

Biomass and Habitat Partitioning of *Desmognathus* on Wet Rock Faces in the Southern Appalachian Mountains

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ABSTRACT.—The importance of plethodontid salamanders in forested ecosystems has been recognized for decades, and studies aimed at quantifying salamander biomass and determining habitat requirements have become more common. However, there is a lack of knowledge on the use and contribution of vertical structures (e.g., wet rock faces) to total salamander biomass within a forested ecosystem. The purpose of our study was to characterize the population density, biomass, and habitat use of a wet rock face by a stream-salamander assemblage. We estimated the population density to be 14.69 salamanders m^{-2} and the total biomass estimate to be 27.16 $g\ m^{-2}$, which is more than two times greater than any salamander biomass reported previously in the eastern United States. We also found significant habitat partitioning of the vertical gradient by the three species of salamanders in the assemblage. The stable microclimate and increased protection from other predators (e.g., mammals, snakes, and ground-foraging birds) provided by wet rock faces likely leads to the increased amount of biomass we found in this study. Although the salamanders are likely protected from most noncaudate predators, the spatial structuring in the assemblage still follows an intraguild predation gradient found in horizontal habitats.

The importance of plethodontid salamanders in forested ecosystems has been recognized for decades (e.g., Hairston, 1949, 1987; Organ, 1961), and studies aimed at quantifying salamander biomass have become more common (Table 1). Burton and Likens (1975) were the first to estimate salamander biomass across a landscape ($0.18\ g\ m^{-2}$ in northeastern U.S. forests). Subsequently, Petranka and Murray (2001) estimated the biomass of a riparian-associated salamander assemblage in the southern Appalachian Mountains to be $1.65\ g\ m^{-2}$. More recently, the biomass of a single stream-breeding plethodontid species (*Desmognathus quadramaculatus*, Black-bellied Salamander) was estimated to be $9.93\ g\ m^{-2}$, which is six times greater than biomass estimates from previous studies (Peterman et al., 2008). Although population and biomass estimates are becoming more precise for plethodontid salamanders, these estimates only account for salamanders on the forest floor (i.e., stream, riparian, and woodland habitat). Currently there is a lack of knowledge on the contribution of vertical structures (e.g., wet rock faces) to total salamander biomass within a forested ecosystem.

Information is somewhat limited on salamander biomass and its overall importance in forested ecosystems, but there is comparatively more information on distribution and habitat use of plethodontid salamanders in the eastern United States (e.g., Organ, 1961; Hairston, 1987; Grover, 2000; Crawford and Semlitsch, 2008). Plethodontid salamanders typically avoid competitive interactions through allopatric geographical or altitudinal distributions (Hairston, 1951; Wake and Lynch, 1976). When *Plethodon* salamanders are present at a site, usually there are only two species present and these differ greatly from one another in size (Fraser, 1976); however, Adams (2007) found that some guild-based *Plethodon* assemblages can contain up to five species. Within stream salamander assemblages it is not uncommon to find several abundant species of *Desmognathus* at one site (Krzysik, 1979; Crawford and Semlitsch, 2007, 2008; Bruce, 2011). Among the stream salamanders, Grover (2000) found that larger species were found closer to water than were smaller species, and the rehydration rates of the smaller species

that were found farther from the stream were higher than those of larger species found closer to the stream. In stream salamander assemblages in western North Carolina, Crawford and Semlitsch (2007) found four species that were spatially separated from one another. The majority of dusky salamanders (*D. quadramaculatus*, *Desmognathus monticola* [Seal Salamander], and *Desmognathus ocoee* [Ocoee Salamander]) were found within 15 m of the stream's edge, whereas brook salamanders (*Eurycea wilderae* [Blue Ridge Two-lined Salamander]) occurred primarily beyond 15–20 m (and up to 100 m) from the stream's edge. This may be due to predation and competition pressures exerted by the larger dusky salamanders on the brook salamanders (Southerland, 1986; Hairston, 1987). Both Black-bellied Salamanders and Seal Salamanders are large-bodied and prey on juvenile and adult Two-lined Salamanders (Beachy, 1993; Crawford, pers. obs.).

Within the southern Appalachian Mountains the steep topography, high rainfall, erosion-resistant rock, and construction of roads have exposed masses of rock on the sides of mountains and gorges. Typically, most of these exposed rock faces are too dry to sustain populations of salamanders, although Green Salamanders (*Aneides aeneus*) prefer drier rock-faces than do other plethodontid salamanders (Corser, 2001). Exposed rock faces with a constant supply of water can provide suitable habitat for certain species of stream salamanders (Huheey and Brandon, 1973). Tilley (1980) found that wet rock face environments provided ample sites for brooding of eggs by females and habitat for larvae, juveniles, and adults of *Desmognathus ochrophaeus* (Allegheny Mountain Dusky Salamander). Tilley (1980) also speculated that wet rock faces provided a refuge from predation for smaller species of salamanders from larger heterospecific species (i.e., larger salamanders are less adept at climbing). The objectives of our study were to characterize the population density, biomass, and habitat use of a wet rock face by a stream salamander assemblage in a Southern Appalachian forested ecosystem.

MATERIALS AND METHODS

Study Site.—The study site was a wet rock face located off of Secondary State Highway 1606 southeast of Highlands, North Carolina ($35^{\circ}2'8''N$, $83^{\circ}8'36''W$) The rock face is not a natural

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TABLE 1. Summary of published density and biomass estimates from salamander studies in the eastern United States.^a

Species	Density (m ⁻²)	Biomass (g m ⁻²)	Reference
DFUS	1.42	N/A	Spight, 1967
DOCH (BVV-1)	7.0–19.0	N/A	Huheey and Brandon, 1973
DOCH (BVV-3)	3.0–9.0	N/A	Huheey and Brandon, 1973
DFUS, EBIS, GPOR, NVIR ^b , PCIN	0.30	0.18	Burton and Likens, 1975
DFUS, DOCH	1.90	2.50	Hall, 1977
DOCH (Whiteside Mountain)	5.80	N/A	Tilley, 1980
DOCH (Dry Falls)	6.90	N/A	Tilley, 1980
DMON, DOCH, DQUA, PGLU, PJOR	N/A	0.23	Hairston, 1987
DORE, PJOR ^c	2.26	2.77	Howard, 1987
DCAR, DWRI, EWIL, PGLU, PJOR, PYON	1.85	1.65	Petranka and Murray, 2001
DQUA, EWIL, GPOR ^d	12.10	7.88	Davic and Welsh, 2004
DQUA ^e	0.40	0.60	Davic and Welsh, 2004
DQUA	1.13	9.93	Peterman et al., 2008
DMON, DOCO, DQUA	14.69	27.16	This study

^a DCAR = *Desmognathus carolinensis* (Carolina Mountain Dusky Salamander); DFUS = *Desmognathus fuscus* (Northern Dusky Salamander); DMON = *D. monticola*; DOCH = *D. ochrophaeus*; DOCO = *D. ocoee*; DORE = *Desmognathus orestes* (Blue Ridge Dusky Salamander); DQUA = *D. quadramaculatus*; EBIS = *Eurycea bislineata* (Northern Two-lined Salamander); EWIL = *E. wilderae*; GPOR = *Gyrinophilus porphyriticus*; NVIR = *Notophthalmus viridescens* (Eastern Newt); PCIN = *Plethodon cinereus* (Eastern Red-backed Salamander); PGLU = *Plethodon glutinosus* (Northern Slimy Salamander); PJOR = *Plethodon jordani* (Jordan's Salamander); PYON = *Plethodon yonahlossee* (Yonahlossee Salamander); N/A = not applicable.

^b Terrestrial eft stage only.

^c Estimation was made using the two numerically dominant species at the site.

^d These species comprise the salamander assemblage found within the stream, including larval forms.

^e Adult life stage only.

feature but is the result of road construction. The rock wall is approximately 2.25 m in height and 25 m in length, of which the first 15 m were studied (the last 10 m of the rock face remained dry throughout the study period and no animals were encountered). Water flowed down from the top of the rock face, accumulating into a wet, seep-like ditch at the base. This ditch drained the length of the rock face, ultimately flowing into an unnamed headwater stream 20 m from the edge of the rock face. The rock face itself had numerous vertical and horizontal cracks and fissures; clumps of moss were patchily distributed across the rock. Three species of salamanders were readily encountered on the rock face: *D. monticola*, *D. ocoee* (formerly *D. ochrophaeus*), and *D. quadramaculatus*. Larval and adult *Gyrinophilus porphyriticus* (Spring Salamanders) were occasionally observed in the ditch at the base.

Field Surveys.—Mark-recapture surveys were conducted approximately once every five nights (2200–0100 h EST); fifteen surveys were conducted from 21 May to 30 July 2005. The rock face was searched for salamanders by two researchers with the aid of battery-powered headlamps. When a salamander was found on the rock face, the height (cm) and temperature (rock surface and animal) were recorded. Temperatures were recorded to the nearest 0.1°C using a Raytek® MiniTemp™ infrared thermometer. Salamanders were captured, weighed (to nearest 0.1 g), and measured to the nearest mm for total length (TL) and snout-vent length (SVL). Newly captured animals were then given a unique toe clip for identification. No more than two digits were clipped from a foot, no adjacent digits were clipped

together, and no salamander had more than four toes clipped during the study. Salamanders were released on the rock face at the point of capture following data collection. Mark-recapture data were analyzed with open population models using Jolly-Seber estimation in Program MARK (version 4.2; available from Gary White at: <http://warnercnr.colostate.edu/~gwhite/mark/mark.htm>). The Jolly-Seber model has three main assumptions: 1) all animals present in the population at time *i* are equally likely to be captured (equal capture probability); 2) every marked animal present in the population at time *i* has the same probability of surviving from *i* to *i* + 1; and 3) marks are not lost or overlooked by the observer (Bailey et al., 2004). Additionally, it is assumed that all emigration from the population is permanent. We are confident that the assumptions of the Jolly-Seber model were met in our study because we sampled over a discrete time period, and home-range data from other wet rock face studies (Huheey and Brandon, 1973; Tilley, 1980) suggest that movements into or out of the population are limited and unlikely. We had no way of determining whether deaths occurred during the study, and newly metamorphosed juveniles were not encountered.

RESULTS

Two-hundred and nine unique salamanders were captured throughout the study with 151 recapture events (Table 2). An average of 24 salamanders were captured per survey (range = 12–58). *Desmognathus ocoee* was the most-abundant species but

TABLE 2. Mark-recapture and habitat data for the wet rock face salamander assemblage in the southern Blue Ridge Physiographic Province. Average height is height from the base of the rock face and average rock temperature is the temperature of the rock surface adjacent to a salamander.

Species	New captures	Recapture events	Total capture events	Avg. height (cm)	Height range (cm)	Avg. rock temp. (°C)
<i>Desmognathus ocoee</i>	141	48	189	120	0–224	15.1
<i>Desmognathus monticola</i>	51	89	140	85	0–196	15.7
<i>Desmognathus quadramaculatus</i>	17	14	31	76	0–193	16.7
Total assemblage	209	151	360	N/A ^a	N/A	N/A

^a N/A = not applicable.

TABLE 3. Capture event history data for the wet rock face salamander assemblage in the southern Blue Ridge Physiographic Province. This table contains information on the total number of times each individual salamander of each species was captured during the course of the study.

Species	Recapture events									
	0	1	2	3	4	5	6	7	8	9
<i>Desmognathus ocoee</i>	113	15	10	1	1	0	1	0	0	0
<i>Desmognathus monticola</i>	21	9	6	6	3	3	1	0	1	1
<i>Desmognathus quadramaculatus</i>	10	3	2	1	1	0	0	0	0	0

had the least number of recaptures (28 individuals were recaptured 1–6 times; Table 3). *Desmognathus monticola* was the second most-abundant and most-frequently recaptured species (30 individuals were recaptured 1–9 times; Table 3). *Desmognathus quadramaculatus* was least abundant on the rock face (7 individuals were recaptured 1–4 times; Table 3). For all statistical analyses we used data from initial salamander capture events only; data from recapture events were not included. The three salamander species exhibited a significant partitioning of the rock face (one-way ANOVA; $F_{2,208} = 10.107$, $P < 0.001$), with the smaller *D. ocoee* inhabiting the higher reaches (mean = 120 cm) and *D. monticola* and *D. quadramaculatus* occupying the lower reaches (means = 85 and 76 cm, respectively). The difference in height is not significant between *D. monticola* and *D. quadramaculatus* (Tukey's honest significance test [HSD] post hoc test, $P = 0.093$). Animal temperatures did not differ from the temperature of rock face where they were found (paired *t*-test, $T_{208} = 0.218$, $P = 0.828$). Of the 141 *D. ocoee*, 40 gravid females were observed. The gravid *D. ocoee* did not utilize the rock face differently than did nongravid *D. ocoee* with regard to height ($F_{1,140} = 1.101$, $P = 0.663$) or surface temperature of the rock space occupied ($F_{1,140} = 0.516$, $P = 0.819$). Of the 51 *D. monticola*, 6 gravid females were observed. The gravid *D. monticola* did not utilize the rock face differently than did nongravid *D. monticola* with regard to height ($F_{1,50} = 0.022$, $P = 0.991$) or surface temperature of the rock space occupied ($F_{1,50} = 0.329$, $P = 0.880$).

Mark-recapture data were analyzed using Jolly-Seber estimation, which makes population estimations using open population models. The total estimated population size of the assemblage on the study area (33.75 m²) was 496 salamanders (95% CI = 374–619; Table 4), which yielded a biomass of 916.56 g (95% CI = 670.90–1,166.27; Table 4).

DISCUSSION

Within various microhabitats of the forest floor (streams, riparian zones, woodland habitat), salamander biomass estimates in the eastern United States have ranged from 1.77 kg ha⁻¹ to 99.30 kg ha⁻¹ (Table 1). We estimated the population density of a wet rock face salamander assemblage to be 74,600 ha⁻¹ (95% CI = 66,400–100,400 ha⁻¹), which leads to a total biomass estimate of 203.8 kg ha⁻¹ (95% CI = 169.4–294.4 kg

ha⁻¹). Although this biomass estimate is more than two times greater than any salamander biomass reported previously in the eastern United States (Table 1), the estimates for two of the three species in our assemblage (*D. quadramaculatus* and *D. ocoee*) are similar to other studies (Table 1). Additionally, the previous high estimate of 99.3 kg ha⁻¹ provided by Peterman et al. (2008) was for only one species (*D. quadramaculatus*) of a multispecies assemblage. When accounting for the additional species in their assemblage, Peterman et al. (2008) estimated a total assemblage biomass of 143.8 kg ha⁻¹.

While the assemblage and population densities of salamanders can vary from site to site (Organ, 1961; Hairston, 1987), our wet rock face study site is not unusual for the southern Appalachian region in terms of diversity or abundance of salamanders (Huheey and Brandon, 1973; Tilley, 1980; JAC and WEP, pers. obs.). Huheey and Brandon (1973) and Tilley (1980) conducted intensive mark-recapture studies of *D. ocoee* at two wet rock faces, each in the southern Blue Ridge region near our study site. Huheey and Brandon (1973) estimated densities of 7–19 individuals m⁻² and 3–9 individuals m⁻² at their two study sites, and Tilley (1980) estimated densities of 5.8 individuals m⁻² and 6.9 individuals m⁻² at his two respective study sites. Tilley (1980) also noted the presence of *D. monticola* and *D. quadramaculatus* at his study sites, although these species were not monitored for population density. Our estimate of 11.97 *D. ocoee* m⁻² is average to above average when compared to the aforementioned studies.

Accompanying the large biomass of the wet rock face was a significant spatial structure in the salamander assemblage. We found that *D. ocoee* inhabited significantly higher reaches of the wet rock face than did both *D. monticola* and *D. quadramaculatus*. Although there was no significant difference between *D. monticola* and *D. quadramaculatus*, *D. monticola* was found an average of 9 cm higher than *D. quadramaculatus*. Within the horizontal gradient, stream salamanders typically align themselves from most aquatic (largest species) to most terrestrial (smallest species) from the stream edge, and the assemblage can include from three to five species or more (Organ, 1961; Krzysik, 1979; Crawford and Semlitsch, 2007). In the region of our wet rock face study site, Crawford and Semlitsch (2007) found that *D. quadramaculatus*, *D. monticola*, and *D. ocoee* were found an average of 3.2, 6.8, and 10.4 m from the stream edge,

TABLE 4. Population and biomass estimates from mark-recapture data for the wet rock face study area (33.75 m²) in the southern Blue Ridge Physiographic Province. Values in parentheses are the standard errors of the population estimates.

Species	Population estimate	Lower 95% CI	Upper 95% CI	Mean mass (g)	Biomass (g)	Lower 95% CI	Upper 95% CI
<i>Desmognathus ocoee</i>	404 (52.0)	302	506	0.95	383.80	286.90	480.70
<i>Desmognathus monticola</i>	66 (5.0)	57	76	4.05	267.30	230.85	307.80
<i>Desmognathus quadramaculatus</i>	26 (5.6)	15	37	10.21	265.46	153.15	377.77
Total assemblage	496 (N/A ^a)	374	619	N/A	916.56	670.90	1,166.27

^a N/A = not applicable.

respectively. This pattern follows the distribution seen in the wet rock face assemblage of salamanders.

In salamander assemblages that are old enough, the members should be well co-adapted and resource competition should be minimal (Krzysik, 1979). Habitat is usually the major resource partitioned between co-occurring species, and partitioning along horizontal gradients has been well documented. Less is known about partitioning of vertical habitats by amphibians. Miyamoto (1982) found that among four species of frogs (*Eleutherodactylus*) there were significant differences in use of vegetation height, with the larger and heavier-bodied species being found closest to the ground. Both Heatwole (1963) and Blair and Doan (2009) also showed that frog species can partition their vertical habitats. For *Desmognathus* salamanders it has been hypothesized that moisture, competition, and predation structure the assemblages in the horizontal gradient from stream edge to upland habitat (Hairston, 1980; Toft, 1985; Hairston, 1986). Within the horizontal habitat, larger species are constrained by moisture and must remain near the stream edge (Grover, 2000), thus decreasing predation on smaller species that are found farther from the stream. In the vertical habitat we found the same distribution, but the larger species were no longer constrained by moisture (i.e., entire rock face is wet). However, the larger a salamander is, the more difficult it is for the animal to climb a vertical structure. Therefore, in these vertical habitats the pattern remains the same although the factors shaping the structure appear to differ.

The enormous quantity of amphibian biomass has been documented in a handful of studies (e.g., Burton and Likens, 1975; Petranka and Murray, 2001; Gibbons et al., 2006; Peterman et al., 2008), with our study being the latest to increase the upper limit of biomass estimates. Wet rock faces represent a unique habitat with relatively homogeneous temperature and moisture regimes. Additionally, the vertical structure likely decreases the threat of predation from other animals such as mammals, snakes, and ground-foraging birds. The stable microclimate and increased protection from other predators could lead to the increased amount of biomass we found in this study. Additionally, the rock face may also be a source of increased prey for the salamanders, which has been shown to increase growth rates drastically (Bernardo and Agosta, 2003). Although the salamanders are likely protected from noncaudate predators, the spatial structuring on the assemblage still follows the intraguild predation gradient seen in horizontal habitats. While the role that salamander biomass plays in ecosystem function has yet to be determined, our study has documented the importance of a unique habitat feature in contributing to overall salamander abundance across a forested landscape. Future research should focus on the role that wet rock face salamander assemblages may play in recolonization events in disturbed habitats such as forests used for timber harvest.

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