

JOURNAL OF HERPETOLOGY

Seasonal Migration by Red-Backed Salamanders, *Plethodon cinereus*

LAWRENCE L. WOOLBRIGHT^{1,2} AND CHRISTOPHER P. MARTIN³

¹Biology Department, Siena College, 515 Loudon Road, Loudonville, New York 12211 USA

³Saratoga National Historical Park, 648 Route 32, Stillwater, New York 12170 USA

Seasonal Migration by Red-Backed Salamanders, *Plethodon cinereus*

LAWRENCE L. WOOLBRIGHT^{1,2} AND CHRISTOPHER P. MARTIN³

¹Biology Department, Siena College, 515 Loudon Road, Loudonville, New York 12211 USA

³Saratoga National Historical Park, 648 Route 32, Stillwater, New York 12170 USA

ABSTRACT.—We report direct observation of seasonal movements of adult *Plethodon cinereus* uphill to a rocky hilltop in the fall and downhill into a wet area in the spring. Counts from arrays of cover boards in both areas showed occupancy patterns that were consistent with seasonal changes in spatial distribution. Soil moisture was markedly higher and pH was slightly lower in the downhill area. Soil temperature did not differ between the two areas. Young age classes do not migrate but apparently stay in the wet area where they hatch. Differences in body size and egg diameter between fall and spring samples suggest that migratory adult salamanders grow and yolk eggs during the winter. The most likely explanation for this behavior is that the rocky hillside provides crevices that allow salamanders to get far enough underground to remain active in winter.

Detailed information on annual movement patterns and cycles of habitat usage is incomplete for many amphibians because of their small size and secretive habits yet is needed to inform management decisions (e.g., placement of roads and culverts [Madison et al., 2010]). *Plethodon cinereus* are small terrestrial-breeding salamanders that can reach high densities in northeastern U.S. forests (Burton and Likens, 1975). They are typically found on the forest floor under cover objects like logs, and they have been reported to maintain territories (Jaeger and Gergits, 1979). Reproduction is terrestrial with direct development of eggs and female parental care of eggs and young. Using mark-recapture techniques, Mathis (1991) estimated the home ranges of adult males and females to be 0.16 m². Their primary response to changing conditions is thought to be vertical movement in the soil (Taub, 1961).

To our knowledge, there have been no reports of seasonal mass movements by *P. cinereus*. However, we encountered a large number of *P. cinereus* moving in the same direction across the tour road at Saratoga National Historical Park (SNHP) on a wet night in April 2005. We assumed that some management activity by park staff had altered the suitability of the habitat and that this movement represented a one-time relocation. However, we returned to that location on wet nights in spring 2007 and 2008 and observed the same phenomenon.

These observations suggested two hypotheses: 1) the existence of source and sink populations (Pulliam, 1988); and 2) seasonal migration. These two hypotheses differ in several key predictions. The source-sink hypothesis would predict unidirectional movement from source to sink but no significant amount of movement in the reverse direction. The seasonal migration hypothesis would predict the occurrence of fall movement in the reverse direction. We tested these predictions by visiting the location on every wet night in the fall of 2009 to determine whether *P. cinereus* were returning across the road in the opposite direction from their spring movements.

The source-sink hypothesis also predicts differences in habitat quality, such that one site has much higher salamander productivity than the other. Wyman (1988) reported a higher mean pH for quadrats with *P. cinereus* than for quadrats without them. Wyman and Hawksley-Lescault (1987) found that *P. cinereus* density is higher at soil pH levels above 3.8, although their results did not show an effect on density of either soil temperature or moisture. Vernberg (1955) reported a pH

tolerance of 4.1–7.4 for *P. cinereus*, with a preference between 6.0 and 6.8. Salamander foraging behavior is known to be limited by moisture, because the ability of salamanders to move away from their refugia to forage depends upon the availability of water (Fraser, 1976; Jaeger, 1972). Spotila (1972) reported that *P. cinereus* prefer temperatures around 16°C, that they dehydrate easily in dry conditions and at warmer temperatures, and that their rehydration depends upon soil moisture levels. Therefore, we might expect the habitat of a source population to be cooler, wetter, or less acidic than the habitat of a sink population.

The seasonal migration hypothesis predicts that there is some seasonal variation in what type of habitat is most successful. A successful habitat for the growing season might resemble the source habitat described above, but the requirements for successful overwintering might be quite different. We tested these predictions by measuring pH, soil temperature, and soil moisture in the two areas.

In addition, the seasonal migration hypothesis predicts that spatial patterns of population density might change through the year. We used artificial cover objects to determine whether occupancy at disjunct sites was related to season.

MATERIALS AND METHODS

As part of a continuing amphibian monitoring effort at SNHP, we used the park's tour road as a driving transect on wet nights in the spring since 2001. On 3 April 2005, we observed small salamanders crossing the road in the vicinity of the six-mile marker (43°00.483'N, 73°38.338'W ± 12') (Etrex Venture HC unit, Garmin Ltd., Olathe, KS). We walked along the section of road to observe numerous (20–30) *P. cinereus* all moving across the road in the same direction, from uphill to downhill. We returned to that same location and saw *P. cinereus* moving in the same direction on 27 April and 10 May 2007 and 1 and 8 April 2008.

In 2009, we marked each meter of a 180-m walking transect along the tour road, centered on the area where we had noted salamanders in prior years. We slowly walked that transect on 11 rainy nights between 1 September and 15 November 2009. These included most wet nights between 1 September 2009 and the onset of hard freezes with the exception of three nights when rain started after midnight. Also, we checked the transect on 20 rainy nights between 13 March and 15 June 2010. These included most wet nights from snow melt to hot weather, with the exception of 10 nights when rain occurred after midnight. Night time checks of the transect were conducted between the

²Corresponding Author. E-mail: lwoolbright@siena.edu
DOI: 10.1670/12-074

onset of darkness and midnight. In addition, we checked the transect on three dry nights following afternoon rainfalls, during one peak season daytime rain storm, and on two rainy nights in the summer. Weather data were obtained from a recording station in SNHP located approximately 500 m from the transect (http://raws.wrh.noaa.gov/cgi-bin/roman/meso_base.cgi?stn=SHPN6).

During each transect check, we noted the location to the nearest 1 m and the direction of movement of each salamander that we encountered. On all nights except the first, we also noted color morph and measured body length (snout to vent, hereafter SVL) on each salamander and determined its sex and reproductive condition by candling (Gillette and Peterson, 2001). This method of sex determination resulted in counting immature individuals without visible testes as females. We collected movement data for 121 *P. cinereus* and morphological data for 97. Early in each season, *P. cinereus* were brought to the laboratory and held in a refrigerated chamber until their guts had cleared of food. Females from these samples were examined more closely to determine the number and approximate size (to the nearest 1 mm on a plastic ruler) of their eggs.

Information from the transect identified the specific location where salamanders were crossing the road. Uphill of this site was a patch of forest featuring rocky outcroppings surrounded by hundreds of meters of mowed grassland. The forest patch provided the only suitable habitat, and we assumed it to be the salamanders' destination in that direction. Downhill of the road crossing was an area of low forested wetland with frequently saturated soils but little standing water, surrounded in all directions by higher ground. We assumed that the wet area provided more suitable habitat and that it was the salamanders' destination in that direction. We defined these two sites of similar size (approximately 0.2 ha) as our focal sites for further investigation. To detect seasonality in occupancy rates of *P. cinereus* at the focal sites from which they were apparently traveling from and to, we established an artificial cover board array (Fellers and Drost, 1994) in each location in fall 2008. The array downhill of the tour road had its center at 43°00.513'N, 73°38.358'W and the array uphill at 43°00.514'N, 73°38.318'W. Arrays consisted of 40 rough-cut hemlock boards measuring 30 × 30 × 2.5 cm and placed on 2 m centers in eight rows of five boards each. The long dimension of each array was oriented perpendicular to the road. All boards were located at least 5 m away from the road under the forest canopy. Arrays were sampled 11 times between April 2009 and August 2010. Sampling was conducted during the daytime by lifting each board and noting the presence of any *P. cinereus*. Cover boards were not checked within three days of the last rainfall to maximize the likelihood that salamanders would be occupying cover objects, and all samples were at least two weeks apart.

Soil moisture was measured adjacent to five randomly chosen boards in each array in September and October 2009 and March, May, and August 2010. At each location, a 2.5-cm wide × 10 cm deep soil core was collected with a standard soil sampler (LaMotte soil sampling tube model EP, LaMotte Co., Chestertown, MD). Each sample was measured for mass and then placed in a drying oven (Model 40GC Lab Oven, Quincy Lab, Chicago, IL) at 35°C until it reached a constant dry mass. Soil moisture for each sample was calculated as follows: (wet mass – dry mass)/wet mass × 100%. Temperature was measured under each cover board in March 2010 and under a randomly chosen sample of 10 boards in each array in August 2010 using a

Reotemp model AA0601F23-PS dial thermometer (Reotemp Instrument Corp., San Diego, CA). Measurements of pH were taken under 10 randomly chosen boards in each array in March and August 2010 using a Kelway model HB2 soil tester (Kel Instruments Co. Inc., Wyckoff, NJ).

The relationships between season and direction of movement, season and body size, and time of season and gender were compared using chi-square tests (Siegel, 1956). Temperature, pH, and soil moisture were compared using Mann-Whitney *U*-tests following Siegel (1956). Cover board results were compared using a Fisher Exact test. Salamander body mass and SVL relationships were compared by regression analysis and Kruskal-Wallis one-way nonparametric analysis of variance using Statistix 8.0 (Analytical Software, Tallahassee, FL). To reduce sampling error, only salamanders measured by LLW were used in regression analyses. An α level of 0.05 was used to evaluate statistical significance.

RESULTS

We observed *P. cinereus* crossing the tour road transect on 10 nights in the spring and seven nights in the fall. We observed movement only at temperatures above 10°C and only during rainfall sufficiently heavy to keep the road surface wet. We did not observe *P. cinereus* movement with rainfall events ≤ 2.5 mm, regardless of temperature, on dry nights when the road was still wet from afternoon rains, during the daytime, or during heavy rains at night in the summer.

Salamander movement was strongly unidirectional in both spring and fall. In the spring, 69 of 71 salamanders were observed to be moving from uphill to downhill, perpendicular to the tour road, whereas the other two were moving more or less parallel to the road. Salamanders sampled in the spring were sluggish and did not appear to react to observers or their flashlights. In the fall samples, the majority of salamanders observed (42 of 50) were moving from downhill to uphill, perpendicular to the tour road. Of the remaining eight, two were moving in the opposite direction, and six were moving away from the observers in apparent response to their approach. Salamanders sampled in the fall were much more active than those in the spring, typically reacting to flashlight beams by running the opposite direction. The direction of travel was related to season ($\chi^2 = 83.56$, $P < 0.001$, $df = 1$).

Also, cover boards surveys revealed a temporal shift in *P. cinereus* occupancy. In samples collected before the migration in the spring and after the migration in the fall, 21 of 29 *P. cinereus* were located uphill of the tour road compared to only seven of 22 in samples taken after the spring migration but before the fall migration (Fisher Exact 1-tailed $P = 0.0003$).

The locations of *P. cinereus* along the transect were distributed unimodally, with most salamanders found between meter 80 and meter 140 on the transect.

These two sites, forested area with rocky outcrops and forested wet area, differed in their soil moisture content. All soil samples collected around the downhill cover boards were wetter than any uphill sample in September 2009 (downhill range 33–52%; uphill 19–24%), October 2009 (downhill 29–40%; uphill 17–27%), May 2010 (downhill 33–46%; uphill 18–31%), and August 2010 (downhill 21–30%; uphill all 11%). Only in the March 2010 sample was there any overlap in moisture readings, with one uphill sample (range 24–33%) higher than one

downhill sample (range 29–42%). The latter still represents a significant difference (Mann-Whitney $U = 1$, $P = 0.008$).

Also, the downhill soils appeared to have a lower pH. In March all downhill samples were at or below 6.6, while eight of the 10 uphill samples were 6.7 or higher (Mann-Whitney $U = 12$, $P < 0.05$). In August the difference was more pronounced, with uphill samples remaining close to pH 6.8, but all downhill samples registering less than pH 6.0 (Mann-Whitney $U = 0$, $P < 0.001$). No pH measurement approached the low levels reported to limit the distribution of *P. cinereus*. Soil temperature did not differ between the locations, either in March (Mann-Whitney $U = 594$, $Z = 0.973$, $P = 0.166$) or in August (Mann-Whitney $U = 38$, $P > 0.10$).

Of the 97 *P. cinereus* used for morphological measurements, 52 (54%) were females, 39 (40%) were males, and six could not be positively determined because of extreme quantities of material in their guts. The sexes appeared to differ with regard to activity within each season. Males were more likely to be found in samples taken early in the season and females more likely to be found in later samples, both in the fall ($\chi^2 = 4.36$, $0.025 < P < 0.05$, $df = 1$) and in the spring ($\chi^2 = 3.89$, $0.025 < P < 0.05$, $df = 1$). The majority of *P. cinereus* (87 of 97) exhibited the typical red stripe on the dorsum, whereas nine lacked it ("leadbacks"), and one had an unusual yellowish dorsal stripe.

The reproductive condition of female *P. cinereus* appeared to differ between seasons. Of the 12 females examined in the laboratory in the fall, seven (58%) had visible eggs and five (42%) did not. Those with eggs had a mean of 9.3 (SD = 1.5, range 7–11) eggs each, and egg diameter was approximately 1 mm. Of the 28 females examined in the spring, 22 (79%) had visible eggs and six (21%) did not. Those with eggs had a mean of 9.1 (SD = 1.5, range 6–11) eggs each. Nineteen had large eggs with an estimated diameter of 3 mm, whereas three had small eggs similar in size to those observed in the fall.

All *P. cinereus* seen during transect censuses were adult size or close to it. The smallest *P. cinereus* measured was 26 mm SVL, whereas the largest was 49 mm. Only 11 of the 97 were smaller than 35 mm SVL. Mean SVL was 39.9 mm (SD = 4.46), and SVL did not vary by gender (Kruskal-Wallis statistic = 2.169, $P = 0.338$). However, it did vary seasonally with *P. cinereus* captured in the spring (mean = 41.3 mm, SD = 3.74) being longer than those captured in the fall (mean = 38.4 mm, SD = 4.74 [Kruskal-Wallis statistic = 9.514, $P = 0.002$] [Fig. 1]). This seasonal difference in body length appeared to result mainly from a difference in female body size between fall (mean = 37.0 mm, SD = 5.30) and spring (mean = 42.2 mm, SD = 3.75 [Kruskal-Wallis statistic = 13.190, $P = 0.0003$]) and not males (mean = 39.5, SD = 3.70), which did not vary seasonally (Kruskal-Wallis statistic = 1.509, $P = 0.219$). Among the adult salamanders captured, larger size classes were more common in spring samples, and smaller size classes were more common in fall samples ($\chi^2 = 9.03$, $0.01 < P < 0.025$, $df = 2$; Fig. 1).

Salamander mass depended strongly on body length according to the regression equation: mass = $0.066(\text{SVL}) - 1.52$ ($F_{1,52} = 126.26$, $P = 0.000$). Comparison of regression lines between the sexes revealed no difference in slope ($F_{23,27} = 0.30$, $P = 0.126$), with males of the same body length (intercept = -1.41) being heavier than females (intercept = -1.53 ; $F_{1,51} = 9.21$, $P = 0.004$). Comparison of regression lines between the seasons also showed no difference in slopes ($F_{1,50} = 0.23$, $P = 0.634$), with *P. cinereus* of the same body length being heavier in the fall (intercept = -1.63) than in the spring (intercept = -2.04 ; $F_{1,51} = 5.32$, $P = 0.025$).

DISCUSSION

Results were not consistent with the predictions of the source-sink population hypothesis and strongly supported the predictions of the seasonal migration hypothesis. Habitat measurements did not reveal major differences between the two locations except in soil moisture. Migrating *P. cinereus* are spending the summer in the wetter downhill location and the winter in the drier uphill one. Cover board occupancy in both locations varied seasonally, with more salamanders at the lower location in the summer and at the higher location in early spring and late fall. We note that this result is the opposite of what would be predicted if salamanders were more likely to use cover boards in drier habitats. Road transects showed directional movement of salamanders in a downhill direction in the spring and an uphill direction in the fall.

Based on salamander body sizes, migration is restricted to mature individuals. Both Saylor (1966) and Nagel (1977) reported three size classes in their populations, two immature and one reproductive. Young hatch at about 14 mm SVL in the fall and then grow about 10 mm their first summer and 8 mm in their second, becoming mature at two years of age (Werner, 1971). Mature females have small (1.3 mm) eggs in the fall of their second year that they can then deposit at 3.0 mm the following summer when they are two and one-half years old (Saylor, 1966). The majority of females we examined in the fall had small eggs and the majority of those in the spring had large ones. Both male and female body sizes were similar to the mature size class reported for other populations. Thus, it appears that reproductive individuals move downhill into the wetland to reproduce and that the young stay in the wetland for their first two years and then migrate uphill for the winter preceding their first reproductive season.

A small number of the females migrating downhill in the spring had small rather than large eggs. These observations are consistent with Werner's (1971) suggestion that the latest hatchlings of their cohort may not be big enough to lay eggs in their third summer. Likewise, a small number of the females migrating uphill in the fall did not have visible eggs and were probably post-reproductive animals.

The seasonal migration may be reproductive in nature. The time spent in the uphill study area corresponds well with the mating period reported for other populations, December to March in Tennessee (Nagel, 1977) and October to April in Maryland (Saylor, 1966). Our data also suggested that the salamanders tend to be bigger in the spring than they were in the fall and that the females have larger eggs in the spring than in the fall. If salamanders are growing, breeding, and yolking eggs during upstate New York winters when the ground is frozen solid and covered with a meter or more of snow, they must be deep underground to remain active. It is possible that the boulders located at the uphill site make it possible for salamanders to get deeper underground than they would be able to in the low wetland site and that warmer temperatures underground facilitate yolking eggs and possibly mating prior to oviposition the following summer.

Reports exist of plethodontids using winter refugia of various types. In Indiana, Caldwell and Jones (1973) reported finding an aggregation of 34 *P. cinereus* over two feet below the surface in December and another group of 42 *P. cinereus* over three feet below the surface in February. Both aggregations were in abandoned ant mounds, and the presence of food in salamander stomachs suggested that they were active. Caldwell (1975) reported finding a third aggregation of 30 *P. cinereus* in the same

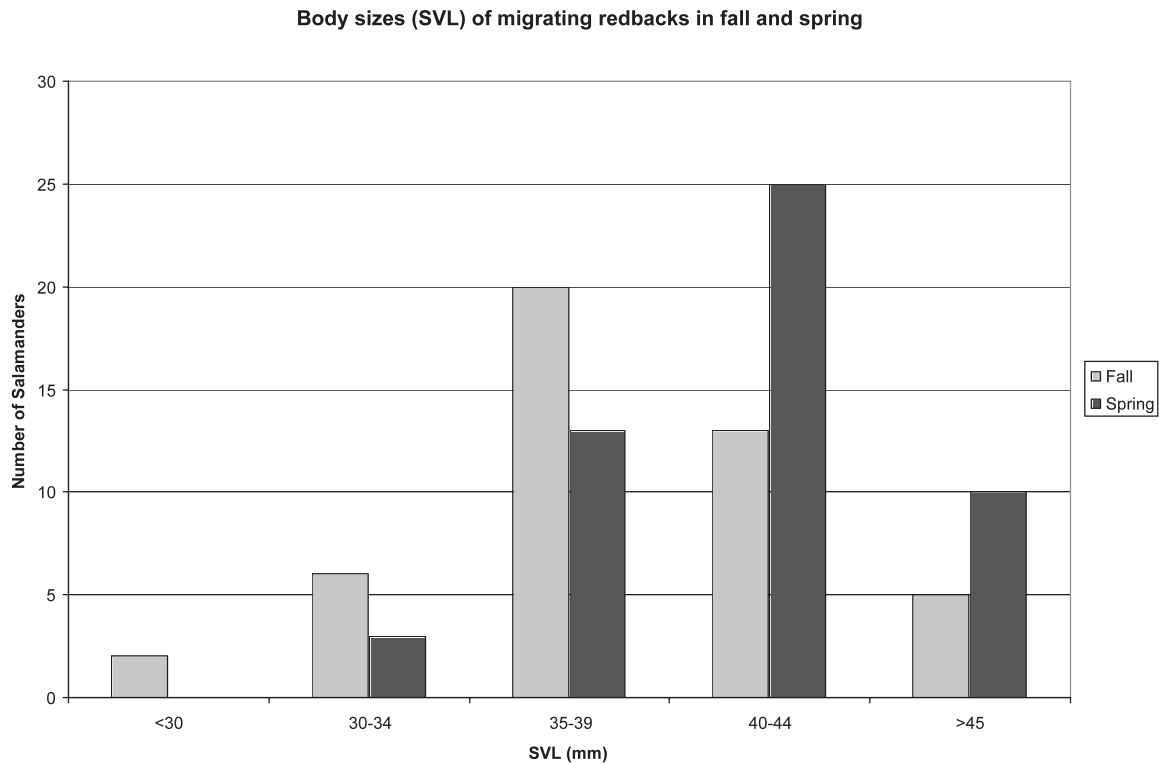


FIG. 1. Body sizes of salamanders captured in the fall (light bars) and spring (dark bars). Distributions among size classes differed seasonally ($\chi^2 = 9.03$, $0.01 < P < 0.025$, 2 df).

location at a depth of 31–75 cm in January. All were mature adults; more than half of the females had mated; one male had a mature spermatophore; and the majority had food in their stomachs. Hoff (1977) reported finding 87 *P. cinereus* at depths between 30 and 36 inches under the stumps of recently cut white oaks in Massachusetts in February. He reported that those animals were found typically in the channels of partially rotted roots, that they were active, and that some had food in their stomachs. Grizzell (1949) found a *P. cinereus* about three feet below the surface in the burrow of a hibernating Woodchuck (*Marmota monax*) in February and remarked on the immediate activity of the salamander. Cooper (1962) reported finding *P. cinereus*, along with several other species of plethodontids, in a cave and speculated about whether seasonal migrations might occur. There are several other reports of plethodontids from karst and cave surveys (e.g., Briggler and Prather, 2006; Camp and Jensen, 2007; Elliott and Ireland, 2002; Fowler, 1951; Jensen et al., 2002; Newman, 1954). Both Fowler (1951) and Newman (1954) noted the apparent seasonal nature of cave occupancy. The combined weight of these reports suggests that *P. cinereus* may take advantage of wintering sites.

If it is possible for *P. cinereus* to stay active longer and grow more during the winter in the uphill habitat, one wonders why immature individuals would not benefit also from seasonal migration. Madison (1969) reported that immature *P. jordani* had less homing ability than adults and suggested that learning might be involved with this behavior. It also seems possible that smaller *P. cinereus* have limited physical ability to disperse, or that, in the absence of breeding behaviors, the selective advantage of migration might be reduced. The smallest salamander we found moving was 26 mm SVL, and only one other was less than 30 mm. It seems likely that the wetter lowland area offers more opportunity for activity, feeding, and

growth than does the dry upland site. Grover (1998) experimentally increased moisture by watering areas with sprinklers and found an increase in abundance and activity of juvenile *P. cinereus*. Also, smaller salamanders are more subject to desiccation than large ones (Spotila, 1972).

We do not know how common seasonal migration might be among *P. cinereus* populations. There are multiple reports of seasonal shifts in *P. cinereus* abundance on the surface of the ground. Nagel (1977) reported that by June individuals were difficult to find. Blanchard (1928) reported that *P. cinereus* in Michigan could be found in early spring and late autumn. Ovaska and Gregory (1989) reported that adults were active from March to June and September to November but disappear in midsummer. Cover board data from the Long Point World Biosphere Reserve show consistently across sites and years that *P. cinereus* are most commonly found in the spring and fall, with lower numbers in the summer (Van Wieren, 2003). Most population studies have assumed, based on the work of Taub (1961), that *P. cinereus* are underground when they are not found in regular retreat locations. Taub's study demonstrated that *P. cinereus* will travel underground, especially under experimental conditions that provide passageways for their travel, but she did not collect data on vertical movement under natural conditions. Our study suggests that seasonal fluctuations in salamander abundance could be explained also by horizontal migration.

Horizontal migration into an abandoned mine for the winter and out again in the spring was documented for a population of *Eurycea longicauda* (Mohr, 1944). He reported that the salamanders were as active in the mine in the winter as they were outside in other seasons and reported finding their eggs in the mine in January.

There have been prior suggestions of horizontal migration in *P. cinereus*. Test and Bingham (1948) removed all *P. cinereus* from a study plot during four extensive searches in May and June and were puzzled by continuing to find substantial numbers each time. They considered the possibility that the later captures had immigrated, although they ultimately favored an explanation based on vertical migration. However, based on the descriptions in their manuscript, the study area was a mesic site, and there was an unusual amount of rainfall throughout their study. We found continued migration at our site with heavy rainfall in May and into June. Indeed, Test and Bingham's (1948) study was prompted by prior censuses by Test that suggested considerable "shifting of individuals" (p. 362), although they did not elaborate on that prior work. LeClair et al. (2006) did weekly checks of drift fences set up across the slope at four sites in Quebec from 29 May to 3 November. The majority of their captures occurred in the first two weeks in October. This result is consistent with a pattern of seasonal migration in which their study dates missed the spring migration and documented the fall migration.

Circumstantial evidence that *P. cinereus* may move more than suspected was provided by Marsh et al. (2004) who reported that *P. cinereus* displaced as much as 55 m were able to return to their initial capture location, and that forest "islands" constructed in fields were colonized by *P. cinereus* within a year. They suggested a possible dispersal stage in the *P. cinereus*'s life history. Kleeberger and Werner (1982) found that *P. cinereus* displaced as much as 90 m returned to their original sites, typically by a direct route within 24 h. In a genetic analysis, Cabe et al. (2007) reported that *P. cinereus* population structure appears consistent with a model of continuous distribution and limited dispersal, but speculated that *P. cinereus* probably have a greater ability to disperse than they typically exhibit.

It is interesting that the migration path we observed involved the crossing of a paved roadway. Roads are frequently viewed as obstacles to the movement of small amphibians. Marsh et al. (2005) reported that displacement across forest roads greatly reduced the return rate of *P. cinereus*. However, they speculated that the true obstacle might be the steepness of the road bank rather than the road itself. In addition, Marsh et al. (2004) reported that *P. cinereus* appear to cross open fields readily, and Marsh et al. (2008) found that only large roads were associated with genetic differentiation among *P. cinereus* populations.

Although we suggest that seasonal horizontal migration should be considered a possibility in other populations of *P. cinereus*, it does not follow that all populations must exhibit the same seasonal behaviors. Plethodontids show considerable intraspecific variation in life-history characteristics (Tilley and Bernardo, 1993) and might be expected to show intraspecific behavioral differences as well. Jaeger (1979) found no difference between *P. cinereus* density between spring and summer in a population in Virginia. Mathis (1989) also found no seasonal difference in cover board use between June and October. Both of these studies were at high elevations with relatively cool, moist conditions and may be examples of populations of *P. cinereus* that do not migrate seasonally. If the climate or the distribution of resources makes it possible for both the summer activity needs and the winter prebreeding needs to occur in the same place, then there would be no pressure to develop seasonal migration. It is only when all of an animal's annual requirements are not met by its main habitat that we would expect to see seasonality in habitat usage.

Acknowledgments.—We appreciate the efforts of L. Fifield and K. Kiley who conducted some of the transects and helped process the animals. Also, J. Battenfield, S. Macica, E. Smassanow, and M. Woolbright provided valuable assistance in the field. P. Terry conducted some of the cover board checks and collected some of the soil data. K. Bak, K. Byrnes, M. Carson, J. Casinelli, A. Davis, T. Golden, E. Merritt, G. Mulero, M. Purcell, F. Sylvester, and B. Towne assisted with one or more transect check. Partial funding for the project was provided by Siena College. We appreciate the extensive logistical support provided by the National Park Service and the Saratoga National Historical Park. D. Fraser and two anonymous reviewers provided valuable comments on previous versions of the manuscript.

LITERATURE CITED

- BLANCHARD, F. N. 1928. Topics from the life history and habits of the red-backed salamander in southern Michigan. *American Naturalist* 62: 156–164.
- BRIGGLER, J. T., AND J. W. PRATHER. 2006. Seasonal use and selection of caves by plethodontid salamanders in a karst area of Arkansas. *American Midland Naturalist* 155:136–148.
- BURTON, T. M., AND G. E. LIKENS. 1975. Salamander populations and biomass in the Hubbard Brook Experimental Forest, New Hampshire. *Copeia* 1975:541–546.
- CABE, P. R., R. B. PAGE, T. J. HANLON, M. E. ALDRICH, L. CONNORS, AND D. M. MARSH. 2007. Fine-scale population differentiation and gene flow in a terrestrial salamander (*Plethodon cinereus*) living in continuous habitat. *Heredity* 98:53–60.
- CALDWELL, R. S. 1975. Observations on the winter activity of the red-backed salamander, *Plethodon cinereus*, in Indiana. *Herpetologica* 31: 21–22.
- CALDWELL, R. S., AND G. S. JONES. 1973. Winter aggregations of *Plethodon cinereus* in ant mounds, with notes on food habits. *American Midland Naturalist* 90:482–485.
- CAMP, C. D., AND J. B. JENSEN. 2007. Use of twilight zones of caves by plethodontid salamanders. *Copeia* 2007:594–604.
- COOPER, J. E. 1962. Cave records for the salamander *Plethodon richmondi richmondi*, with notes on additional cave-associated species. *Herpetologica* 17:250–255.
- ELLIOTT, W. R., AND L. IRELAND. 2002. The Missouri cave life survey. In G. T. Rea (ed.), *Proceedings of the National Cave and Karst Management Symposium*, pp. 123–130. Tucson, Arizona, October 16–19, 2001.
- FELLERS, G. M., AND C. A. DROST. 1994. Sampling with artificial cover. In W. R. Heyer, M. A. Donnelly, R. W. McDiarmid, L. C. Hayak, and M. S. Foster (eds.), *Measuring and Monitoring Biological Diversity. Standard Methods for Amphibians*, pp. 146–150. Smithsonian Institution Press, Washington, D. C.
- FOWLER, J. A. 1951. Preliminary observations on an aggregation of *Plethodon dixi*. *Herpetologica* 7:147–148.
- FRASER, D. F. 1976. Empirical evaluation of the hypothesis of food competition in salamanders of the genus *Plethodon*. *Ecology* 57:459–471.
- GILLETTE, J. R., AND M. G. PETERSON. 2001. The benefits of transparency: candling as a simple method for determining sex in red-backed salamanders (*Plethodon cinereus*). *Herpetological Review* 32:233–235.
- GRIZZELL, R. A. 1949. The hibernation site of three snakes and a salamander. *Copeia* 1949:231–232.
- GROVER, M. C. 1998. Influence of cover and moisture on abundances of the terrestrial salamanders *Plethodon cinereus* and *Plethodon glutinosus*. *Journal of Herpetology* 32:489–497.
- HOFF, J. G. 1977. A Massachusetts hibernation site of the red-backed salamander, *Plethodon cinereus*. *Herpetological Review* 8:33.
- JAEGER, R. G. 1972. Food as a limited resource in competition between two species of terrestrial salamanders. *Ecology* 53:535–546.
- . 1979. Seasonal spatial distributions of the terrestrial salamander *Plethodon cinereus*. *Herpetologica* 35:90–93.
- JAEGER, R. G., AND W. F. GERGITS. 1979. Intra- and interspecific communication in salamanders through chemical signals on the substrate. *Animal Behaviour* 27:150–156.

- JENSEN, J. B., C. D. CAMP, AND J. L. MARSHALL. 2002. Ecology and life history of the Pigeon Mountain salamander. *Southeastern Naturalist* 1:3–16.
- KLEEGER, S. R., AND J. K. WERNER. 1982. Home range and homing behavior of *Plethodon cinereus* in northern Michigan. *Copeia* 1982: 409–415.
- LECLAIR, M. H., M. LEVASSEUR, AND R. LECLAIR JR. 2006. Life-history traits of *Plethodon cinereus* in the northern parts of its range: variations in population structure, age, and growth. *Herpetologica* 62:265–282.
- MADISON, D. M. 1969. Homing behaviour of the red-cheeked salamander, *Plethodon jordani*. *Animal Behaviour* 17:25–39.
- MADISON, D. M., V. R. TITUS, AND V. S. LAMOUREUX. 2010. Movement patterns and radiotelemetry. In C. K. Dodd Jr. (ed.), *Amphibian Ecology and Conservation*, pp. 183–202. Oxford University Press, Oxford.
- MARSH, D. M., K. A. THAKUR, K. C. BULKER, AND L. B. CLARKE. 2004. Dispersal and colonization through open fields by a terrestrial woodland salamander. *Ecology* 85:3396–3405.
- MARSH, D. M., G. S. MILAM, N. P. GORHAM, AND N. G. BECKMAN. 2005. Forest roads as partial barriers to terrestrial salamander movement. *Conservation Biology* 19:2004–2008.
- MARSH, D. M., R. B. PAGE, T. J. HANLON, R. CORRITONE, E. C. LITTLE, D. E. SEIFERT, AND P. R. CABE. 2008. Effects of roads on patterns of genetic differentiation in red-backed salamanders, *Plethodon cinereus*. *Conservation Genetics* 9:603–613.
- MATHIS, A. 1989. Do seasonal spatial distributions in a terrestrial salamander reflect reproductive behavior or territoriality? *Copeia* 1989:788–791.
- . 1991. Territories of male and female terrestrial salamanders: costs, benefits, and intersexual spatial associations. *Oecologia* 86: 433–440.
- MOHR, C. E. 1944. A remarkable salamander migration. *Proceedings Pennsylvania Academy Sciences* 18:51–54.
- NAGEL, J. W. 1977. Life history of the red-backed salamander, *Plethodon cinereus*, in northern Tennessee. *Herpetologica* 33:13–18.
- NEWMAN, W. B. 1954. A new plethodontid salamander from southwestern Virginia. *Herpetologica* 10:9–14.
- OVASKA, K., AND P. T. GREGORY. 1989. Population structure, growth and reproduction of *Plethodon vehiculum*. *Herpetologica* 45:133–143.
- PULLIAM, H. R. 1988. Sources, sinks, and population regulation. *American Naturalist* 132:652–661.
- SAYLER, A. 1966. The reproductive ecology of the red-backed salamander, *Plethodon cinereus*, in Maryland. *Copeia* 1966:183–193.
- SIEGEL, S. 1956. *Nonparametric Statistics for the Behavioral Sciences*. McGraw Hill, New York.
- SPOTILA, J. R. 1972. Role of temperature and water in the ecology of lungless salamanders. *Ecological Monographs* 42:95–125.
- TAUB, F. B. 1961. The distribution of the red-backed salamander, *Plethodon c. cinereus*, within the soil. *Ecology* 42:681–698.
- TEST, F. H., AND B. A. BINGHAM. 1948. Census of a population of the red-backed salamander (*Plethodon cinereus*). *American Midland Naturalist* 39:362–372.
- TILLEY, S. G., AND J. BERNARDO. 1993. Life history evolution in plethodontid salamanders. *Herpetologica* 49:154–163.
- VAN WIEREN, J. 2003. Long Point World Biosphere Reserve *Plethodon cinereus* monitoring program: data analysis. EMAN/Parks Canada National Monitoring Report, University of Waterloo, Ontario, Canada.
- VERNBURG, F. J. 1955. Correlation of physiological and behavioral indexes of activity in the study of *Plethodon cinereus* (Green) and *Plethodon glutinosus* (Green). *American Midland Naturalist* 54:382–393.
- WERNER, J. K. 1971. Notes on the reproductive cycle of *Plethodon cinereus* in Michigan. *Copeia* 1971:161–162.
- WYMAN, R. L. 1988. Soil acidity and moisture and the distribution of amphibians in the forests of southcentral New York. *Copeia* 1988: 394–399.
- WYMAN, R. L., AND D. S. HAWKSLEY-LESCAULT. 1987. Soil acidity affects distribution, behavior, and physiology of the salamander *Plethodon cinereus*. *Ecology* 68:1819–1827.

Accepted: 31 December 2013.