RESISTANCE AND RESILIENCE OF A STREAM SALAMANDER TO SUPRASEASONAL DROUGHT

STEVEN J. PRICE[1,2,3], ROBERT A. BROWNE[1], AND MICHAEL E. DORCAS[2]

[1]*Department of Forestry, University of Kentucky, Lexington, KY 40546, USA*
[2]*Department of Biology, Davidson College, Davidson, NC 28035-7118, USA*

ABSTRACT: Drought represents a significant stressor to aquatic animals. However, empirical data regarding the response of many aquatic animals, particularly amphibians, to drought are limited. The southeastern United States experienced a supraseasonal drought in 2007–2008, which provided an opportunity to examine the resistance and resilience of salamanders to drought. In this study, we used 5 yr of presence–absence data at 17 first-order streams and 61 mo of mark–recapture data at one stream to examine the effects of drought on occupancy and vital rates of the salamander *Desmognathus fuscus* (Northern Dusky Salamander). We tested three hypotheses regarding the effects of drought: larvae would decrease in occupancy during drought conditions, but adult occupancy would remain stable; adult temporary emigration rates would be greatest during supraseasonal drought conditions; and adult survivorship would be equal or nearly equal during nondrought conditions and drought conditions due to higher rates of temporary emigration. We found that adult salamander occupancy remained stable through the 5 yr of sampling; however, larval salamander occupancy decreased by an average of 30% during the supraseasonal drought. We found that adult temporary emigration probabilities were twice as high during supraseasonal drought conditions than during nondrought or typical drought conditions. Monthly survival of adults was relatively high during nondrought ($S = 0.89 \pm 0.02$), typical drought ($S = 0.97 \pm 0.02$), and severe drought conditions ($S = 0.90 \pm 0.01$). Our findings suggest that high survivorship of adult *D. fuscus* likely buffers the negative effects of drought on larvae and high rates of temporary emigration allow adult salamanders to be resilient to supraseasonal drought conditions.

Key words: Amphibians; Capture–mark–recapture; *Desmognathus fuscus*; Northern Dusky Salamander; Occupancy; Survivorship; Temporary emigration

DROUGHT represents a major disturbance affecting populations of freshwater biota (Lake, 2003). Two distinct types of droughts exist: the somewhat predictable, periodic droughts (e.g., Gasith and Resh, 1999) and the unpredictable and lengthy exceptional or supraseasonal droughts (e.g., Humphries and Baldwin, 2003). Most freshwater biota, especially those inhabiting intermittent systems, often exhibit high resistance and resilience to seasonal droughts (Yount and Niemi, 1990; Magoulick and Kobza, 2003; DiStefano et al., 2009). Conversely, supraseasonal droughts generally are thought to reduce population densities (Hakala and Hartman, 2004), change species composition (Love et al., 2008), and alter life-history scheduling (i.e., reproduction and recruitment; Cowx et al., 1984).

The ability of stream animals to survive drought is often dependent upon their refugium-use strategies (Lake, 2003; Davey et al., 2006). Refugium-use strategies include those occurring between generations and those

within generations (Lake, 2003). Complex life cycles are considered a between-generation strategy as one stage can buffer the negative effects of drought on another stage (Boulton, 2003). Within-generation refugium-use strategies involve estivation either through movement from surface water to subterranean retreats (Clinton et al., 1996) or surviving in microhabitats that lack water but have high humidity (Boulton, 1989).

Stream salamanders in the family Plethodontidae can occur at high densities and represent the dominant vertebrates of stream communities in eastern North America (Burton and Likens, 1975; Petranka and Murray, 2001; Davic and Welsch, 2004; Peterman et al., 2008). Deterioration of habitat as a result of drought may lead to decreased survivorship of adult and larvae and subsequent lower recruitment, as noted in wetland-breeding salamanders (Church et al., 2007), stream fishes (Hakala and Hartman, 2004), and invertebrates (Boulton, 2003). Yet, the resistance and resilience of stream salamander populations to supraseasonal drought conditions are unknown.

---

[3] CORRESPONDENCE: e-mail, steven.price@uky.edu
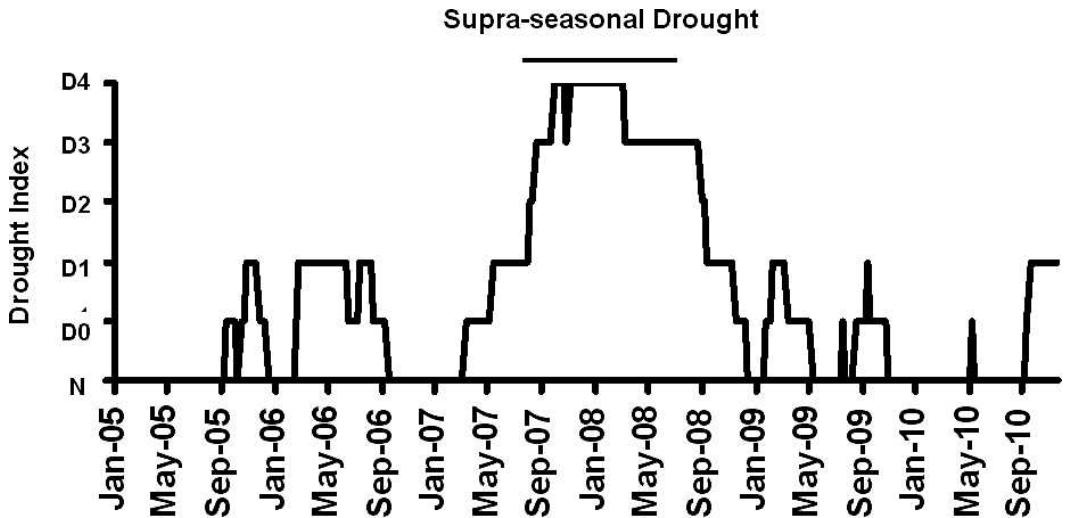
Supra-seasonal Drought

Fig. 1.—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). Supraseasonal drought conditions occurred from October 2007 to August 2008, when stream levels were at 110-yr lows.

The Piedmont region of North Carolina, USA experienced a supraseasonal drought beginning in 2007 and continuing through late summer 2008. Stream flows were at 110-yr low levels, and the drought was classified at exceptional (D4) from October 2007 through March 2008 and extreme drought conditions (D3) continued until August 2008 (Fig. 1, North Carolina Department of Environment and Natural Resources; www.ncwater.org/ Drought_Monitoring/dmhistory/; accessed online March 2011). Many intermittent streams completely dried for an extended period (i.e., 2–3 mo) during this supraseasonal drought. As part of an ongoing investigation on stream salamander populations started in March 2005 and continuing to May 2009, data were collected on salamander occupancy at 17 first-order streams in the western Piedmont of North Carolina. Additionally, capture–mark–recapture (CMR) data were collected at one stream from October 2005 through November 2010. These data allow for an in-depth investigation on the effects of drought on salamander populations as well as providing insights into possible refugium-use strategies salamanders used during supraseasonal drought conditions.

In this study, our first objective was to assess occupancy dynamics of larvae and adult *Desmognathus fuscus* (Northern Dusky Salamanders) in 17 streams during presupraseasonal drought conditions, supraseasonal drought conditions, and postsupraseasonal drought conditions. We hypothesized that larvae would decrease in occupancy during drought conditions, but adult occupancy would remain stable, suggesting a possible between-generation strategy to overcome drought conditions. Our second objective was to determine the role of within-generation strategies by examining the probability of temporary emigration and adult survivorship patterns during typical seasonal drought, supraseasonal drought, and nondrought conditions. We hypothesized that adult temporary emigration rates would be greater during supraseasonal drought conditions and survivorship would be equal to or nearly equal to nondrought conditions. If our second hypothesis is supported, high temporary emigration rates would give support to a within-generation strategy that allows adult salamanders to resist exceptional drought conditions.

MATERIALS AND METHODS

Study System

Desmognathus fuscus is a species of lungless salamander (Family Plethodontidae) that is

widely distributed throughout eastern North America. Individuals of this species are ubiquitous in first-order streams, where adults inhabit the streambed and stream margins, often occurring under logs, rocks, and within leafy debris. Females brood, on average, 21–33 eggs during summer months and hatching occurs in late summer (Petranka, 1998). The fully aquatic larvae undergo metamorphosis after spending 9–12 mo within the stream (Danstedt, 1975). Population densities can be exceptionally high (e.g., 1.42 postmetamorphic individuals/m^2; Spight, 1967).

Occupancy assessments of adult and larval salamanders were conducted in 17 streams in Cabarrus, Gaston, Iredell, Lincoln, and Mecklenburg counties in the western Piedmont of North Carolina annually beginning in 2005 and continuing through 2009 (See Price et al., 2011 for a description of study sites). Stream catchments were primarily forested with second-growth forest and streams were generally semipermanent, having low water levels during the late summer or early fall of each year. During the supraseasonal drought of 2007–2008, however, all streams had significantly lower water levels from August 2007 through October 2008, where surface water, if remaining, largely occurred in isolated pools in the streambed.

Intensive CMR surveys were conducted in a 100-m reach segment of one first-order, semipermanent stream located at Stephen's Road Nature Preserve (SRNP) in Huntersville, NC (Universal Transverse Mercator coordinates E0504913, N3917456, Zone 17; datum = NAD83). The stream originates as two seeps; an upstream seep was dammed to form a small pond at the headwaters, and a secondary seep feeds the stream approximately 200 m upstream from our sampling location. The total length of the stream was 929 m until reaching a second-order stream that flows into the Catawba River. The stream substrate varied throughout the stream, but coarse substrate (boulders and cobbles), sand, silt, and detritus were dominant components in the 100-m study reach. The 100-m reach contained surface water continuously from October 2005 until July 2007, when surface flow ceased until October 2007. From July to October 2007, only the first 10 m and the final

10 m of the 100-m sampling section contained surface water. Surface flow resumed at low levels in late October 2007 but again ceased in late May 2008 until July 2008, with only the first 20 m and final 10 m of stream containing surface water. Surface flow was regularly maintained through the entire 100-m sampling area from October 2008 until November 2010.

Salamander Sampling Methods

To estimate salamander occupancy, three sampling methods were used; 30 min of dipnetting within a linear, 10-m section; a 15-min survey of leaf litter and cover objects along the bank of each 10-m section; and a 1-wk-long trapping period of a second 10-m section of each stream (Price et al., 2011). The three methods were repeated twice each spring: once in March/early April and again in mid-April or early May, at which point all streams had surface water. Following capture of a salamander, we identified stage and species, measured (snout–vent length [SVL] and total length [TL] to nearest 0.1 mm) each individual, and returned the salamander to the sampling transect. During the trapping period, to avoid counting individuals on multiple occasions, captured individuals were either retained in the laboratory until the final day of trapping that portion of the stream or uniquely marked with visible implant elastomer (VIE; Northwest Marine Technologies, Shaw Island, Washington, USA) before release. Fourteen of the 17 streams were sampled each year from 2005 to 2009. One stream was not sampled during 2008 and 2009 and two streams were not sampled in 2009.

CMR surveys were used at SRNP to estimate survivorship and temporary emigration probabilities of adult stream salamanders. Using robust design sampling, we captured salamanders in the entire 100-m reach of the SRNP stream twice per month from October 2005 to November 2010. Sampling of salamanders consisted of turning over cover objects (e.g., rocks and logs) and searching leaf litter within the stream or up to 1 m from the stream bank (Price et al., 2012). To provide additional captures, coverboards (73 cm × 73 cm, 1.1 cm thick) were placed at 5-m intervals along the stream bank and checked

during each survey. After an animal was captured, we recorded its longitudinal position within the stream. All animals captured were returned to the lab, where they were anesthetized with 1 g of maximum strength Orajel® per 1 L of tap water (Del Pharmaceuticals, Uniondale, NY; Cecala et al., 2007), uniquely marked using VIE, measured (SVL and TL), and weighed. Animals were released at their exact point of capture within 1–2 d of processing. Subsequent (i.e., secondary) sampling occurred <3 d from the release date. Population closure was assumed between first and second samples.

Drought Data

Drought index data, collected by the North Carolina Department of Environment and Natural Resources, Division of Water Resources (www.ncdrought.org, accessed March 2011) for Mecklenburg County, NC, were used to assess drought conditions. The categories North Carolina Department of Environment and Natural Resources uses to define drought conditions include: normal, abnormally dry (D0), moderate drought (D1), severe drought (D2), extreme drought (D3), and exceptional drought (D4). We simplified the categories and assumed typical drought conditions to include the "abnormally dry" and the "moderate drought" indices. We identified supraseasonal drought conditions occurring from October 2007 through August 2008, when stream levels were at 110-yr lows and drought categories included severe drought, extreme drought, and exceptional drought (Fig. 1).

Occupancy Modeling and Parameter Estimation

To evaluate our first hypothesis, we used dynamic occupancy models (Royle and Kéry, 2007; Royle and Dorazio, 2008), which allow for estimation of initial site occupancy, colonization and extinction probabilities, and detection probability. These models rely on repeated presence–absence surveys conducted during multiple sampling events or secondary samples across primary sampling periods. Secondary samples are assumed to be closed to birth, death, immigration, and emigration. However, occupancy status may change among primary periods because of extinction and colonization events.

We used yearly samples from 2005–2009 as our primary sampling periods, with two secondary sampling periods each year. The outcome of sampling in each secondary sampling period was categorized separately for adult and larval *D. fuscus* as either detection or nondetection. Following the notation of Royle and Dorazio (2008), $z(i,t)$ is the true occupancy state of site i at time t and can either be occupied ($z = 1$) or unoccupied ($z = 0$). As a result of imperfect detection, $z(i,t)$ is unobserved or partially unobserved. However, two secondary samples (i.e., $y_j[i, t]$) at each site accounted for imperfect detection. Our sampling data were condensed from the three methods (i.e., dipnetting, trapping, bank search) to reflect detection by at least one method or nondetection by all methods for each secondary sampling event. We assumed our secondary samples were independent and identically distributed Bernoulli trials with parameter p_{it} (i.e., detection probability; see Price et al., 2011).

The dynamic occupancy model is a hierarchical model, expressed by two components: a submodel for the observations conditional on the unobserved state process, such that $y(i, t)|z(i, t)$, and a submodel for the unobserved state process ($z[i, t]$). The state model is formulated by initial occupancy probability (ψ_1), local survival (Φ_t; i.e., remains occupied), and colonization (γ_t; i.e., recruitment) probabilities. Royle and Dorazio (2008) provide a description of parameter calculation in initial and subsequent time periods. We derived occupancy probability for adult and larvae for each year using finite sample manifestations of occupancy probabilities as our scope of interest was with the actual sample sites rather than a theoretically infinite number of sites (Royle and Kéry, 2007).

To estimate occupancy probability for *D. fuscus*, Bayesian analysis in the software package WinBUGS (Version 1.4; Spiegelhalter et al., 2003) was used through the R add-in library R2WinBUGS. We used Bayesian analysis rather than a maximum likelihood (ML) approach due to our small sample size (i.e., 17 streams surveyed). For small sample

sizes, inference based on ML estimates may be biased (Le Cam, 1990), yet Bayesian inference is exact for finite samples (Kéry, 2010). We used uninformative priors, following the standard uniform distribution. Posterior summaries were based on 35,000 Markov chain Monte Carlo iterations. The first 5000 iterations were disregarded as burn-in and the models had a thinning rate of 10. The mean and standard deviation of the model coefficients were calculated, as were the 95% Bayesian credible intervals. Annual estimates of occupancy were compared using 95% credible intervals, where we assumed that nonoverlapping credible intervals indicated a difference in occupancy probability.

CMR Modeling and Vital Rate Estimation

To test our second hypothesis, we used Program MARK (v. 6.0; White and Burnham, 1999) to construct models and evaluate the effects of drought on adult survival and temporary emigration probabilities. We defined adult salamanders as those exhibiting SVL $\geq$ 35 mm (Orser and Shure, 1975; Jones, 1986). The Huggins closed-captures form of the robust design model (Huggins, 1989, 1991) was used to estimate population parameters. Huggins robust design models are composed of three parameters: capture probability, apparent survival rate, and probability of temporary emigration. Huggins robust design models derive population estimates separate from the model likelihood and often tend to perform better than traditional closed-captures robust design models with sparse data (Huggins, 1989, 1991).

A step-down approach advocated by Lebreton et al. (1992) was used to evaluate capture probability, temporary emigration, and apparent survival rate (see also Muths et al., 2006). We first constructed candidate models that varied in capture probability (p) and capture response (c) to find the best-fit model for salamander detection. We assumed p and c within primary periods to be constant. Candidate models 1–5 for p and c included: constant capture probability with capture response ($p[.]c[.]$), month-specific capture probability with capture response ($p[month]c[month]$), time-specific capture probability with capture response ($p[time]c[time]$), capture probability

dependent on drought (i.e., all drought indices with same parameter, $p[drought]c[drought]$), capture probability differs among nondrought conditions, typical drought conditions (i.e., D0, D1), and supraseasonal drought conditions (October 2007–August 2008; i.e., $p[drought severity]c[drought severity]$). Models 6–11 contained the same parameterization as models 1–5 but contained no capture response (i.e., $p = c$). Models 1–11 contained constant, random, temporary emigration and constant survival. We compared the fit of the candidate models using Akaike's information criterion (AIC; Akaike, 1973) adjusted for small sample sizes (AIC$_c$; Burnham and Anderson, 2002).

After identifying the most parsimonious model for p and c, we used that model to compare various parameterizations of temporary emigration. Temporary emigration can either be random or Markovian and is represented by two parameters, γ''_i and γ'_i, respectively (Kendall et al., 1997). Random temporary emigration is the probability that movement between availability states between primary occasions i and $i + 1$ is independent of the previous state of the individual. On the other hand, Markovian temporary emigration is the probability that movement between availability states is dependent on the previous availability of the animal. Two probabilities are associated with Markovian temporary emigration: γ''_i, defined as the probability that an animal available at time $i - 1$ temporally emigrates from the sampling area and is unavailable for encounter at time i, and γ'_I, defined as the probability that an animal not present in the sampling area at time $i - 1$ is also not present at time i. Permutations for γ included: no temporary emigration ($\gamma'' = \gamma' = 0$), constant and random temporary emigration ($\gamma'' = \gamma'[.]$), constant and random temporary emigration with all drought indices having the same parameter ($\gamma'' = \gamma'[drought]$), and constant and random temporary emigration dependent on nondrought conditions, typical drought conditions (i.e., D0, D1), and supraseasonal drought conditions (October 2007–August 2008; i.e., $\gamma'' = \gamma'$ [drought severity]). We compared random and no temporary emigration models with Markovian models that included the identical parameters as random temporary emigration models. The fit of the
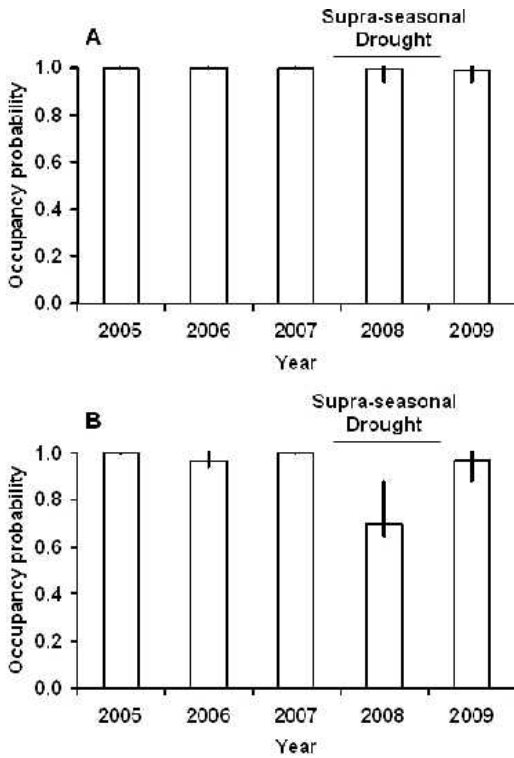
FIG. 2.—Estimated annual occupancy probabilities of adult (A) and larval (B) Northern Dusky Salamanders (*Desmognathus fuscus*) detected in 17 first-order streams in the western Piedmont of North Carolina, USA (error bars, 95% credible intervals).

candidate models were compared using AIC_c (Burnham and Anderson, 2002).

Finally, using the top model for temporary emigration and capture probability, we evaluated three models for apparent survival rate (S): apparent survival is constant over time($S[.]$), apparent survival is dependent on drought ($S[drought]$), and apparent survival differs among normal, typical drought conditions (D0, D1), and supraseasonal drought conditions ([S{drought severity}]). Again, AIC_c was used to select our best models(s) using Akaike weights (w) to indicate the probability that the model was the best among the whole set of candidate models (Burnham and Anderson, 2002). In all mark–recapture models, ML was used to estimate parameters and their standard errors.

RESULTS

Occupancy Patterns

Adult *D. fuscus* occupancy probability, assessed in March and April of each year, remained near or at 1.0 throughout the 5 yr of sampling and we found no change in occupancy during the 2007–2008 supraseasonal drought (Fig. 2a). Using the aforementioned combination of sampling methods, adult *D. fuscus* detection was ≥ 0.76 (95% credible interval 0.61–0.89) in all years of the study. Similarly, larval *D. fuscus* occupancy was ≥ 0.97 in 2005, 2006, 2007, and 2009. During the 2007–2008 supraseasonal drought, however, larval occupancy probabilities decreased to an average of 0.70 (95% credible interval 0.65–0.82; Fig. 2b). Detection of larvae was ≥ 0.83 (95% credible interval 0.69–0.94) in all years.

Temporary Emigration and Survival

We recorded 2303 captures of 1381 adult *D. fuscus* individuals from October 2005 through

TABLE 1.—Model rankings for estimating capture (p) and recapture (c) probabilities for the Northern Dusky Salamander (*Desmognathus fuscus*) sampled at one first–order stream in Mecklenburg County, North Carolina, USA, from October 2005 to November 2010. Survivorship was held constant and temporary emigration was random in all models.

Model	Number of parameters	AIC_c[1]	ΔAIC_c	AIC_c wt
p(month)c(month)	26	10,329.62	0.00	0.93
p(t)=c(t)	63	10,334.69	5.06	0.07
p(month)=c(month)	14	10,360.54	30.91	0.00
p(t)c(t)	124	10,371.09	41.46	0.00
p(severe)c(severe)	8	10,389.08	59.45	0.00
p(.)c(.)	4	10,389.92	60.30	0.00
p(drought)c(drought)	6	10,393.41	63.79	0.00
p(severe)=c(severe)	5	10,407.20	77.58	0.00
p(.)=c(.)	3	10,411.76	82.14	0.00
p(drought)=c(drought)	4	10,413.60	83.98	0.00

[1] AIC_c, Akaike's information criterion adjusted for small sample sizes.

TABLE 2.—Model rankings for estimating temporary emigration (γ) in the Northern Dusky Salamander (*Desmognathus fuscus*) sampled at one first-order stream in Mecklenburg County, North Carolina, USA, from October 2005 to November 2010. Survivorship was held constant and recapture and capture probabilities were month specific.

Model	Number of parameters	AIC_c[1]	ΔAIC_c	AIC_c wt
γ(Markovian, severe)	31	10,236.96	0.00	1.00
γ(Markovian, drought)	29	10,251.70	14.74	0.00
γ(Markovian)	27	10,254.97	18.01	0.00
γ(random, severe)	28	10,320.34	83.38	0.00
γ(random, drought)	27	10,321.99	85.03	0.00
γ(random)	26	10,329.62	92.67	0.00
γ(0)	25	10,359.60	122.64	0.00

[1] AIC_c, Akaike's information criterion adjusted for small sample sizes.

November 2010 at SRNP. Our top model for dusky salamander detection indicated month-specific capture and recapture probabilities (Akaike weight = 0.93; Table 1). We found support for models that included Markovian temporary emigration. These models generally performed significantly better than the models with random temporary emigration or no temporary emigration (i.e., fixed to zero). The top model for temporary emigration indicated Markovian temporary emigration with a response based on drought severity (Akaike weight = 1.00; Table 2). Our top model for *D. fuscus* survival indicated that survivorship varied according to drought severity (Akaike weight = 0.81; Table 3).

Real parameter estimates of capture probability for adult *D. fuscus* ranged from 0.16 (1 SE = 0.03, 95% confidence interval [CI] = 0.11–0.22) in April to 0.04 (1 SE = 0.01, 95% CI = 0.03–0.07) in June. We found evidence of capture response, with salamanders exhibiting greater or lesser probability of capture depending on month. Real parameter estimates for recapture probability ranged from 0.19 (1 SE = 0.05, 95% CI = 0.11–0.30) in July to 0.02 (1 SE = 0.02, 95% CI = 0.01–0.09) in December.

Temporary emigration parameter estimates varied in accordance with drought severity. Although the real parameter estimates had large confidence intervals, γ''_i, (i.e., the probability that an animal available at time $i - 1$ temporally emigrates from the sampling area) during the supraseasonal drought was approximately twice as large as γ''_i during nondrought and typical drought conditions (Fig. 3). The immigration parameter, γ'_i (i.e., the probability that an animal not present in the sampling area at time $i - 1$ is also not present in at time i) was greatest during typical drought conditions and roughly equal during nondrought and supraseasonal drought conditions.

Survival of *D. fuscus* was greatest during typical drought conditions, with a real parameter estimate of 0.97 (1 SE = 0.02, 95% CI = 0.91–0.99). During normal conditions and supraseasonal drought conditions, survival estimates were 0.89 (1 SE = 0.02, 95% CI = 0.84–0.91) and 0.90 (1 SE = 0.01, 95% CI = 0.87–0.91), respectively.

DISCUSSION

We used empirical methods to evaluate the effects of supraseasonal droughts on the stream salamander *D. fuscus*. Our results

TABLE 3.—Model rankings for estimating survival (*S*) in the Northern Dusky Salamander (*Desmognathus fuscus*) sampled at one first-order stream in Mecklenburg County, North Carolina, USA from October 2005 to November 2010. Temporary emigration was Markovian and dependent on drought severity and recapture and capture probabilities were month-specific.

Model	Number of parameters	AIC_c	ΔAIC_c	AIC_c wt
S(severe)	33	10,233.22	0.00	0.81
S(.)	31	10,236.96	3.74	0.12
S(drought)	32	10,238.12	4.90	0.07

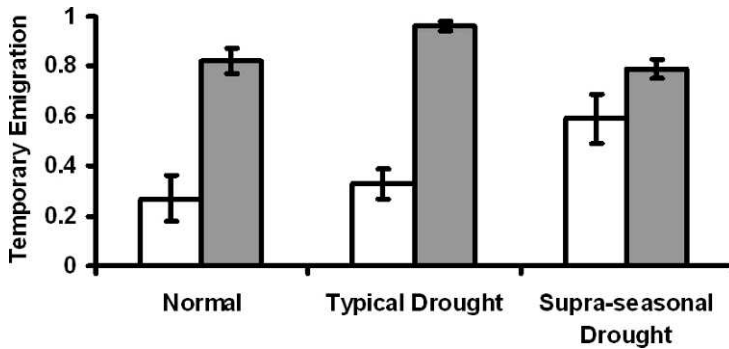AIC_c, Akaike's information criterion adjusted for small sample sizes.

F<small>IG</small>. 3.—Estimates of Markovian, drought severity-specific temporary emigration probabilities of Northern Dusky Salamanders (*Desmognathus fuscus*) sampled from October 2005 to November 2010 in one first-order stream in Mecklenburg County, NC. Components of Markovian temporary emigration include γ'' (white bars), defined as the probability that an animal available at time $i - 1$ temporally emigrates from the sampling area (e.g., likely moving underground or to the terrestrial environment for salamanders) and is unavailable for encounter in time i, and γ' (gray bars), defined as the probability that an animal not present in the sampling area at time $i - 1$ is also not present in the sampling area at time i. Typical drought conditions consist of time periods when drought conditions were either abnormally dry or moderate drought; supraseasonal drought conditions occurred from October 2007 to August 2008, when drought conditions were either severe, extreme, or exceptional. Error bars, ±1 SE.

illustrated that occupancy of larvae declined during supraseasonal droughts but that adults were resistant to supraseasonal drought, as their occupancy probabilities did not differ between nondrought and supraseasonal drought conditions. Adult survival remained relatively high during supraseasonal droughts due to high rates of temporary emigration. Thus, *D. fuscus* appear to use both between- and within-generation refugium-use strategies to persist through periods of supraseasonal drought.

Our findings of reduced resistance of *D. fuscus* larvae during the supraseasonal drought suggest either increased mortality of larvae or eggs, failure of adult females to oviposit, or the use of hyporheic zones by larval salamanders. *Desmognathus* larvae in the North Carolina Piedmont generally hatch from August to October and reside in streams until metamorphosis in May through July (Danstedt, 1975). Thus, maintenance of free-flowing water during this time period is likely critical for larval survival. During the 2007–2008 supraseasonal drought, surface water in the majority of the study streams was minimal or altogether absent, possibly resulting in higher mortality rates than those during nondrought years. Indeed, drought is a well-known stressor on survivorship and recruitment of larval pond-breeding salamander

populations (e.g., Semlitsch, 1987) and other amphibians (Kagarise Sherman and Morton, 1993). In a related study of stream biota, Davies et al. (1998) found that recruitment by trout (*Salmo trutta* and *Oncorhynchus mykiss*) was severely limited both during and after drought, which led to the conclusion that drought-induced mortality was the most likely cause. It is also possible that limited oviposition or loss of eggs could have occurred during the supraseasonal drought, leading to the reduced occupancy of larval *D. fuscus*. Camp and Tilley (2005) reported limited oviposition and the loss of clutches by female Ocoee Salamanders (*Desmognathus ocoee*) during a drought, resulting in an eventual extirpation. Finally, larval salamander occupancy may have decreased due to an increase in use of the hyporheic zone. Feral et al. (2005) found that larval Pacific Giant Salamanders (*Dicamptodon tenebrosus*) used hyporheic zones in intermittent streams in California, with most captures occurring when there was no surface flow. Although studies on *D. fuscus* use of hyporheic zones are nonexistent, it is possible that *D. fuscus* larvae use hyporheic zones during supraseasonal droughts as a within-generation refugium-use strategy.

The lack of a response by adult *D. fuscus*, as measured through occupancy rates, to supraseasonal drought suggests an important be-

tween-generation refugium-use strategy. Complex life cycles have been shown to allow persistence of stream biota during droughts: high survival of one stage can buffer the low survival of another stage (Boulton, 2003). For example, many macroinvertebrates found in intermittent streams have eggs or juvenile stages that can survive desiccation (Miller and Golladay, 1996). Our CMR analysis indicated that adult *D. fuscus* had high survivorship probabilities during supraseasonal droughts despite the deterioration of the in-stream habitat. These survivorship probabilities differed little from survival during nondrought conditions. Thus, it is likely that the high survival of adult *D. fuscus* during supraseasonal drought conditions buffers the negative effects of drought on larval *D. fuscus*.

Our results also highlight the importance of temporary emigration as a within-generation refugium-use strategy used by *D. fuscus*. We found that during supraseasonal droughts, the probability that a salamander emigrated from the sampling area to a refuge between samples was approximately twice as probable as emigration during nondrought and typical drought conditions. Thus, our data indicate that *D. fuscus* moves from the streambed surface to an underground or high-humidity refuge. The specific refuge type utilized by adult *D. fuscus* was not detected during our study; however, we speculate that the refuge occurs within the stream, as *D. fuscus* rarely move more than a few meters from the stream margin (Petranka, 1998). Refuge use by other stream animals during drought include migration to the hyporheic zone (Griffith and Perry, 1993), movements to permanent pools in otherwise dry streams (Labbe and Fausch, 2000), movements to headwater seeps (Davey et al., 2006), and movements into substratum or interstitial spaces (Morrison, 1990). These refuges could likewise be utilized by *D. fuscus*. Crayfish burrows (DiStefano et al., 2009) and large rocks (Keen, 1982) may be particularly important refuges for stream-dwelling salamanders; Ashton (1975) documented that *D. fuscus* moved into crayfish burrows when stream temperatures rose to 22°C. Regardless of the specific type of refugium use, our results concluded that temporary emigration rates are much higher during supraseasonal

drought conditions than during typical droughts and nondrought conditions.

We found that the highest survival probability occurred during typical drought conditions (i.e., D0 and D1 drought indices). We also found that during these typical drought conditions, the probability of temporarily emigrating between samples was slightly greater than during nondrought conditions, but far less than supraseasonal drought conditions. More importantly, the probability that a salamander was not present during a sample as well as the previous sample was substantially greater than during both nondrought and supraseasonal drought conditions. These findings are consistent with low immigration rates due to the use of refuge for extensive amounts of time during typical seasonal drought conditions. Our data also indicate that individual survival probability is extremely high during these periods of refuge use. Although speculative, lower survival during nondrought conditions may be a reflection of greater activity and foraging by *D. fuscus* during periods of preferred moisture levels (Barbour et al., 1969; Keen, 1984), which can increase susceptibility to predation (Zaret and Rand, 1971; Karlin and Pfingsten, 1989; Schlosser et al., 2000). Somewhat reduced survival and higher probability of being an immigrant during supraseasonal drought conditions compared with typical drought conditions indicates that refugia that may be suitable during typical droughts may not hold the moisture necessary to combat significant water loss, thus reducing overall survival. Furthermore, higher return rates of temporary emigrants indicate that surface activity, particularly movement from a refuge to the surface, still occurred. Surface activity during the supraseasonal drought may have not only resulted in a significant desiccation risk, but also may have led to high predation rates on salamanders.

Our study of drought effects on *D. fuscus* has implications into the consequences for stream-inhabiting salamander populations in the face of climate change. Climate-change models project that globally many regions will experience episodic precipitation patterns and longer, more severe droughts (Schindler, 1997; Bates et al., 2008; Dai, 2011). Isolated,

aquatic ecosystems, which are dependent on a balance of precipitation and evaporation, may be at particular risk as increased drought severity could increase mortality risks of larvae and possibly result in early metamorphosis and subsequent declines in salamander fitness and adult size (Brooks, 2009). Yet, empirical evidence on the effects of drought on stream salamander populations was limited before our investigation. We showed that *D. fuscus* utilize both between-generation and within-generation refugium-use strategies that provide resistance and resilience to especially severe drought conditions. However, climate change may increase the temporal duration of droughts beyond the 11 mo of supraseasonal drought seen in our study (Dai, 2011). The probability of an adult surviving for 1 yr during supraseasonal drought conditions is 28% (i.e., 0.9^{12}); for 2 yr survival is estimated at 8%; surviving for 3 yr is approximately is 2%; and surviving for 4 yr is 0.06%. Thus, if no recruitment from the larval class occurs during extended (e.g., >4 yr) supraseasonal droughts, adult populations will likely have a low probability of persisting. However, long-term studies are needed to fully assess the resistance and resilience of amphibians and other stream biota to lengthy supraseasonal droughts.

Literature Cited

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. Pp. 267–281 in B.N. Petrov and F. Csáki (Eds.), Second International Symposium on Information Theory, Akademiai Kiadó, Hungary.

Ashton, R.E., Jr. 1975. A study of the movement, home range, and winter behavior of *Desmognathus fuscus* (Rafinesque). Journal of Herpetology 9:85–91.

Barbour, R.W., J.W. Hardin, J.P. Schafer, and M.J. Harvey. 1969. Home range, movement, and activity of the Dusky Salamander, *Desmognathus fuscus*. Copeia 1969:293–297.

Bates, B.C., Z.W. Kundzewicz, S. Wu, and J.P. Palutikof (Eds.), 2008. Climate Change and Water. Technical Paper of the Intergovernmetnal Panel on Climate Change, IPCC Secretariat, Geneva. Available at http://www.ipcc.ch/pdf/technical-papers/climate-change-water-en.pdf. Archived by WebCite at http://www.webcitation.org/67gEQSmeQ on 15 May 2012.

Boulton, A.J. 1989. Over-wintering refuges of aquatic macroinvertebrates to two intermittent streams in central Victoria. Transactions of the Royal Society of South Australia 113:23–34.

Boulton, A.J. 2003. Parallels and contrasts in the effects of drought on stream macroinvertebrate assemblages. Freshwater Biology 48:1173–1185.

Brooks, R.T. 2009. Potential impacts of global climate change on hydrology and ecology of ephemeral freshwater systems of the forests of the northeastern United States. Climatic Change 95:469–483.

Burnham, K.P., and D.R. Anderson. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. Springer-Verlag, USA.

Burton, T.M., and G.E. Likens. 1975. Salamander populations and biomass in the Hubbard Brook Experimental Forest, New Hampshire. Copeia 1975:541–546.

Camp, C.D., and S.G. Tilley. 2005. *Desmognathus ocoee*, Ocoee Salamander, Pp. 719–721 in M. Lannoo (Ed.), Amphibian Declines: The Conservation Status of United States Species, University of California Press, USA.

Cecala, K.K., S.J. Price, and M.E. Dorcas. 2007. Diet of larval red salamanders (*Pseudotriton ruber*) examined using a nonlethal technique. Journal of Herpetology 41:741–745.

Church, D.R., L.L. Bailey, H.M. Wilbur, W.L. Kendall, and J.E. Hines. 2007. Iteroparity in the variable environment of the salamander *Amybstoma tigrinum*. Ecology 88:891–903.

Clinton, S.M., N.B. Grimm, and S.G. Fisher. 1996. Response of a hyporheic invertebrate assemblage to drying disturbance in a desert stream. Journal of the North American Benthological Society 15:700–712.

Cowx, I.G., W.O. Young, and J.M. Hellawell. 1984. The influence of drought on the fish and invertebrate populations of an upland stream in Wales. Freshwater Biology 14:165–177.

Dai, A. 2011. Drought under global warming: A review. Wiley Interdisciplinary Reviews: Climate Change 2:45–65.

Danstedt, R.T., Jr. 1975. Local geographic variation in demographic parameters and body size of *Desmognathus fuscus* (Amphibia: Plethodontidae). Ecology 56:1054–1067.

Davey, A.J.H., D.J. Kelly, and B.J.F. Biggs. 2006. Refuge use strategies of stream fishes in response to extreme low flows. Journal of Fish Biology 69:1047–1059.

Davic, R.D., and H.H. Welsh, Jr. 2004. On the ecological roles of salamanders. Annual Review in Ecology, Evolution and Systematics 35:405–434.

Davies, P.E., R.D. Sloane, and J. Andrew. 1998. Effects of hydrological change and the cessation of stocking on a stream population of *Salmo trutta* L. Australian Journal of Marine and Freshwater Research 39:337–354.

DiStefano, R.J., D.D. Magoulick, E.M. Imhoff, and E.R. Larson. 2009. Imperiled crayfishes use hyporheic zone during seasonal drying of an intermittent stream. Journal of the North American Benthological Society 28:142–152.

Feral, D., M.A. Camann, and H.H. Welsch, Jr. 2005. *Dicamptodon temebrosus* larvae within hyporheic zones of intermittent streams in California. Herpetological Review 36:26–27.

Gasith, A., and V.H. Resh. 1999. Streams in Mediterranean climate regions: Abiotic influences and biotic response to predictable seasonal events. Annual Review in Ecology and Systematics 30:51–81.

Griffith, M.B., and S.A. Perry. 1993. The distribution of macroinvertebrates in the hyporheic zone of two small Appalachian headwater streams. Archiv für Hydrobiologies 126:373–384.

Hakala, J.P., and K.J. Hartman. 2004. Drought effect on stream morphology and brook trout (*Salvelinus fontinalis*) populations in forested headwater streams. Hydrobiologia 515:203–213.

Huggins, R.M. 1989. On the statistical analysis of capture–recapture experiments. Biometrika 76:133–140.

Huggins, R.M. 1991. Some practical aspects of a conditional likelihood approach to capture experiments. Biometrics 47:725–732.

Humphries, P., and D.S. Baldwin. 2003. Drought and aquatic ecosystems: An introduction. Freshwater Biology 48:1141–1146.

Jones, R.L. 1986. Reproductive biology of *Desmognathus fuscus* and *Desmognathus santeetlah* in the Unicoi Mountains. Herpetologica 42:323–334.

Kagarise Sherman, C., and M. L. Morton. 1993. Population declines of Yosemite toads in the eastern Sierra Nevada of California. Journal of Herpetology 27:186–198.

Karlin, A.A., and P.A. Pfingsten. 1989. *Desmognathus fuscus* (Rafinesque), dusky salamander. Pp. 174–180 in R. A. Pfingsten and F. L. Downs (Eds.), Salamanders of Ohio. Ohio Biological Survey Bulletin, New Series Volume 7.

Keen, W.H. 1982. Habitat selection and interspecific competition in two species of plethodontid salamanders. Ecology 63:94–102.

Keen, W.H. 1984. Influence of moisture on the activity of a plethodontid salamander. Copeia 1984:684–688.

Kendall, W.L., J.D. Nichols, and J.E. Hines. 1997. Estimating temporary emigration using capture–recapture data with Pollock's robust design. Ecology 78:563–578.

Kéry, M. 2010. Introduction to WinBUGS for Ecologists: A Bayesian Approach to Regression, ANOVA, Mixed Models and Related Analyses. Academic Press, USA.

Labbe, T.R., and K.D. Fausch. 2000. Dynamics of intermittent stream habitat regulate persistence of a threatened fish at multiple scales. Ecological Applications 10:1774–1791.

Lake, P.S. 2003. Ecological effects of perturbation by drought in flowing waters. Freshwater Biology 48:1161–1172.

Lebreton, J. -D., K.P. Burnham, J. Clobert, and D.R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: A unified approach with case studies. Ecological Monographs 62:67–118.

Le Cam, L. 1990. Maximum likelihood: An introduction. International Statistical Review 58:153–171.

Love, J.W., C.M. Taylor, and M.P. Warren. 2008. Effects of summer drought on fish and macroinvertebrate assemblage properties in upland Ouachita mountain streams, U.S.A. American Midland Naturalist 160:265–277.

Magoulick, D.A., and R.M. Kobza. 2003. The role of refugia for fishes during drought: A review and synthesis. Freshwater Biology 48:1186–1198.

Miller, A.M., and S.W. Golladay. 1996. Effects of spates and drying on macroinvertebrate assemblages of an intermittent and a perennial prairie stream. Journal of the North American Benthological Society 15:670–689.

Morrison, B.R. 1990. Recolonisation of four small streams in central Scotland following drought conditions in 1984. Hydrobiologia 208:261–267.

Muths, E., R.D. Scherer, P.S. Corn, and B.A. Lambert. 2006. Estimation of temporary emigration in male toads. Ecology 87:1048–1056.

Orser, P.N., and D.J. Shure. 1975. Population cycles and activity patterns of the dusky salamander, *Desmognathus fuscus fuscus*. American Midland Naturalist 93:403–410.

Peterman, W.E., J.A. Crawford, and R.D. Semlitsch. 2008. Productivity and significance of headwater streams: Population structure and biomass of the black-bellied salamander (*Desmognathus quadramaculatus*). Freshwater Biology 53:347–357.

Petranka, J.W. 1998. Salamanders of the United States and Canada. Smithsonian Institution Press, USA.

Petranka, J.W., and S.S. Murray. 2001. Effectiveness of removal sampling for determining salamander density and biomass: A case study in an Appalachian streamside community. Journal of Herpetology 35:36–44.

Price, S.J., K.K. Cecala, R.A. Browne, and M.E. Dorcas. 2011. Effects of urbanization on occupancy of stream salamanders. Conservation Biology 25:547–555.

Price, S.J., E.A. Eskew, K.K. Cecala, R.A. Browne, and M.E. Dorcas. 2012. Estimating survival of a streamside salamander: Importance of temporary emigration, capture response, and location. Hydrobiologia 679:205–215.

Royle, J.A., and R.M. Dorazio. 2008. Hierarchical modeling and inference in ecology: The analysis of data from populations, metapopulations and communities. Academic Press, USA.

Royle, J.A., and M. Kéry. 2007. A Bayesian state-space formulation of dynamic occupancy models. Ecology 88:1813–1823.

Schindler, D.W. 1997. Widespread effects of climatic warming on freshwater ecosystems in North America. Hydrological Processes 11:1043–1067.

Schlosser, I.J., J.D. Johnson, W.L. Knoteck, and M. Lapinksa. 2000. Climate variability and size-structured interactions among juvenile fish along a lake–stream gradient. Ecology 8:1046–1057.

Semlitsch, R.D. 1987. Relationship of pond drying to the reproductive success of the salamander *Ambystoma talpoideum*. Copeia 1987:61–69.

Spiegelhalter, D.J., A. Thomas, N.G. Best, and D. Lunn. 2003. WinBUGS user manual. Version 1.4. MRC Biostatistics Unit, UK.

Spight, T.M. 1967. Population structure and biomass production by a stream salamander. American Midland Naturalist 78:437–447.

White, G.C., and K.P. Burnham. 1999. Program MARK: Survival estimation from populations of marked animals. Bird Study 46:120–139.

Yount, D.D., and G.D. Niemi. 1990. Recovery of lotic communities and ecosystems from disturbance—A narrative view of case studies. Environmental Management 14:547–569.

Zaret, T.M., and A.S. Rand. 1971. Competition in tropical stream fishes: Support for the competitive exclusion principle. Ecology 52:336–342.