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Postbreeding Emigration and Habitat Use by Jefferson and Spotted Salamanders in Vermont

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ABSTRACT.—**In New England, temporary pool-breeding salamanders inhabit terrestrial forested habitats for the majority of the year. Wetland regulations and forestry Best Management Practices rarely consider the upland areas surrounding breeding pools for protection. Those that do, generally establish buffer zones that are insufficient to protect salamander populations. A better understanding of the area requirements and upland habitat preferences of pool-breeding salamanders is needed to develop biologically relevant buffers for conservation. I used radiotelemetry to investigate the postbreeding emigration and terrestrial habitat use of two syntopic mole salamander species. Sixteen adult salamanders (eight *Ambystoma jeffersonianum*, and eight *Ambystoma maculatum*) were radiotracked for a mean of 164 days (SE = 5.1). Eleven individuals were tracked to overwintering sites (five *A. jeffersonianum*, and six *A. maculatum*). Emigration distances from breeding pool edge varied widely (range = 30–219 m) with a mean of 112.8 m (SE = 19.9) for both species combined. Combining data from this and other studies, a salamander "life zone" that would encompass 95% of the population was calculated, resulting in an area extending 175 m from a pool's edge. Two types of small mammal burrows (deep vertical tunnels, and highly branched horizontal tunnels) were used almost exclusively as terrestrial refuges. In general, Jefferson and Spotted Salamanders used well-shaded, deciduous forest stands with abundant logs and stumps. Their habitat use also showed a strong association with vertical mammal tunnels, suggesting that this resource may be limiting. Biologically defined salamander life zones should be identified as critical wildlife habitat and considered in forest management strategies.**

During the past decade, apparent amphibian declines, increased malformation rates, and local extinction events have resulted in global concerns for conservation of amphibian populations (Barinaga, 1990; Pechmann et al., 1991; Blaustein et al., 1994; Lips, 1998; Alford and Richards, 1999). Development of strategies to address these complex issues has been complicated by a lack of ecological data to guide conservation efforts. Recently, the Northeast Endangered Species Technical Committee listed the Jefferson Salamander as a species of regional conservation concern, indicating that (1) the species is at high risk of extirpation from the region, (2) a significant portion of the species' range occurs in the Northeast, (3) few data exist with which to address conservation concerns, and (4) without conservation attention, the global population could be at risk (Therres, 1999).

Temporary pool-breeding amphibians, such as Jefferson and Spotted Salamanders, use terrestrial forested habitats for the majority of the year ($\geq$ 11 months). These areas are where they must acquire enough food to grow and prepare for breeding and seek protection from predation, dehydration, and freezing for long periods of time (Madison, 1997). While breeding sites are critical to the viability of populations, upland areas surrounding temporary pools must also be included in conservation strategies. Semlitsch (1998) reviewed the literature on terrestrial habitat use by six species of *Ambystoma* and found that all postbreeding adults and metamorphs were found outside the current federal delineated wetland boundary, and 76% occurred beyond the 30.8 m (100 ft) extended "buffer zone" recommended in some states (see Murphy and Golet, 1998). These data led Semlitsch (1998) to suggest that the habitat surrounding breeding pools be considered a "life zone," vital for the maintenance of the entire juvenile and adult breeding populations.

Numerous studies have identified a variety of habitat features that provide salamanders with necessary forest floor microclimate, as well as surface and subterranean refuges. These include deep, uncompacted leaf litter (Pough et al., 1987; DeGraaf and Rudis, 1990; Bonin, 1991; deMaynadier and Hunter, 1998), coarse woody debris (Bury and Corn, 1988; Petranka et al., 1994; Dupuis et al., 1995; Windmiller, 1996), stumps and roots (Aubry et al., 1988; Corn and Bury, 1991; deMaynadier and Hunter, 1998, 1999), dense understory vegetation (Pough et al., 1987), a closed forest canopy (deMaynadier and Hunter, 1998), and the presence of small mammal runways (Williams, 1973; Semlitsch, 1981; Windmiller, 1996; Madison, 1997). Even small-scale habitat disturbances that affect the forest floor environment may impact local

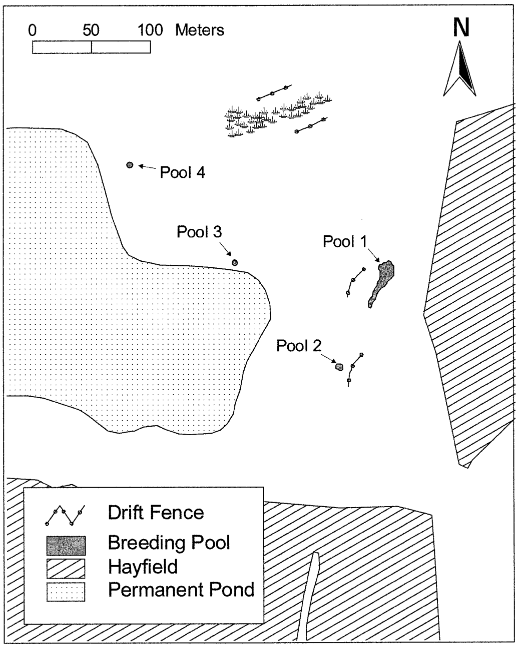

FIG. 1. Study area and location of temporary breeding pools and drift fence arrays at the Marsh-Billings-Rockefeller National Historical Park, Woodstock, Vermont.

populations of salamanders (deMaynadier and Hunter, 1995).

In Maine, New Hampshire, and Vermont, where more than 80% of the landscape is classified as forested and a large proportion of that is privately owned and managed for forest products (National Association of State Foresters, 2002), there is a critical need to develop biologically based management guidelines that will protect biodiversity within working forests. Natural resource managers who strive to balance forest management activities with biological resource needs often rely on accepted Best Management Practices (BMPs) for guidance. However, forestry BMPs for the Northeast vary considerably, and, with the exception of recently developed guidelines in Maine (Calhoun and deMaynadier, 2002), most focus on protecting the vernal pool depression itself with limited consideration of the surrounding forest. For example, Welsch et al. (1995) recommend maintaining 50% crown cover within a 40.2 m buffer zone around vernal pools, whereas New Hampshire guidelines recommend maintaining a shaded, minimally disturbed buffer within 15.4 m of a vernal pool (New Hampshire Division of Forests and Lands et al., 1997). In contrast, Maine BMPs recommend maintaining canopy closures of at least 75% within a 30.5 m "Protection Zone," and 50–60% between 30.5 m and 121.9 m from the pool edge (Calhoun and deMaynadier, 2002).

In developing Maine BMPs, the authors benefited from several recent studies (e.g., Madison, 1997; Semlitsch, 1998), suggesting that other state and federal guidelines were not adequate to conserve amphibian populations at most sites. Semlitsch (1998) indicated a need for still more data for pool-breeding salamanders based on direct monitoring techniques and additional documentation of habitat requirements. To this end, I used radiotelemetry to investigate the postbreeding movement patterns, emigration distances, and microhabitat use of syntopic Jefferson and Spotted Salamanders in central Vermont.

MATERIALS AND METHODS

Study Site.—The study area was located within the Marsh-Billings-Rockefeller National Historical Park (MABI), Windsor County, Vermont (43°37′N, 72°32′W). The 225-ha park ranges in elevation from 210–433 m and has a long history of careful land stewardship and sustainable forest management (Foulds et al., 1994). Vegetation is dominated by northern hardwood forest, primarily American beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), and yellow birch (*Betula alleghaniensis*), with some stands containing a significant component of eastern hemlock (*Tsuga canadensis*). In addition, there are several conifer plantations of various sizes and species composition, including red pine (*Pinus resinosa*), Scotch pine (*P. sylvestris*), Norway spruce (*Picea abies*), European larch (*Larix decidua*), and white pine (*P. strobus*), as well as several hayfields totaling 13.4 ha. The park contains an extensive network of hiking trails and unimproved carriage roads that are open to foot and horse traffic. This study was centered around 4 temporary breeding pools located in a beech/maple/hemlock stand at an elevation of 350 m (Fig. 1).

Methods.—Between 1 and 24 May 2000, Jefferson and Spotted Salamanders were captured in drift fence arrays previously established at the study area during a herpetological inventory (Fig. 1). Eight (4 M, 4 F) adult Jefferson Salamanders and eight (5 M, 3 F) adult Spotted Salamanders were randomly selected for radio tagging. Eleven individuals were from known breeding pools. Of these, five (four Jefferson, one Spotted) were from pool 1, and six (two Jefferson, four Spotted) were from pool 2 (Fig. 1). The remaining five salamanders were captured away from breeding sites, and their precise breeding location could not be determined, if they bred at all.

Radio transmitter units (model BD-2GH, Holohil Systems Ltd., Carp, Ontario, Canada) with an estimated battery life of six months were surgically implanted using a technique similar to Madison (1997). Each transmitter unit (including radio, battery, and internal helix antenna) was completely encapsulated by inert marine epoxy, resulting in pear-shaped implants measuring 16 mm × 9 mm and weighing 1.75 g. Prior to surgery, salamanders were immersed in a 0.1% (1 g/l) solution of MS-222 (tricaine methanesulfonate) at room temperature. All instruments and transmitter implants were sterilized with ethyl alcohol. Average induction time was 31 min ± 12.4 SD (range 14–50 min). To implant the radio unit, I made a 12 mm longitudinal incision in the left ventrolateral abdominal wall 10 mm anterior to the left hind leg. A transmitter was placed through the incision with the transmitter's wide end posterior. Five to seven sutures using 5-0 silk were used to close the incision. Immediately following surgery, salamanders were briefly immersed in fresh water at room temperature to remove residual anesthesia and then placed in individual plastic boxes with moist paper towels.

Less than 24 h postsurgery, all implanted salamanders were released at a suitable cover object (e.g. log, stump, accumulations of leaf litter, etc.) within 2 m of their point of capture. Locations of salamanders in underground refuges were obtained by using direct overhead localization with a handheld antenna. In addition, I occasionally conducted limited searches to visually confirm an individual salamander's precise location, refuge use, and postoperative condition. Searches included delicate removal of leaf litter, turning of cover objects, illuminating tunnel entrances with a small flashlight, and occasional limited hand-excavation of tunnel systems. Radio telemetry was conducted following rain events or at least once per week during daylight hours through 15 November 2000. All new locations were marked with small ground flags on which the transmitter frequency, date, and species was recorded with permanent marker. Salamander positions were later spatially referenced using a Trimble GPS unit and plotted in ArcView.

Emigration was considered to have occurred if salamanders moved at least 20 m from their release point. Spring emigrants were arbitrarily defined as those completing at least 67% of their maximum distance from release point between 17 May and 16 July; summer emigrants, at least 67% between 17 July and 15 September; fall emigrants, at least 67% between 16 September and 15 November; and "split" emigrants, those completing more than 33% during any two periods. Local precipitation data for Woodstock, Vermont were obtained via the National Weather Service web page (http://www.nws.noaa.gov/er/btv/).

TABLE 1. Habitat variables measured at Jefferson and spotted salamander locations and random plots at the Marsh-Billings-Rockefeller National Historical Park, Vermont, 2000.

Habitat variable
3-m radius plot
Ground cover[a]
Total green cover
Shrubs
Ferns
Grass/sedge
Forbs
Moss
Deciduous leaf litter
Coniferous leaf litter
Downed logs > 5 cm diameter
Bare ground
Standing water
Coarse woody debris
Saplings
Coniferous canopy
Deciduous canopy
Mid-story canopy
Shrub/sapling density
Plot aspect
Plot slope
1-m^2 plot
Tunnel substrate
Tunnel type
Length of horizontal type tunnels
Number of vertical type/other tunnels
Litter depth
Number of CWD objects (>5 cm diameter)
Distance to nearest CWD
Number and decay class of logs/stumps (>10 cm diameter)
Soil moisture

[a] Based on visual estimates of percent cover below 50 cm.

Refuge and Habitat Sampling.—Habitat variables were selected on the basis of previously described habitat associations (deMaynadier and Hunter, 1995, 1998; Wyman, 1988) and on their relevance to forest management practices (Table 1). Refuge characteristics and habitat variables were sampled at each unique salamander refuge location (N = 89) and at 50 random plots within the study area. Random plots were selected using a random numbers table to generate a compass direction in degrees and distance in meters. If a random plot occurred in nonforested habitat, another point was selected.

Within a 3-m radius plot centered on each salamander location, I made visual estimates of percent cover by 13 categories of ground cover, measured coniferous and deciduous canopy closure (> 3 m in height) and mid-story canopy closure (1.5–3 m in height) using a convex mirror densiometer, classified shrub/sapling stem density by visual estimates as either low

(0–10 stems), medium (11–50 stems), or high (> 50 stems), and recorded plot aspect and slope.

Within a 1-m^2 plot centered on each salamander location, I classified known tunnel refuges into three categories—horizontal, vertical, or eastern chipmunk (*Tamias striatus*). Horizontal tunnels consisted of highly branched, 2.0–2.5 cm diameter tunnels oriented horizontally in the organic layer just beneath the litter, whereas vertical tunnels consisted of smaller, 1.5–2.0 cm diameter burrows oriented vertically into the soil, usually without horizontal runways under the litter. Chipmunk tunnels were characterized by vertical burrows with a diameter of 4–6 cm. Tunnels were classified as unknown if they did not fit into any of these categories or if the precise refuge used could not be confirmed. I also identified any habitat feature(s) associated with the occupied tunnel refuge (e.g., log, stump, leaf litter, root, coarse woody debris [CWD], root bole, pit or mound topography, rock rubble, snag, or road-bank). I counted the number of CWD objects (> 5 cm diameter) and measured the distance from plot center to the nearest one. I also counted large diameter logs and stumps (> 10 cm) and placed them into one of the following decay classes: Class 1 = freshly fallen, supported above soil by branches; Class 2 = structurally sound, bark-covered but resting on soil; Class 3 = relatively intact but beginning to rot and lose bark; Class 4 = soft, with little bark remaining and; Class 5 = almost completely incorporated into soil (Monti, 1997). Organic litter depth was measured with a ruler (to nearest mm) at the plot corners and center, and after removing all leaf litter and CWD from the plot, I measured the length of horizontal tunnels using a tape (to nearest centimeter) and counted the number of vertical and chipmunk tunnel entrances. Finally, using a bulb planter, I collected a soil sample at the plot center to estimate relative soil moisture content. Soil samples were weighed, air dried for 21 days, and then weighed again. Soil water content was calculated using the following formula: [(Soil Wet Weight–Soil Dry Weight)/Soil Dry Weight]. Field measurements of all habitat variables were collected in July of 2001.

Data Analyses.—Data for emigration distances from release point deviated from normal distributions and did not normalize following standard transformations. Therefore, I used nonparametric Mann-Whitney *U*-tests to compare net emigration distances from release point between species and sexes. Following Semlitsch (1998), I used the mean emigration distance from known breeding pools to calculate a terrestrial life zone that would encompass 95% of the *A. jeffersonianum* and *A. maculatum* populations. I used the following formula to calculate the distance that would encompass 95% of the adult population: [95% confidence limits = mean ± 2.23 (t-distribution; $\alpha = 0.05$, df = 10) × standard deviation/$\sqrt{n}$].

Multiple logistic regression was used to describe the relationships between salamander presence/absence and microhabitat characteristics, as well as to describe habitat associations between the two species. In constructing models to compare salamander-use sites (1) with random sites (0), data from both salamander species were pooled to improve power. For between-species habitat comparisons, the dependent variable was defined as *A. jeffersonianum* (1) or *A. maculatum* (0). I used forward stepwise selection methods (P to enter and remove = 0.05), and only those variables with tolerance values greater than 0.2 were included in the best-fit models. I evaluated the significance of variable coefficients using Chi-square tests of Wald statistics (Hosmer and Lemeshow, 1989). I used Mann-Whitney *U*-tests to compare habitat variables between salamander overwintering and non-overwintering sites with random sites because data were not normally distributed and did not normalize following transformations. Salamander use of horizontal and vertical tunnel refuges by month was analyzed with a Chi-square test of an $r \times c$ contingency table. All statistical analyses were conducted with SYSTAT 8.0, and used $\alpha = 0.05$; however, Bonferroni adjustments were made to P-levels for Mann-Whitney *U*-tests to account for multiple tests of a single data set (Zar, 1996). Means are given ± 1 SE.

RESULTS

Sixteen salamanders (eight *A. jeffersonianum*, eight *A. maculatum*) were radiotracked between 17 May and 15 November 2000 for a total of 466 telemetry fixes (Table 2). The average number of days tracked was 164 ± 5.1 (range 119–182), although radio contact with four individuals (two *A. jeffersonianum*, two *A. maculatum*) was lost prematurely (before day 150). One of these lost signals was caused by suspected transmitter/battery failure (J-M-446), whereas three were caused by unknown causes (J-M-488, S-M-211, S-F-288).

Eleven of the 16 individuals (five *A. jeffersonianum*, six *A. maculatum*) were tracked to overwintering sites where their implant either expired or could not be detected because of depth underground. Although no mortality among the study animals was documented, I found Jefferson Salamander male J-M-409 on 21 August lying on the soil surface adjacent to a rotten stump in which it often found refuge. It was highly desiccated, and its tail was scarred, presumably with bite marks from a depredation attempt by a shrew. When checked one week later, its signal emanated from deep within the

TABLE 2. Inventory, fate, and movement data of 16 Jefferson and Spotted Salamanders radiotracked at the Marsh-Billings-Rockefeller National Historical Park, Vermont, 2000. Provided for each salamander is their sex, initial mass at implant surgery, subsequent mass (^{a} = 21 August, ^{b} = 3 October), the number of days tracked, and the number of positions (Fixes). The fates include animals alive at their last position when their transmitters expired (A), animals with suspected transmitter failures (T), and animals whose fate was unknown (U). The distances moved include total distance during radio tracking (TD), the net maximum distance from the release point (ND), and the maximum distance in a single movement (SD).

ID	Sex	Initial mass (g)	Autumn mass (g)	Days tracked	Date of last fix	No. of fixes	Fate	TD (m)	ND (m)	SD (m)	Type of emigrant
Jefferson Salamander (*A. jeffersonianum*)											
J-M-392	M	12.4	11.8^a	182	15 Nov	33	A	92	89	36	Summer
J-M-409	M	11.9		180	13 Nov	35	A	66	61	30	Spring
J-M-446	M	13.1		146	3 Oct	24	T	125	97	83	Spring
J-M-488	M	11.7		133	27 Sep	24	U	83	64	42	Spring
J-F-309	F	13.6	15.9^a	177	15 Nov	31	A	424	405	355	Spring
J-F-461	F	17.1		153	13 Oct	29	T	93	11	14	
J-F-508	F	17.2		182	15 Nov	34	A	119	57	44	Fall
J-F-526	F	15.4		182	15 Nov	35	A	244	194	125	Spring
Spotted Salamander (*A. maculatum*)											
S-M-211	M	18.9		119	13 Sep	18	U	104	94	70	Spring
S-M-228	M	19.0	22.9^b	175	15 Nov	28	A	62	46	54	Spring
S-M-246	M	11.9		176	15 Nov	29	A	18	12	7	
S-M-268	M	15.2		176	15 Nov	31	A	73	58	39	Spring
S-M-328	M	20.1	22.5^b	181	15 Nov	35	A	196	182	133	Spring
S-F-288	F	23.1		141	3 Oct	23	U	237	181	106	Spring
S-F-349	F	24.0		155	19 Oct	28	A	243	218	156	Summer
S-F-371	F	16.4		161	25 Oct	29	A	59	18	13	

stump. Two attempts to excavate this salamander to confirm its fate were unsuccessful, although changes in signal strength and intensity during these attempts suggested that the animal moved in response to my digging.

Limited searches were conducted to confirm an individual's presence and refuge use, often resulting in visual and/or physical contact. All 16 individuals were located visually at least once after release. Of 57 visual contacts, 11 animals (five Jefferson, six Spotted) were captured on 18 occasions to briefly inspect their suture lines and assess their general health. Those inspected less than 30 days postsurgery appeared in good health with well healed, but noticeable, suture lines. Those handled greater than 60 days following surgery showed no scarring or other indications of suturing and appeared to be in good health. Four individuals were weighed in the field and their masses compared to those taken during implant surgery (Table 2).

Emigration.—Although emigratory movements occurred in all directions, most were to the north/northwest or south/southeast, consistent with the two major emigration barriers (permanent pond and hayfield) east and west of the study site (Fig. 1). By mid- to late-June, most individuals had settled into a defined home range (approximately 15–20 m^2) where they remained all summer. Of the 16 individuals tracked, 13 (seven Jefferson, six Spotted) moved more than 20 m from their release points and therefore could be categorized as to occurrence and type of emigration (Table 2). Ten salamanders (five Jefferson, five Spotted) were spring emigrants, one of each species were summer emigrants, one Jefferson was a fall emigrant, and three (one Jefferson, two Spotted) were nonemigrants. Of the 10 spring emigrants, major movements of nine individuals occurred during rain events on 12 June, and 3 and 7 July. On 12 June, one Jefferson and three Spotted Salamanders moved an average of 103.4 ± 17.4 m (range = 54–133 m), whereas on 3 and 7 July, three Jefferson and two Spotted Salamanders moved an average of 107.1 ± 62.4 m (range = 30–355 m). The earliest emigration occurred on 24 May—just one week after implant surgery—when J-M-446 moved 83 m northwest to a hemlock-dominated forest stand where it remained until its transmitter prematurely expired on 3 October. The only fall emigration occurred on 19 October when J-F-508 moved 30 m to an overwintering site. All emigrations apparently occurred on nights with precipitation.

Mean distance moved from release point to last location for all 16 salamanders was 111.9 ± 25.7 m (range = 11–405 m). There was no difference between species, with Jefferson Salamanders moving an average of 122.6 ± 44.4 m (range = 11–405 m), and Spotted 101.1 ± 28.8 m

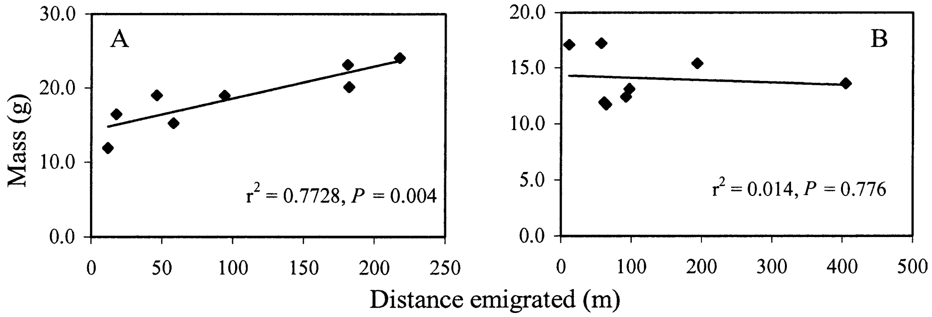

FIG. 2. Relationship between mass and distance emigrated from release site for radio-tagged (A) Spotted and (B) Jefferson Salamanders, Marsh-Billings-Rockefeller National Historical Park, Vermont.

(range = 12–218 m; $U = 35.00$, $P = 0.753$). Although the mean distance moved from release point for females (154.9 ± 53.0 m, range = 18–405 m) was nearly twice that of males (78.4 ± 15.8 m, range = 12–182 m), the difference was not significant because of the wide variability ($U = 38.00$, $P = 0.491$). Similarly, among the 13 individuals that were considered emigrants (Table 2), females moved considerably but not significantly farther from their release point (mean = 211.0 ± 55.9 m, range = 57–405 m) than males (mean = 86.8 ± 15.2 m, range = 46–182 m; $U = 32.00$, $P = 0.079$). In addition, there was a significant positive relationship between salamander mass and net distance moved from release site for *A. maculatum* but not for *A. jeffersonianum* (Fig. 2).

Movement distances from known breeding pools could be determined for 11 individuals in this study, 10 of which were captured exiting pools 1 or 2, and one that was found in close proximity to pool 1. For both species combined, the mean distance moved from the closest pool edge was 112.8 ± 19.9 m. The mean distance traveled from pool edge for *A. jeffersonianum* was 92.8 ± 25.1 m (range = 30–205 m, $N = 6$) and 136.8 ± 31.0 m for *A. maculatum* (range = 52–219 m, $N = 5$). Because the distances salamanders moved away from known breeding pools were normally distributed (test of normality of data for both species combined; $W = 0.892$, $P = 0.145$), then by definition, the mean distance traveled from a breeding pool for these two species (112.8 m) represents an area that would include just 50% of the population. For the breeding pools at MABI, a life zone encompassing 95% of both populations would extend 157.1 m from a pool's edge. Adding the mean distances traveled from pool edge for *A. Jeffersonianum* and *A. maculatum* from this study (92.8, 136.8, respectively) to the means for these species from other studies summarized by Semlitsch (1998), I again calculated the 95% life zone using the same formula (see Materials and Methods). This resulted in a salamander life zone that would extend at least 175 m from a pool's edge.

Refuge Use.—Within a few days of release, most animals moved into subterranean refuges, primarily small mammal tunnel systems. Salamanders were observed in refuges on 56 occasions, 52 of which (91.2%) were within mammal runway systems. Forty-one refuges (73.2%) were horizontal runways, four (7.1%) were vertical runways, seven (12.5%) were in tunnels that could not be classified as to type, two (3.6%) were underneath rotten logs, and two (3.6%) were under slabs of bark. *Ambystoma jeffersonianum* was never observed in vertical runways, whereas two *A. maculatum* were twice observed using vertical burrows.

In addition to direct observations, salamander use of mammal runways was inferred from radio telemetry locations. Based on signal strength and habitat features, 444 of 466 radio fixes (95.3%) were pinpointed to tunnel systems. One hundred sixty-three of these (36.7%) were horizontal tunnels, 106 (23.9%) were vertical tunnels, three (0.7%) were eastern chipmunk tunnels, and 172 (38.7%) either could not be classified as to type, or the precise tunnel system used could not be determined. A significant seasonal shift in tunnel use was evident for both species ($\chi^2_7 = 41.75$, $P < 0.001$). During summer (May through August), 44% of radio locations were from horizontal burrow systems, whereas 16% were from vertical tunnels. During fall (September through November), however, the use of horizontal tunnels dropped to 25%, whereas vertical tunnel use increased to 36%. By November, 54% of radio locations were inside deep, vertical burrows, 6% were in horizontal runways, and 40% could not be identified to tunnel type (Fig. 3).

Microhabitat Characteristics.—The best-fit multiple logistic regression model for salamander refuge sites and random sites was highly significant ($\chi^2_7 = 145.96$, $P < 0.0001$). The model correctly classified 93.5% of salamander refuge locations and 88.3% of random sites. The variables that best discriminated salamander sites from random plots included percent cover of deciduous leaf litter and low shrubs (< 50 cm in height), the number of logs and stumps, soil moisture, slope, and number of vertical tunnels (Table 3). Midstory canopy cover was negatively associated with salamander locations.

The best-fit multiple logistic regression model for discriminating between Jefferson and Spotted refuge sites was also significant ($\chi^2_4 = 36.96$, $P < 0.0001$). Percent cover of logs and saplings were most important at *A. maculatum* sites, whereas *A. jeffersonianum* selected locations with abundant CWD and low shrubs (Table 3). This model, however, correctly classified only 68.7% of 89 sites used by these two species.

Several microhabitat characteristics were associated with tunnel refuges occupied by salamanders significantly more often than expected based on their availability at random plots. Salamanders frequently selected refuges within or under pit/mound topography ($U = 1{,}925.0$, $P = 0.007$), live root boles ($U = 1{,}900.0$, $P = 0.005$), logs ($U = 1{,}858.5$, $P = 0.012$), and stumps ($U = 1{,}944.5$, $P = 0.018$). In addition, overwintering sites had significantly more vertical tunnels than did random sites ($U = 21.0$, $P < 0.001$; Table 4).

Discussion

Although the radio implant technique employed here has been used successfully with other amphibians, this appears to be the first study in which the procedure has been used to track Jefferson Salamanders and to simultaneously track two syntopic species. I documented no mortality among the 16 animals studied, although the fates of three individuals were unknown because of premature loss of radio contact (Table 2). These three "losses" could be attributed to undetected emigrations, transmitter/battery failures, depredation, or an individual retreating too deep underground to be detected.

Emigration.—Radio-tagged animals emigrated during overnight rain events, but movement timing, direction, and distance traveled varied widely among individuals. Some remained at or near their release site for a month or longer, whereas others made an initial movement within a day or two of release. Some individuals were consistently found in the same location, whereas others made frequent moves within their home range. Although Madison (1997) found that emigratory movements of *A. maculatum* in New York occurred almost exclusively in April and May or October and November, most emigration in this study occurred in June and the first week of July. This pattern could be attributed to weather or to a later breeding season than that of *A. maculatum* in New York. Rainfall during May and June 2000 was well above normal. This trend continued during the first week of July, although overall, July rainfall was below normal. Unusually damp conditions may have prompted salamanders to initiate emigration that in other years may occur during autumn rains. In addition, implanted salamanders in this study were released in mid-May, more than a month later than those in Madison's (1997) study.

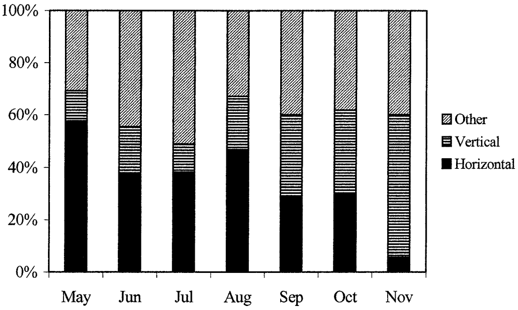

FIG. 3. Proportion of small mammal tunnel types used each month by radio-tagged Jefferson and Spotted Salamanders, Marsh-Billings-Rockefeller National Historical Park, Vermont, 2000.

I expected more individuals to make additional autumn movements, although it is possible that the three salamanders with which I lost radio contact during September and early October made sudden, long-distance movements that went undetected. Although Madison (1997) speculated that salamanders showed a strong bimodal, spring/fall emigration and avoided above-ground movements during summer because of a high risk of snake predation, my results do not support this hypothesis. Predation pressure from snakes may generally be lower at more northern latitudes, such as those of central Vermont. In addition, snake activity during the summer of 2000 appeared to be depressed at MABI because of frequent rains and below normal temperatures (pers. obs.).

For both species combined, the average minimum emigration distance to overwintering sites from release point (112 m) and from breeding pool edge (113 m) is consistent with previous research (Williams, 1973; Douglas and Monroe, 1981; Madison, 1997). However, it should be emphasized that these are minimum distance estimates because they include five individuals that were incompletely radiotracked (Table 2). Therefore, the 157-m life zone value calculated for MABI breeding pools probably underestimates the actual area needed to encompass 95% of most populations. It is likely that the 175-m life zone value derived by adding data from this study to those summarized in Semlitsch (1998) is

TABLE 3. Summary of multiple logistic regression analyses for microhabitat relationships between salamander use sites and nonuse (random) sites, and between Jefferson and Spotted Salamanders, Marsh-Billings-Rockefeller National Historical Park, Vermont, 2000.

Dependent variable	Model variables	Regression coefficient	Standard error	Wald Chi-square	P
Salamander use to nonuse	Number of vertical type tunnels	2.892	0.889	10.593	0.001
	Percent deciduous leaf litter	6.368	2.822	5.092	0.024
	Number of logs/stumps > 10 cm diameter	4.988	1.602	9.695	0.002
	Percent midstory canopy (1.5–3.0 m)	−6.318	2.440	6.704	0.010
	Percent shrub cover	66.971	23.611	8.045	0.005
	Percent slope	0.261	0.090	8.398	0.004
	Percent soil moisture	6.951	3.257	4.556	0.033
A. jeffersonianum to *A. maculatum*	Percent log cover	−18.893	4.917	14.767	<0.001
	Percent sapling cover	−9.583	3.553	7.275	0.007
	Percent CWD	14.578	6.257	5.429	0.020
	Percent shrub cover	8.392	4.238	3.921	0.048

more robust because it includes natural variations caused by geographic location, climate, patch size, type of terrestrial habitat, and other variables. For an isolated vernal pool surrounded by contiguous forest, a 175-m life zone would encompass roughly 10 ha of forested habitat. Whether salamanders require this much habitat, or could successfully use a smaller area should habitat be lost, is unknown. However, some data suggest that an increase in the terrestrial density of adults and/or juveniles would result in decreased survivorship and productivity (Pechmann, 1994). It is also important to realize that the life zones calculated here do not consider the complex nature of metapopulation dynamics, a topic that is only beginning to be explored for pond-breeding amphibians (Semiltsch, 1998, 2000; Marsh and Trenham, 2001). A better understanding of dispersal and colonization rates, isolation effects, extinction risks, and area sensitivities of various pond-breeding species is needed to fully comprehend their area requirements on a landscape scale. Clearly, additional forested habitats are necessary between neighboring pools to provide dispersal corridors and maintain sustainable source-sink dynamics.

Small Mammal Runway Use.—This study suggests that an important ecological relationship exists between ambystomatid salamanders and small mammals that excavate and/or maintain tunnel systems. Both salamander species used horizontal and vertical type small mammal runways as subterranean refuges almost exclusively. Moreover, since salamanders selected microhabitats with significantly higher densities of vertical tunnels based on their availability at random sites, the distribution and abundance of tunnels across the landscape may be limiting to these salamander species. Madison (1997) showed that access to small mammal runways, particularly in the hours before sunrise, is crucial to salamander survival. The distinct seasonal shift that I detected in salamander runway use, from horizontal tunnels in summer to deeper, vertical tunnels in fall, supports the findings of Madison (1997) and suggests that populations of small mammal species may be important to maintaining viable salamander populations by providing both summer and winter refuges. Loredo et al. (1996) demonstrated the importance of ground squirrel burrows for *Ambystoma californiense* and suggested that loss of these habitat features might have strong negative consequences for salamander populations. Results from pitfall trapping in this study indicate that *Sorex cinereus* and *Blarina brevicauda* were the most abundant small mammals present, followed by *Microtus pennsylvanicus* and *Peromyscus leucopus* and *Peromyscus maniculatus* (unpubl. data). These results are similar to those of Brooks and Doyle (2001), who sampled shrew species composition and richness around vernal pools in central Massachusetts. Management strategies that influence the abundance of these and other small mammals may affect salamander populations as well.

Further investigations should focus on whether small mammal density, and therefore the proportion of unoccupied tunnels that are available in a given area may also contribute to the area requirements of these salamander species. Additionally, future studies investigating how salamanders detect, select, and use mammal runways and the length of time that unmaintained tunnels remain suitable for salamander occupancy are crucial to better understand the terrestrial ecology of these and possibly other, ambystomatid salamanders.

Habitat Characteristics.—Microhabitat features associated with ambystomatid salamander loca-

TABLE 4. Values for habitat variables measured at Jefferson and Spotted Salamander locations, random sites, and overwintering sites, Marsh-Billings-Rockefeller National Historical Park, Vermont, 2001. Means given ± 1 SE.

Habitat variable	*A. jeffersonianum* ($N = 50$)	*A. maculatum* ($N = 39$)	Random sites ($N = 50$)	Overwinter sites ($N = 10$)
Total green cover (%)	87.46 ± 2.10	89.95 ± 2.10	93.90 ± 1.40	82.70 ± 5.40
Shrub cover (%)	6.40 ± 1.10*	4.39 ± 0.90*	1.24 ± 0.40	3.80 ± 1.30
Fern cover (%)	1.96 ± 0.60*	5.00 ± 1.30	10.84 ± 2.50	2.00 ± 1.00
Grass/sedge cover (%)	0.22 ± 0.10*	1.00 ± 0.30	5.60 ± 1.80	0.200 ± 0.20
Forb cover (%)	2.70 ± 0.40	5.51 ± 1.30	4.44 ± 0.90	2.50 ± 1.50
Moss cover (%)	7.02 ± 1.00	5.62 ± 0.80	4.84 ± 0.80	7.00 ± 1.80
Deciduous leaf litter (%)	56.54 ± 3.20*	48.54 ± 3.30	32.56 ± 3.70	52.00 ± 7.00
Coniferous leaf litter (%)	5.60 ± 1.60	5.64 ± 1.90	14.16 ± 3.70	6.00 ± 4.30
Downed logs > 5 cm diameter (%)	7.84 ± 0.90	14.87 ± 1.70	9.42 ± 0.90	8.40 ± 1.40
Bare ground (%)	12.34 ± 2.10	10.05 ± 2.10	6.10 ± 1.40	17.30 ± 5.40
Coarse woody debris (%)	9.09 ± 1.30	6.26 ± 0.70	7.46 ± 0.80	5.30 ± 0.90
Saplings (%)	8.22 ± 1.20*	12.67 ± 1.80	13.04 ± 1.20	15.00 ± 4.10
Coniferous canopy (%)	13.64 ± 3.20	16.26 ± 4.00	15.38 ± 3.00	7.30 ± 4.60
Deciduous canopy (%)	74.20 ± 4.40	71.92 ± 4.80	61.10 ± 5.20	80.00 ± 0.08
Mid-story canopy (%)	22.92 ± 2.80	28.92 ± 4.60	43.88 ± 4.90	25.00 ± 8.30
Shrub/sapling density	1.28 ± 0.09	1.31 ± 0.08	1.22 ± 0.06	1.30 ± 0.21
Slope (%)	19.02 ± 1.62	20.28 ± 1.89	18.00 ± 1.52	26.20 ± 4.79
Soil moisture (%)	47.70 ± 4.10	66.64 ± 8.80*	32.73 ± 1.70	62.80 ± 14.60
Litter depth (cm)	2.61 ± 0.19	2.60 ± 0.20	2.34 ± 0.14	1.80 ± 0.21
Number of CWD objects > 5 cm	0.74 ± 0.14	0.82 ± 0.15	0.28 ± 0.10	0.80 ± 0.33
Distance to nearest CWD (cm)	91.38 ± 14.59	61.69 ± 13.96	128.54 ± 16.34	101.50 ± 36.13
Number of logs/stumps > 10 cm	0.68 ± 0.13*	0.77 ± 0.15*	0.08 ± 0.04	0.80 ± 0.33
Length of horizontal tunnels (cm)	100.14 ± 12.81	170.08 ± 37.46	113.64 ± 16.00	111.60 ± 19.94
Number of vertical type tunnels	5.62 ± 0.82*	4.15 ± 0.76*	0.44 ± 0.11	6.30 ± 1.60*

* Significantly different from random value (Mann-Whitney *U*-test), Bonferroni adjusted *P*-value ≤ 0.002.

tions were consistent with those found in mature, deciduous forest stands with low ambient light levels and include a well-developed layer of deciduous leaf litter, abundant coarse woody debris objects > 10 cm diameter, a dense low shrub layer, and relatively high soil moisture content. These habitat features provide a suitable forest floor microclimate, as well as surface and additional subterranean refuges for salamanders. The strong relationship between salamander refuge locations and CWD in this study supports the results of Windmiller (1996), who found that radio-tagged Spotted Salamanders in Massachusetts were usually directly under or within 0.5 m of coarse woody objects, most of which were > 4.5 cm in diameter. This is in contrast to the results of deMaynadier and Hunter (1998), who found that percent cover of CWD had a negative relationship with the abundance of *Ambystoma* species along clearcut-induced forest edges in Maine. Although slash accumulation was high on their study sites, they theorized that the habitat value of downed woody material may be limited if it is of recent decay class or small in diameter and if it is isolated from other important habitat variables such as canopy cover. In this study, logistic regression identified two variables for each salamander species that differentiated between them, percent downed logs and sapling cover for *A. maculatum* and percent CWD and low shrub cover for *A. jeffersonianum*. Biologically the differences appeared insignificant since both involved measures of CWD and shading by understory vegetation.

I located salamanders in refuges associated with pit/mound topography, logs, stumps, live tree root boles, and rotten stumps more often than expected based on availability. The use of pit/mound topography appears not to have been documented in previous published studies. A fairly common feature of mature forest stands, pit/mound topography results when a large diameter tree is blown down, pulling up soil attached to the root system as it falls and leaving a pit in its place (Wessels, 1997). As the trunk and root ball decay, a mound of loose, organic matter remains. Pits often accumulate deep layers of leaf litter that may provide highly favorable microclimatic conditions for short-tailed shrews (Hamilton, 1943; Pruitt, 1959) and, hence, for salamanders seeking refuge. Deep litter maintains a moist forest floor, provides cover for amphibians and invertebrates, and influences the forest floor chemistry. In contrast, the mounds used by salamanders in this study were often devoid of deep litter accumulations, although most contained numerous, small mammal tunnels which may provide high-quality refuge sites for salamanders. However, it is important to note that I only measured whether an association existed with pit and mound topography and did not attempt to discriminate between them. Therefore, it is possible that one of the two features was driving the association.

Management Implications.—Forest management practices may directly affect the ecological integrity of vernal pools and adjacent postbreeding habitats used by amphibians. Although it is imperative that amphibian breeding pools be protected from degradation during forestry operations, it is also critical that protection of the surrounding forest be incorporated in management strategies. Management plans that focus only on protecting breeding pools may fail to maintain viable amphibian breeding populations; therefore, identifying and protecting necessary terrestrial habitat should be a priority (Marsh and Trenham, 2001). The terrestrial habitat used by *A. jeffersonianum* and *A. maculatum* populations in this study extended at least 157 m from the edge of their temporary breeding pools. This "salamander life zone" should be identified as critical wildlife habitat and included in forest management plans. Although more research is needed to better understand the short- and long-term effects of forest management in uplands surrounding temporary breeding pools, a variety of habitat characteristics have been identified as important to mole salamander populations in this and other studies (see review in deMaynadier and Hunter, 1995). Forest managers who strive to maintain these habitat features within the salamander life zone will help preserve the ecological integrity of temporary breeding pools and their associated amphibian breeding populations.

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