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Author(s): Grant M. Connette, Steven J. Price and Michael E. Dorcas
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Influence of Abiotic Factors on Activity in a Larval Stream Salamander Assemblage

Grant M. Connette[1,2,*], Steven J. Price[1,3], and Michael E. Dorcas[1]

Abstract - Larval stream salamanders are the numerically dominant predators in many headwater stream systems. Nonetheless, little is known about their activity patterns or the extent to which their movements are influenced by prevailing environmental conditions. In this study, we used capture rates from passive trapping as an index of activity level and sought to identify the environmental variables most responsible for fluctuations in larval stream salamander activity. Over the course of two months, we captured stream salamanders in aquatic funnel traps during both day- and night-trapping sessions at a first-order stream in the North Carolina Piedmont. Using an information-theoretic approach, we constructed models to elucidate the effects of (1) water temperature, (2) cloud cover, (3) days since last rainfall, and (4) time of day on larval salamander activity. We found that the model incorporating time of day and cloud cover was the best predictor of larval salamander activity. In our study, larval salamander activity was highest at night and also demonstrated a weak positive correlation with increasing cloud cover. Using model-averaging, we further determined that our time of day and cloud cover variables demonstrated a significant correlation with observed activity levels. This pattern of peak activity under low light conditions could be a behavioral adaptation that limits predation risk for larval salamanders.

Introduction

Understanding the activity patterns of a species is a critical step towards understanding how that species interacts with its environment. In many cases, the daily activity pattern of an individual may be dictated by competing requirements for resource acquisition and predator avoidance (Werner and Anholt 1993, Yurewicz 2004). For many salamanders, this has been shown to result in shifts in active periods or patterns of microhabitat use during times of perceived predation risk (Barr and Babbitt 2007, Holomuzki 1986, Madison et al. 1999, Maerz et al. 2001). Furthermore, the activity patterns of adult stream salamanders have been shown to correspond with daily peaks in prey abundance (Holomuzki 1980). Stream salamander activity can also be broadly shaped by cyclical factors such as season or reproductive cycle (Orser and Shure 1975). Over the short term, however, much of the observed variability in the activity levels of adult stream salamanders may be correlated with changes in environmental conditions such as temperature, rainfall, or substrate moisture (Barbour et al. 1969, Hairston 1949, Keen 1984, Orser and Shure 1975).

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[1] Department of Biology, Davidson College, Davidson, NC 28035-7118. [2] Division of Biological Sciences, University of Missouri, Columbia, MO 65211-7400. [3] Department of Biology, Wake Forest University, Winston-Salem, NC 27109. [*] Corresponding author - gmcz7c@mail.mizzou.edu.

Stream salamanders often serve as the dominant vertebrate predators in headwater streams (Davic and Welsh 2004) and may constitute a considerable biomass reservoir in these systems (Hairston 1987, Peterman et al. 2008, Petranka and Murray 2001). In the eastern United States, the majority of stream-affiliated species are lungless salamanders of the family Plethodontidae, and most have complex life cycles consisting of an aquatic larval stage followed by a semi-terrestrial adult stage (Petranka 1998). In many cases, larval salamanders may be more numerous than adults and likely represent a larger part of the total species biomass (Davic and Welsh 2004). Because adult stream salamanders rely entirely on cutaneous respiration, they are highly susceptible to water loss across the moist, permeable surface of their skin and may be forced to reduce their terrestrial activity until optimal temperature and moisture conditions occur (Feder 1983). Being fully aquatic, the larvae of these species may show fundamentally different responses to prevailing environmental conditions.

Despite its ecological relevance in headwater stream systems, few studies have examined the timing of daily activity patterns in larval salamanders (but see Barr and Babbitt 2007, Orser and Shure 1975, Petranka 1984) and few studies have specifically examined the environmental correlates of activity patterns in stream salamanders (but see Johnson and Goldberg 1975). Although Orser and Shure (1975) found surface densities of larval *Desmognathus fuscus* (Rafinesque) Dusky Salamander to be no higher at night than during the day, a second study (Petranka 1984) described a tendency for nocturnal activity in larval *Eurycea bislineata* (Green) Northern Two-lined Salamander. Interestingly, another study found that Northern Two-lined Salamander larvae demonstrated aperiodic activity patterns until a fish predator was added, causing larvae to adopt primarily nocturnal activity (Barr and Babbitt 2007). It is also possible that observed nocturnal activity in certain salamanders is a product of light level (Placyk and Graves 2001, Sites 1978), suggesting that periods of high cloud cover may also correspond with increased activity.

Although numerous studies have demonstrated the sensitivity of terrestrial amphibian activity to moisture and temperature conditions associated with desiccation risk (e.g., Gibbons and Bennett 1974, Hairston 1949, Keen 1984, Mazerolle 2001, Orser and Shure 1975, Semlitsch 1985, Todd and Winne 2006), larval stream salamanders are entirely aquatic, and their foraging activity is not physiologically limited by water loss. Johnson and Goldberg (1975) found a general lack of larval salamander movement during high-flow periods, but observed that larval activity peaked as flow levels stabilized following heavy rainfall. Increased stream discharge following rainfall has been shown to increase invertebrate drift (O'Hop and Wallace 1983), which represents a potential influx of prey for larval salamanders. As a result, rainfall could function as an important determinant of foraging activity. Finally, water temperature has been shown to limit the swimming efficiency of salamanders (Marvin 2003a), suggesting that low water temperatures may cause increased susceptibility to downstream drift (Cecala et al. 2009) or an overall tendency for reduced activity.

In this study, we used capture rates from a passive trapping technique as an index of overall movement activity and sought to examine the influence of several abiotic factors on the observed activity patterns of larval stream salamanders. We consider the following factors to be potentially important as determinants of larval salamander activity: time of day (day vs. night), temperature, rainfall, and cloud cover. We used regression analysis and employed an information-theoretic approach to model selection in order to determine which abiotic factors best predict patterns of larval salamander activity.

Field-site Description

We captured salamanders in a first-order stream located in the Cowans Ford Wildlife Refuge in Mecklenberg County, NC (35.3775°N, 80.9658°W). This 150-m perennial stream originates from two seeps and passes through a secondary, mixed-hardwood forest before flowing into Mountain Island Lake (Cecala et al. 2009). Five salamander species have been identified at this site during previous research, including Northern Dusky Salamander*,* Southern Two-lined Salamander*, Eurycea guttolineata* Holbrook (Three-lined Salamander)*, Pseudotriton montanus* Baird (Mud Salamander)*,* and *P. ruber* Dunn (Red Salamander) (K. Cecala, University of Georgia, Athens, GA, pers. comm.).

Methods

We sampled larval salamanders using one-liter plastic, inverted bottle funnel traps (Willson and Dorcas 2003). Capture rates from passive sampling techniques, such as funnel trapping, are dependent on both the density of animals within the study area as well as the activity levels of those animals (Willson and Gibbons 2009). Thus, capture rates from passive trapping would reflect changes in activity levels during short-term studies where amphibian population densities remain relatively constant (Willson and Gibbons 2009). As a result, passive sampling using drift fences has been employed to study both seasonal (Gibbons and Bennett 1974, Mazerolle 2001, Todd and Winne 2006) and daily (Semlitsch and Pechmann 1985) patterns of migratory activity in pond-breeding amphibians, as well as environmental correlates of activity patterns (Gibbons and Bennett 1974, Mazerolle 2001, Semlitsch 1985, Todd and Winne 2006). Although the use of funnel traps has been previously used to define patterns of surface activity in a pond-breeding salamander, *Ambystoma tigrinum* (Green) (Eastern Tiger Salamander; Holomuzki and Collins 1983), this technique has not been applied to studies of the activity levels of stream-associated salamanders. In this study, we used capture rates from funnel traps (total number of captures per sampling period) as an index of overall larval salamander activity.

Traps were arranged in one of four blocks containing ten traps each. Traps within each block were arranged in pairs, with each pair containing one upstream-facing and one downstream-facing trap. All pairs of traps within each block were separated by 3 m. We conducted five trapping sessions between 4 October and 4 December 2007. During each trapping session, we checked all traps within one hour of sunrise and sunset each day over the course of four days. An individual captured before traps were checked at sunrise was considered a night capture, whereas an individual captured before traps were checked at sunset was considered a day capture. We alternated whether day or night trapping was conducted first during each trapping session in order to mitigate the influence of any behavioral changes resulting from previous sampling intervals. For each individual captured, we recorded both the location and orientation of the trap in which it was captured. Because we were interested in examining the activity patterns of larval salamanders, the few adults captured were excluded from all analyses. After measuring each salamander, we released the individual 1 m downstream from the trap to ensure that it was not washed immediately back into the trap. Total processing time did not exceed two minutes per salamander.

To determine the effects of environmental variation on salamander activity, we took measurements on a number of abiotic variables, including air temperature, water temperature, recent rainfall, and cloud cover. Water temperature was collected at 15-minute intervals by a datalogger (TidbiT v2, UTBI-001, Onset Computer Inc., Pocasset, MA) which was submerged in the center of the stream. Air temperature was also measured every 15 minutes with a datalogger (Hobo Pro RH/Temp, H08-032-08, Onset Computer Inc.). Because of a high degree of correlation between water temperature and air temperature ($r > 0.92$), we included only mean water temperature in our analyses. The mean water temperature for a trapping period was classified as the mean of all 15-minute intervals during the approximately 12-hour period since traps were last checked. Recent rainfall was recorded as the number of days since the last rainfall event. We also visually estimated percent cloud cover from a nearby clearing each time we checked traps and categorized these values as either low (<33%), medium (34–67%), or high (>67%) (see Girard et al. 2003).

We modeled count data (total number of captures per visit) with a generalized linear model following a Poisson distribution and created 15 a priori models using combinations of four environmental variables to compare their ability to predict stream salamander activity. We employed an information-theoretic approach to model selection (Burnham and Anderson, 2002) to determine the relationship between the abiotic variables and stream salamander activity. The information-theoretic approach ranks each model based on the strength of evidence for that model relative to the complete set of models. The models we constructed were (1) GLOBAL (includes day vs. night, mean water temperature, cloud cover, and days since last rainfall), (2) Night (day vs. night), (3) Temp (mean water temperature), (4) Cloud (cloud cover), (5) Rain (days since last rainfall), (6) RainCloudTemp, (7) RainCloudNight, (8) RainTempNight, (9) CloudTempNight, (10) RainCloud, (11) RainTemp, (12) RainNight, (13) CloudTemp, (14) CloudNight, and (15) TempNight.

For each model, we calculated the $QAIC_c$ value, which is a measure of the strength of evidence for a given model, adjusted for overdispersion and small sample size, as follows:

$$QAIC_c = -2(log - likelihood) / \hat{c} + 2K(K + 1) / (n - K - 1)$$

When calculating $QAIC_c$ values for each model, we used the dispersion parameter ($\hat{c}$) of the global model (Mazerolle 2006). We then calculated $\Delta QAIC_c$ for each model, which is the difference in $QAIC_c$ between each model and the best model in the set. A $\Delta QAIC_c$ less than 2 suggests that there is substantial support for the model, a $\Delta QAIC_c$ between 3 and 7 suggests that there is considerably less support for the model, and a $\Delta QAIC_c$ greater than 10 suggests that the model is very unlikely to best explain reality (Burnham and Anderson 2002). We also calculated Akaike weights (ω_i), which represent the probability that the given model is the best among the entire set of candidate models.

We first developed models that incorporated data for all larval salamander captures together and then developed species-specific models for larval Red Salamander, which was the most commonly encountered species over the course of our study. Because there were two or more models competing for first place in both sets of analysis, we also calculated model-averaged parameter estimates and corresponding unconditional standard errors for each of the four environmental variables incorporated in the models (Burnham and Anderson 2002, Mazerolle 2006). Confidence intervals were calculated for each model-averaged parameter estimate as the individual estimate ± (1.96) multiplied by the unconditional standard error for that estimate (Burnham and Anderson 2002, Mazerolle 2006).

Results

We captured a total of 96 salamanders (17 adult, 79 larvae), representing each of the five species known to be present at our study site: Dusky Salamander (10 adult, 20 larvae), Southern Two-lined Salamander (3 larvae)*,* Three-lined Salamander (21 larvae)*,* Mud Salamander (6 adult, 2 larvae), and Red Salamander (1 adult, 33 larvae). Of the larvae captured in this study, 65 (82%) were captured during night-trapping intervals, while 14 (18%) were captured during day-trapping. We captured a mean of 1.92 ± 2.06 SD (n = 24) salamanders under low cloud cover (0–33%), 1.00 ± 0.82 SD (n = 7) under medium cloud cover (34–66%), and 4.78 ± 4.52 SD (n = 8) under high cloud cover. Traps facing upstream captured only two more salamanders (n = 49) than those facing downstream (n = 47), suggesting that capture rates were not merely a product of downstream drift (Bruce 1986). When larval captures from all species were combined, the model incorporating cloud cover and time of day best predicted stream salamander activity (ω_i = 0.43; Table 1). There was also substantial support for the model incorporating cloud cover, water temperature, and time of day (ω_i = 0.19) and the model incorporating cloud cover, rainfall, and time of day (ω_i = 0.12). Of the four variables considered, only the model-averaged parameter estimates for time of day and cloud cover had 95% confidence intervals which did not overlap zero (Table 3), indicating that these variables were the most important predictors of larval salamander activity.

The models that best predicted larval Red Salamander activity consisted of the model incorporating only time of day ($\omega_i = 0.28$), the model including cloud cover and time of day ($\omega_i = 0.19$), the model including water temperature and time of day ($\omega_i = 0.18$), and the model including rainfall and time of day ($\omega_i = 0.14$; Table 2). In the separate analyses for larval Red Salamanders, the top model again had a low probability of being the "best" model among the entire set. Of the model-averaged parameter estimates, only time of day had 95% confidence

Table 1. Regression models best explaining the influence of abiotic variables on captures of all stream salamander larvae.

Model[A]	Log-likelihood	K[B]	$QAIC_c$[C]	$\Delta QAIC_c$[D]	ω_i[E]
CloudNight	-64.13	4	98.53	0.00	0.43
CloudTempNight	-63.41	5	100.16	1.63	0.19
RainCloudNight	-64.10	5	101.12	2.59	0.12
TempNight	-66.42	4	101.72	3.19	0.09
Night	-68.54	3	102.20	3.67	0.07
Global	-63.04	6	102.42	3.89	0.06
RainNight	-67.90	4	103.79	5.26	0.03
RainTempNight	-66.42	5	104.34	5.81	0.02
Cloud	-80.43	3	118.78	20.25	0.00

[A] Night: day vs. night, Temp: mean daily water temperature, Cloud: percent cloud cover at time of sampling, Rain: days since last rainfall.

[B] Parameters = number of variables + intercept + variance inflation factor ($\hat{c}$).

[C] $QAIC_c$ values are based on the variance inflation factor of the global model.

[D] Difference between $QAIC_c$ value of the current model vs. the best model.

[E] Akaike weight. Probability that the model is the best among the set of all candidate models.

Table 2. Regression models best explaining the influence of abiotic variables on captures of larval *Pseudotriton ruber* (Red Salamander).

Model[A]	Log-likelihood	K[B]	$QAIC_c$[C]	$\Delta QAIC_c$[D]	ω_i[E]
Night	-46.34	3	74.63	0.00	0.28
CloudNight	-45.15	4	75.37	0.74	0.19
TempNight	-45.23	4	75.49	0.86	0.18
RainNight	-45.63	4	76.08	1.45	0.14
CloudTempNight	-44.60	5	77.18	2.55	0.08
RainCloudNight	-45.00	5	77.77	3.13	0.06
RainTempNight	-45.13	5	77.97	3.34	0.05
Global	-44.59	6	79.96	5.32	0.02
Cloud	-53.45	3	85.07	10.43	0.00

[A] Night: day vs. night, Temp: mean daily water temperature, Cloud: percent cloud cover at time of sampling, Rain: days since last rainfall.

[B] Parameters = number of variables + intercept + variance inflation factor ($\hat{c}$).

[C] $QAIC_c$ values are based on the variance inflation factor of the global model.

[D] Difference between $QAIC_c$ value of the current model vs. the best model.

[E] Akaike weight. Probability that the model is the best among the set of all candidate models.

intervals which did not overlap zero (Table 3). The magnitude and precision of this parameter estimate suggests that time of day was a strong predictor of Red Salamander activity, indicating a clear tendency for nocturnal activity in larvae of this species.

Discussion

The goal of this study was to determine important abiotic correlates of activity in larval stream salamanders. We found that time of day (e.g., day vs. night) appeared to be the best predictor of stream salamander activity in the models we compared. In the separate analyses for both Red Salamander and all species combined, we observed a clear tendency for nocturnal activity. This pattern of nocturnal activity has been consistently demonstrated for adult stream salamanders (Barbour et al. 1969, Hairston 1949, Orser and Shure 1975, Shealy 1975), as well as in a previous study of larval stream salamanders (Petranka 1984). Although Orser and Shure (1975) found larval salamander densities to be no higher at night than during the day, Barr and Babbitt (2007) observed a shift towards increased nocturnal activity in the presence of a fish predator. This suggests that the extent of nocturnal behavior for some salamanders may be partially a response to predator cues. Daily peaks in adult stream salamander activity have also been found to coincide with the peak activity of their potential prey (Holomuzki 1980). Larval salamanders consume primarily aquatic invertebrates (Cecala et al. 2007, Davic 1991, Petranka 1984), which may show daily periodicity in drift, with peaks in abundance occurring at either dusk (Elliot 1967) or dawn (Waters 1972). Thus, foraging during these periods may allow stream salamanders to optimize their resource acquisition while limiting their vulnerability to predators in comparison to daytime activity.

Previous studies have also proposed that nocturnal behavior in adult salamanders may be a direct response to light level (Placyk and Graves 2001, Shealy 1975), suggesting that low light conditions may also correlate with an increase in activity. One possible explanation for increased activity under low-light conditions is

Table 3. Model-averaged parameter estimates and 95% confidence intervals for all variables included in analysis.

Parameter^A	Model-averaged estimates	Lower 95% C.I.	Upper 95% C.I.
$\text{Night}_{\text{Total}}$	1.50	0.81	2.20
$\text{Temp}_{\text{Total}}$	0.05	-0.03	0.13
$\text{Cloud}_{\text{Total}}$	0.35	0.05	0.65
$\text{Rain}_{\text{Total}}$	0.01	-0.08	0.09
$\text{Night}_{\text{Pserub}}$	1.71	0.60	2.83
$\text{Temp}_{\text{Pserub}}$	0.06	-0.05	0.18
$\text{Cloud}_{\text{Pserub}}$	0.26	-0.18	0.70
$\text{Rain}_{\text{Pserub}}$	-0.04	-0.16	0.08

^{A}Total: parameter estimates from count data including all individuals captured, Pserub: parameter estimates from count data of all *P. ruber* captures.

that salamanders forgo active foraging during high light levels in order to reduce their risk of predation (Madison et al. 1999). Alternatively, salamanders may conduct passive, sit-and-wait foraging until low light levels preclude the use of visual cues (Placyk and Graves 2001). This trend only achieved significance in our analysis of combined larval captures, and the magnitude of the parameter estimate for cloud cover was greatly surpassed by the estimate for time of day in both sets of analyses. Furthermore, the higher observed capture rates under high cloud cover conditions were primarily driven by much higher capture rates during a handful of night-trapping intervals. Because only five trapping intervals took place during conditions of high nighttime cloud cover, we feel that further research is required to determine whether differing light levels between nights correlate significantly with variability in larval salamander activity.

Warm temperatures are needed to sustain both metabolic rate and growth rate in amphibians (Beachy 1995, Fitzpatrick 1973), and low temperatures have also been shown to cause a significant reduction in locomotor performance, especially endurance (Else and Bennett 1987; Marvin 2003a, b). Ashton (1975) reported that Northern Dusky Salamanders began moving into sub-surface winter retreats when stream temperature dropped below 7 °C, and Orser and Shure (1975) noted a decrease in activity when water temperature dropped below 12 °C. Mean water temperatures during our study ranged from 8.1 °C to 19.5 °C. Although no adult salamanders were captured when water temperatures dropped below 14 °C, our analyses found no response of larval salamanders to water temperature. In fact, 29% of larval captures ($n = 23$) occurred during trapping intervals where mean water temperature fell below 14 °C. Even the highest water temperatures observed during our study (19.6 °C) fell within the thermal preferences of the adults of many stream salamander species (Spotila 1972). Cecala et al. (2007) found a negative relationship between water temperature and the presence of prey items in larval salamander stomach contents. They proposed that this could be due to reduced foraging activity at warm water temperatures or limited food availability during the summer months. Our study was conducted during the fall and found that overall, larval salamander activity was not related to water temperature. Our study, however, did not distinguish between local foraging activity and other in-stream larval movements such as long-range movements, which can exceed 100 m for Red Salamander (Cecala et al. 2009).

Unlike many previous studies of amphibian movement and activity patterns (Barbour et al. 1969, Gibbons and Bennett 1974, Keen 1984, Orser and Shure 1975), the results of our study were based entirely on captures of larval salamanders, which exhibit movement patterns free from physiological limitation by moisture conditions. Although rainfall could be a potential cause of downstream drift in larval salamanders, one previous study found that larvae exhibited a peak in movement as stream flow stabilized following periods of high flow rate (Johnson and Goldberg 1975). Because salamanders were less active during peak stream discharge (Johnson and Goldberg 1975), it is likely that downstream drift is not accidental, but could instead be a density-dependent dispersal mechanism, as proposed by Bruce (1986). This resilience to accidental drift was also suggested by the upstream-biased dispersal described by Lowe et al. (2003). Cecala et al. (2009) also found upstream-biased dispersal in large Red Salamander larvae and found that no size class demonstrated downstream-biased movement. In this study, upstream- and downstream-facing traps captured nearly equivalent numbers of salamanders. Although we hypothesized that an influx of prey items following rainfall could also trigger an increase in larval salamander foraging activity, we found no effect of rainfall on the observed capture rates of larval salamanders.

Understanding activity patterns is a critical step towards understanding the way in which organisms relate to their environment and interact with other members of their community. Activity patterns of larval salamanders are particularly of interest due to the fact that larvae are often more numerous than adults and likely represent a larger part of the total salamander biomass in many systems (Davic and Welsh 2004). Furthermore, variation in activity may also have an important influence on individual detection probabilities and the effectiveness of population-monitoring techniques (Orser and Shure 1975, Peterson and Dorcas 1992). This study demonstrated a clear tendency for nocturnal activity in larval stream salamanders and also found a weak positive correlation between activity levels and cloud cover. Furthermore, we found that larval stream salamanders may remain active across a broader range of environmental temperatures than adults in our study system. We hope that our work leads to future research on stage-specific variation in salamander activity patterns.

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