March, and April, during which males are actively courting females and females are nesting. Both males and females are found in close proximity to the stream during reproductive season. We considered May through November being non-reproduction months when individuals use stream, streamside, and terrestrial habitats. Although *E. cirrigera* may guard eggs in May in some parts of their range (i.e., Ohio; Pfingsten, 2013), we never witnessed females guarding eggs at this site (and several nearby streams) during the month of May. Drought records were obtained from the North Carolina Department of Environment and Natural Resources, Division of Water Resources (www.ncdrought.org; accessed March 2011) for Mecklenburg County, NC. North Carolina Department of Environment and Natural Resources uses the following categories to define drought: normal (N), abnormally dry (D0), moderate drought (D1), severe drought (D2), extreme drought (D3), and exceptional drought (D4; Fig. 1). All conditions above abnormally dry (D0) were considered drought conditions. The best-fit model for capture probability was based on Akaike's Information Criterion (AIC; Akaike, 1973), adjusted for small sample sizes (AIC_c; Burnham and Anderson, 2002).

Table 1. Cormack-Jolly-Seber model set analyzing the effects of drought and reproductive season on capture probability (p) of *Eurycea cirrigera*.

Model	AIC _c	ΔAIC _c	w _i	NP	Deviance
{Φ(.)p(reproduction.drought)}	688.90	0	0.6237	5	360.60
{Φ(.)p(.)}	691.10	2.20	0.2073	2	368.88
{Φ(.)p(reproduction)}	692.86	3.96	0.0861	3	368.61
{Φ(.)p(drought)}	692.93	4.04	0.0828	3	368.69

AIC_c = Akaike Information Criterion values adjusted for small sample sizes and overdispersion; w_i = Akaike weight; NP = number of parameters; Φ = survivorship; p = capture probability

Using the most parsimonious model for capture probability, we compared various parameterizations of apparent survivorship. Permutations of survivorship included 1) constant (Φ[.]) survival, 2) survival dependent on drought (Φ [drought]), 3) survival dependent on reproduction season (Φ [reproduction]), and 4) survival dependent on drought and reproduction season (Φ [reproduction × drought]).

Goodness-of-fit was evaluated for the CJS models using a parametric bootstrapping method of the most parametrized model (i.e., Φ(reproduction.drought)p(season.drought)) with 1000 iterations (as described in “Program MARK: A Gentle Introduction” by Cooch and White; available at <http://www.phidot.org/software/mark/docs/book/>). The overdispersion factor, \hat{c} , was calculated as the observed global model deviance divided by the mean expected model deviance from the bootstrapping results. Model selection was based on Akaike’s Information Criterion (AIC; Akaike, 1973) values adjusted for small sample sizes (AIC_c; Burnham and Anderson, 2002). If overdispersion was evident from goodness-of-fit testing ($\hat{c} > 1$), then the AIC_c values adjusted for overdispersion (QAIC_c) were used (Burnham and Anderson, 2002).

RESULTS

From October 2005 to November 2010, we had 691 total capture events of 583 post-metamorphic individuals of *E.*

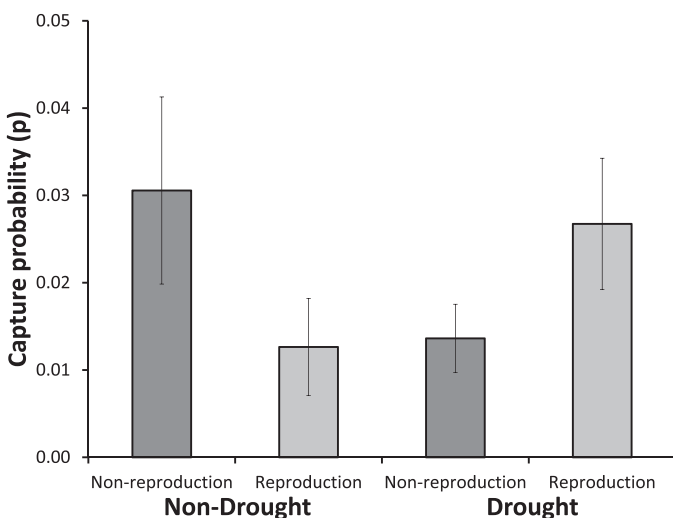


Fig. 2. Individual capture probability (p) of *Eurycea cirrigera* during reproduction (December–April) and non-reproduction (May–November) seasons during drought and non-drought conditions with standard error bars. *Eurycea cirrigera* were sampled from October 2005 to November 2010 in one first order stream in the Piedmont region of North Carolina, USA.

cirrigera (Fig. 1). The number of individuals captured each month varied from 0–113, and the number of monthly captures averaged 16.93 ± 4.64 (s.e.) during drought and 7.09 ± 1.38 (s.e.) during non-drought conditions. We averaged 1.77 recaptures/month with a maximum of 14 recaptures occurring in July 2010. Our top model for capture probability (p) of *E. cirrigera* indicated reproduction season and drought-specific capture probability (AIC w_i = 0.6237, Table 1). Although capture probabilities were generally low, drought conditions lead to increased capture probability in reproduction months, December through April, compared to non-drought conditions (Fig. 2). However, droughts during the non-reproduction months, May through November, lead to decreased capture probabilities in comparison to non-drought conditions (Fig. 2).

The goodness-of-fit testing based on 1000 bootstraps suggested the data were overdispersed, and therefore, a \hat{c} correction of 1.19 was necessary to adjust the AIC_c scores and the QAIC_c were used. The best-supported model for survivorship of *E. cirrigera* suggested that survival was influenced by drought conditions (AIC w_i = 0.8012; Table 2). Real parameter estimates for monthly survivorship of adult *E. cirrigera* decreased from 0.96 ± 0.03 (s.e.) during non-drought conditions to 0.79 ± 0.03 (s.e.) during drought conditions (Fig. 3).

DISCUSSION

We quantified capture probability and survivorship of *E. cirrigera* in drought and non-drought conditions. Our resulting models showed that both capture probability and survivorship of *E. cirrigera* were affected by drought conditions. Specifically, we found strong support for models that suggested monthly survivorship decreased significantly during drought conditions despite the fact that during most of the reproduction season, salamanders were captured in the stream at higher probabilities during drought conditions. Although our findings are the first investigations to examine survivorship of *E. cirrigera* during drought and non-drought conditions, we caution that our findings may not be representative of the response of *E. cirrigera* throughout its geographic range due to our limited geographic scope of sampling.

Studying the movements of *E. bislineata* in Quebec, MacCulloch and Bider (1975) found 98% of activity to be correlated with precipitation and salamanders return to aquatic habitats due to dry conditions, independently of breeding behavior. In our study, capture probability (i.e., the probability that a marked salamander available for capture at time t is captured at time t) during reproductive season (i.e., December–April) was higher during drought conditions. This finding suggests that *E. cirrigera* tend to forgo migrations to the terrestrial environment and remain in the

Table 2. Cormack-Jolly-Seber model set analyzing the effects of drought and reproductive season on survivorship (Φ) of *Eurycea cirrigera*.

Model	QAIC _c	Δ QAIC _c	w_i	NP	QDeviance
{ Φ (drought) ρ (reproduction.drought)}	572.71	0.00	0.8012	6	293.18
{ Φ (reproduction.drought) ρ (reproduction.drought)}	575.85	3.14	0.1664	8	292.23
{ Φ (.) ρ (reproduction.drought)}	580.52	7.81	0.0162	5	303.02
{ Φ (.) ρ (.)}	581.40	8.69	0.0104	2	309.98
{ Φ (reproduction) ρ (reproduction.drought)}	582.55	9.84	0.0059	6	303.02

QAIC_c = Akaike Information Criterion values adjusted for small sample sizes and overdispersion; w_i = Akaike weight; NP = number of parameters; Φ = survivorship; ρ = capture probability; QDeviance = deviance adjusted for small sample sizes and overdispersion

stream throughout the drought, resulting in enhanced capture probabilities compared to non-drought conditions. Conversely, capture probability may be lower during non-drought conditions because of frequent use of terrestrial habitats. However, during non-reproductive months capture probabilities were lower during droughts than during non-drought conditions. Low capture probabilities may be explained by high rates of temporary emigration to stream refugia, as seen in the salamander *Desmognathus fuscus* during exceptional droughts (Price et al., 2012).

Drought reduces survivorship in a wide variety of aquatic and semi-aquatic animal taxa (Semlitsch, 1987; Boulton, 2003; Hakala and Hartman, 2004; Church et al., 2007; Boulton and Lake, 2008). Our findings suggest that droughts negatively impact survivorship of the common, semi-aquatic stream amphibian *E. cirrigera*. Studies on the physiology of plethodontid salamanders, such as *E. cirrigera*, suggest that survivorship may be reduced because of dehydration and restriction of activities during drought conditions (Spotila, 1972). However, Price et al. (2012) found that survivorship of adult *D. fuscus* in drought conditions was similar to survivorship estimates during non-drought conditions, with the use of in-stream refugia possibly responsible for the lack of an effect. Thus, reduced survival of *E. cirrigera* during droughts may be the result of other mechanisms. For example, predation and competition play a large role in structuring salamander communities (Hairston, 1987; Beachy, 1997), and prolonged interactions between *E.*

cirrigera and other salamanders in the local assemblage may influence survival of *E. cirrigera*. Indeed, *D. fuscus*, an abundant salamander in our study site (Price et al., 2012), induces avoidance behavior, a form of interference competition, in *E. cirrigera* (Ransom and Jaeger, 2006). Furthermore, survivorship may have been reduced due to high predation rates. We observed higher than normal densities of salamander predators, especially small woodland snakes (i.e., ringneck snakes [*Diadophis punctatus*], brown snakes [*Storeria dekayi*], and red-bellied snakes [*Storeria occipitomaculata*]), undercover within the stream bed during droughts.

Climate change models predict that many regions will experience increased magnitude of episodic precipitation, warmer summer temperatures, and longer, more severe droughts in the near future (Brooks, 2009; Walls et al., 2013a). Recent research suggests habitat suitable for many lungless salamander species will decrease due to these climatic changes, resulting in significant population declines as early as 2020 (Milanovich et al., 2010). Yet, empirical data on the influence of drought on lungless salamanders is limited. While our results are specific to a single species at a single study location, our data highlight the negative effect of drought on adult salamander survivorship. Future studies examining larval survivorship, recruitment, immigration, and emigration are needed to fully understand the impacts of drought on stream amphibians and other stream biota.

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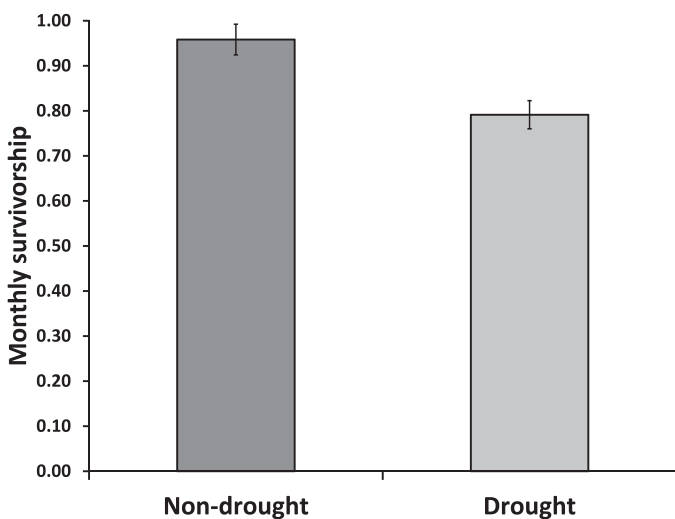


Fig. 3. Monthly survival estimates of *Eurycea cirrigera* during drought and non-drought conditions with standard error bars. *Eurycea cirrigera* were sampled from October 2005 to November 2010 in one first order stream in the Piedmont region of North Carolina, USA.

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