

Postbreeding Habitat Use of the Rare, Pure-Diploid Blue-spotted Salamander (*Ambystoma laterale*)

KEVIN J. RYAN^{1,2} AND ARAM J. K. CALHOUN¹

¹Department of Wildlife Ecology, 5755 Nutting Hall, University of Maine, Orono, Maine 04469 USA

ABSTRACT.—The pure-diploid Blue-spotted Salamander (*Ambystoma laterale*) is among the rarest amphibians in northeastern North America, and data on its ecology are sparse. We assessed the movement ecology and terrestrial habitat use of *A. laterale* using radio- and passive integrated transponder (PIT) tag- telemetry. We radio-tracked 22 *A. laterale* for a median of 54 days (range 6–126 days) in the spring and summer of 2009 and 2010. Using a modified PIT tag reader, we conducted 34 in situ surveys during the spring and summer of 2009 through 2011, resulting in 42 relocations. We detected salamanders at a median straight-line distance of 67 m (range 7–281 m) from their breeding wetland. The life zone (i.e., critical terrestrial habitat), encompassing 95% of observed salamander movements, extended 152 m from the edge of the breeding wetland. Eighteen radio-tracked salamanders migrated to upland forest, three to a wet meadow, and one to a red maple (*Acer rubrum*) swamp. Salamanders used upland forest and wet meadow more often than the availabilities of those habitats would predict. We recorded habitat data at 10-m and 1-m-diameter circular plots centered on animal locations. At the 10-m scale, salamander presence was correlated positively with percent cover of slash and correlated negatively with percent cover of grass, total basal area of trees, and relative humidity. At the 1-m scale, salamander locations had deeper leaf litter and moister soil than did random locations. Our results suggest existing, published recommendations for the conservation of vernal pool species are applicable to *A. laterale*.

Pure-diploid Blue-spotted Salamanders (*Ambystoma laterale*) are among the rarest amphibians in the northeastern United States, documented at only three localities: the eastern tip of Long Island, New York at Montauk; Hockomock Swamp in Massachusetts; and the Quinebaug River watershed in eastern Connecticut (Klemens, 1993). Unisexual *A. laterale*—*jeffersonianum* individuals are far more common. In New York and Massachusetts, both *A. laterale* and *A. laterale*—*jeffersonianum* are listed as “Species of Special Concern” by those states. Connecticut lists *A. laterale*—*jeffersonianum* a “Species of Special Concern” but has recently listed *A. laterale* as “Endangered.”

Empirical data on *A. laterale* ecology are sparse, and most published material pertains to the genetics of populations of the Blue-spotted Salamander complex (e.g., Bogart et al., 2009; Bi and Bogart, 2010; Greenwald and Gibbs, 2012). These populations consist of both *A. laterale* and *A. laterale*—*jeffersonianum*, the latter individuals being polyploid (LJ, LLJ, LLJJ, or LLLJ; each letter designates a genome) unisexuals (female) (Bogart and Klemens, 1997, 2008) which reproduce via “kleptogenesis,” using sperm from donors of sympatric, closely related species (Bogart et al., 2009).

Ambystoma laterale breeds in the early spring, typically in fish-free pools similar to those used by other ambystomatids (Klemens, 1993; Bogart and Klemens, 1997; Gibbs et al., 2007), but information on terrestrial habitat use is limited. They are reported to occur in or around wooded swamps (Klemens, 1993) and to be more tolerant of dry, sandy conditions than are other ambystomatid salamanders within their range (Minton 1972, 2001; Voght 1981, cited in Lannoo, 2005). *Ambystoma laterale* also may be more willing to move across open fields and roads than are other salamander species (Regosin et al., 2005). Klemens (1993) and Gibbs et al. (2007) report that *A. laterale* tend to be more surficial than other *Ambystoma*, being found more readily under cover objects (rocks, logs) in spring, summer, and fall. deMaynadier and Hunter (1998) found their presence to be positively correlated with canopy cover, presence of roots, litter depth, and nonvascular plants and negatively correlated with ambient light, woody cover, and midstory cover. Although

these studies do provide information on *A. laterale* ecology, none examined the ecology and habitat use of *A. laterale* exclusively and, thus, generalizations derived from these studies may obscure the specific behaviors of this species.

In New England and elsewhere, wetland buffers (i.e., regulated areas of terrestrial habitat typically extending 30 m or less from wetland edges) were first implemented to maintain water quality (Burne and Griffin, 2005; Rittenhouse and Semlitsch, 2007a). These narrow buffers have also been used by regulators to conserve amphibians, as most species are perceived to be primarily aquatic (Gamble et al., 2006). They have been shown to be insufficient, however, for conserving pool-breeding amphibians because of the animals’ extensive use of terrestrial habitats beyond 30 m from breeding pools (Semlitsch, 1998; Calhoun et al., 2005; Gamble et al., 2006; Skidds et al., 2007). Semlitsch (1998) summarized data from the literature on terrestrial habitat use for six ambystomatid species, not including *A. laterale*, and suggested that a 164-m buffer zone would suffice to encompass the migration distance of 95% of the individuals within a breeding population. (Note that the vernacular has since changed from “buffer” to “critical terrestrial habitat” [Calhoun et al., 2005] or “life zone” [Faccio, 2003; McDonough and Paton, 2007].)

Vernal pool regulations, where they exist, have since used circular life zones (but see Baldwin et al., 2006) around the high-water mark of pools in an effort to protect some of the terrestrial habitat requirements of pool-breeding amphibians. To date, there are no published results on the distances *A. laterale* travels from breeding pools nor on postbreeding habitat use by this species. These are critical information gaps that must be filled to devise effective conservation guidelines for this and other vernal pool-breeding species, which are sensitive to alterations of the landscapes in which they reside. Studying the ecology of *A. laterale* also serves as a baseline for examining the influence of other species’ genes on the ecology of Blue-spotted Salamander-complex populations.

We conducted a study over 3 yr (2009 through 2011) investigating adult postbreeding habitat use of an *A. laterale* population in a heterogeneous, human-dominated landscape in eastern Connecticut. Our specific objectives were to 1) assess postbreeding migration distances of adult salamanders and the

²Corresponding Author. E-mail: kevin.j.ryan@maine.edu
DOI: 10.1670/13-204

area needed to encompass 95% of these movements, 2) assess selection of habitat patches within individual home ranges, and 3) assess selection of specific microhabitats within the habitat patches used (third- and fourth-order selection, respectively, following Johnson, 1980). Based on our previous experience with *A. laterale* and *A. laterale-jeffersonianum*, in general, we hypothesized that salamanders would be found primarily underneath cover objects within forest patches, with deep leaf litter over moist soil. We hypothesized that salamanders would avoid dry, open-canopy habitats such as agricultural fields.

MATERIALS AND METHODS

Research Sites.—We conducted our study on 28.8 ha of privately owned farm in the Quinebaug River drainage in Windham County, Connecticut, USA. The site is in the middle of the known distribution of *A. laterale* in Connecticut, which falls entirely within the USGS 7.5 minute Plainfield quadrangle (M. Klemens, American Museum of Natural History, pers. com.). The ploidy of the salamander at our research site has been confirmed by karyotyping work previously conducted by Bogart and Klemens (1997; sites 57 and 60, 28 individuals total) (2008; site 204, 20 individuals) and James Bogart (unpubl. data, 164 individuals).

Major land cover types present on the site include hayfields, mixed oak/pine forest (*Quercus rubrum* and *Pinus strobus*), and red maple (*Acer rubrum*) forested wetlands. Two breeding pools are present: a 0.24-ha semipermanent kettle-depression scrub-shrub vernal pool; and a 0.15-ha kettle-depression unvegetated pool with a short hydroperiod. The former serves as the primary breeding habitat for the population of Blue-spotted Salamanders inhabiting the site. Also present are five human-created permanent ponds ranging in size from 0.03 to 0.24 ha. An approximately 30-yr-old gravel extraction area at the center of the site formed three of these permanent ponds and a 0.34-ha area of wet meadow (Fig. 1).

Capture and Tagging.—We installed approximately 2 km of drift fence/pitfall trap arrays at the site and monitored them daily from late winter through the late fall/early winter during each year of this study (Fig. 2). We captured *A. laterale* primarily in the drift fence/pitfall trap array completely enclosing the scrub-shrub vernal pool. Upon capture of each individual, we measured the snout-vent length (SVL; to the nearest 0.1 cm), determined mass (to the nearest 0.1 g), and implanted each with a passive integrated transponder (PIT) tag following Madison et al. (2010). We anesthetized salamanders using 3.1 mM tricaine methane sulfonate (MS-222) neutralized to pH 7.0 using aqueous NaOH. When the righting response and response to touch were completely suppressed (following Faccio, 2003; McDonough and Paton, 2007), we made a 1-mm incision in the ventral posteriolateral abdominal wall and inserted a single PIT tag (bathed in chlorhexidine and rinsed with well water) into the peritoneal cavity. Due to the small incision, we deemed sutures unnecessary (but see Ryan et al., 2014). We then rinsed animals with well water and kept them overnight, separately, in plastic containers lined with wet paper towels. We released salamanders the day after surgery directly across from the pitfall trap in which they were captured.

In 2009 and 2010, we implanted subsets of captured *A. laterale* with both PIT tags and radio transmitters (Model NTC-M-3, mass = 0.5 g; Lotek Wireless Fish and Wildlife Monitoring, Newmarket, Ontario, Canada [2009] or Model A2415, mass = 0.4 g; Advanced Telemetry Systems, Isanti, Minnesota, USA

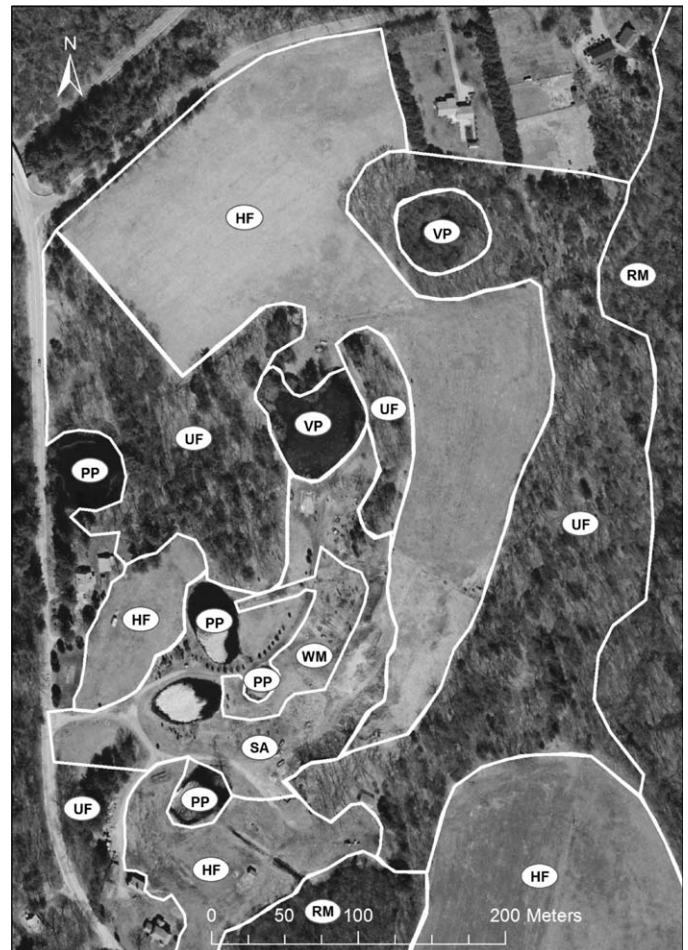


FIG. 1. Major land cover types present at the study site. Letters within ellipsoids indicate cover type: HF = hayfield; RM = red maple swamp; SA = scarified area; PP = permanent pond; UF = upland forest; VP = vernal pool; WM = wet meadow. Note the southern vernal pool is the scrub-shrub pool and the northern is the open-water pool.

[2010]). We implanted radio transmitters only in salamanders that were at least 5.0 g in 2009 and 4.0 g in 2010, such that radio transmitters did not exceed 10% of the individuals' body mass. The transmitter implant procedure differed slightly from the PIT tag procedure in that we made a 5-mm incision in the ventral posteriolateral abdominal wall to facilitate insertion of transmitters, and we closed the incision with dissolvable sutures (Model PDS II, RB-1 taper, Size 5-0, Ethicon Inc., Somerville, New Jersey, USA).

In 2009, we captured postbreeding *A. laterale* ($n = 10$) in the pitfall trap arrays surrounding the scrub-shrub pool. In 2010, we captured salamanders for implantation in the same pitfall trap array ($n = 6$), other on-site pitfall arrays ($n = 3$), or by locating previously PIT tag-implanted individuals ($n = 3$) with a portable PIT tag reader (Pocket Reader; Biomark, Boise, Idaho, USA; hereafter "backpack scanner") (See Ryan et al., 2014). Regardless of their point of capture, all salamanders were confirmed to have bred in the scrub-shrub vernal pool based on pitfall trapping data. We released animals captured in pitfall traps directly across from their point of capture and we released animals detected with the portable PIT tag reader at the exact location where they were found.

Radio Telemetry.—We located salamanders using a Lotek receiver (Model SRX400; 2009) or an ATS receiver (Model R410;



FIG. 2. Pitfall trap array layout.

2010) and an ATS three-element yagi antenna. We assessed daily the location of each salamander to within approximately 10 cm. In addition, we occasionally conducted searches to visually confirm a salamander's location (e.g., under leaf litter or in a small mammal burrow) and to track postoperative condition. We placed pin flags next to salamanders' locations so we could subsequently relocate individuals. We marked all movements >1 m from previous locations with new flags. We recorded all animal locations using a handheld GPS unit (GPSmap 76Cx, Garmin International, Inc., Olathe, Kansas, USA), which was typically accurate within 10 m. We imported GPS points into ArcMap (Version 9.0; Environmental Systems Research Institute, Redlands, California, USA).

PIT Telemetry.—From 2009 through 2011, using the backpack scanner we methodically scanned the cover types within 164 m (13.37 ha) surrounding the scrub-shrub pool to detect PIT tag-implanted *A. laterale* in situ. In all years, we began scanning shortly after the postbreeding adult salamanders emigrated from the pool (late-April or May). We conducted scanning until August in 2009 and 2010 and until July in 2011. Each survey consisted of scanning along 20, evenly spaced straight-line transects radiating out from the wetland (Fig. 3). We conducted scanning transects opportunistically, only on nonrainy days during daylight hours, but independent of previous days' weather conditions. We were able to detect PIT tags reliably from 1–22 cm below the ground surface (see Ryan et al., 2014).

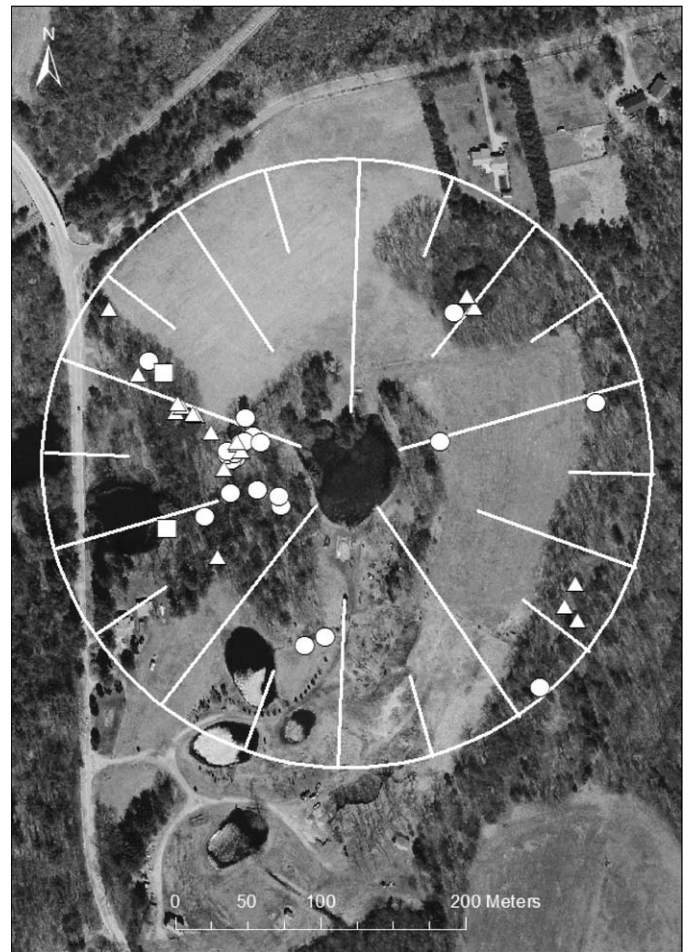


FIG. 3. Sample schematic of scanning transects and locations of Blue-spotted Salamanders scanned in situ. Transects are centered on the scrub-shrub swamp vernal pool. The large circle demarcates the scanning area. Small circles represent 2009 salamander locations, and triangles and squares represent 2010 and 2011 salamander locations, respectively.

Upon detection, we confirmed salamander presence by carefully searching through the leaf litter while scanning with a hand-held PIT tag reader (Pocket Reader; Biomark) until the salamander with the implanted tag was found. We assessed postoperative condition upon finding salamanders. We recorded all salamander locations using a handheld GPS unit and ArcMap, as we did with telemetry locations.

Habitat Data.—We collected and analyzed habitat use at two scales: 3rd-order selection (use of habitat patches within the salamanders' home ranges) and 4th-order selection (microhabitat) (Johnson, 1980). For both telemetry and PIT tag scanning, we collected 22 macro- and microhabitat-related variables at each unique animal location (Table 1). We chose these variables based on previous work on habitat relationships of ambystomatid salamanders (i.e., Faccio, 2003; Montieth and Paton, 2006) and on our observations of the habitat variables of our site. We based visual estimates on cover classes (based on Daubenmire and Daubenmire, 1968, cited in Tiner, 1997) ranging from "trace" ($<1\%$ cover) to "10" (100% cover). We recorded habitat data for both 1-m and 10-m-diameter circular plots centered on animal locations.

For salamanders located via radio telemetry, we collected identical habitat data at two random plots immediately

TABLE 1. Habitat variables collected at 1-m and 10-m-diameter circular plots to assess Blue-spotted Salamander habitat use. Variables were collected at or near the center of each plot. An initial set of 22 variables was chosen based on literature and field observations. This set of 22 was reduced to 14 by excluding from analysis all highly correlated variables ($r \geq 0.7$) and variables that had a value of zero for >50% of sample locations.

Variable	Description
general habitat class	Classes include mixed upland forest, scarified area, deciduous forested wetland, wet meadow, hayfield, and lawn.
airtemp	Ambient air temperature (°C) measured at a height of ~1.5 m above ground using a Kestrel 4100 Pocket Air Flow Tracker (Nielsen-Kellerman, Boothwyn, Pennsylvania, USA).
relhum	Relative humidity (%) measured at a height of ~1.5 m above ground using a Kestrel 4100 Pocket Air Flow Tracker (Nielsen-Kellerman).
canopy	Percent canopy openness above plot. Assessed via analysis of digital images (using a fisheye lens) of the canopy using Gap Light Analyzer computer software (Carey Institute of Ecosystem Studies, Millbrook, New York, USA).
trees	Sum of the diameter at breast height (dbh; cm) of trees >10-cm diameter at that height. Measured using a dbh tape.
shrubs	Visual estimate of percent cover of woody vegetation with stems <10 cm diameter.
herbs	Visual estimate of percent cover of herbaceous/woody vegetation <1 m in height.
slash	Visual estimate of percent cover woody debris 1–10 cm in diameter.
leaflitter	Visual estimate of percent cover of leaf litter.
baresoil	Visual estimate of percent cover of bare soil.
mosslichen	Visual estimate of percent cover of moss and lichen.
grass	Visual estimate of percent cover of grass.
water	Visual estimate of percent cover of standing water.
logsstumps	Number of logs and/or stumps >10 cm in diameter.
norocks	Number of rocks >10 cm in any direction.
perrocks	Visual estimate of percent cover of rocks <10 cm in any direction.
litterdepth	Leaf litter depth measured to the nearest 1 cm with a ruler.
dufftemp	Soil temperature (°C) just below duff layer. Measured using a Hanna HL145 Digital Soil Thermometer (Hanna Instruments, Inc., Woonsocket, Rhode Island, USA). Measured for 1-m-diameter plot only.
soiltemp	Soil temperature (°C) 11 cm below soil surface. Measured using a Hanna HL145 Digital Soil Thermometer (Hanna Instruments, Inc.). Measured for 1-m-diameter plot only.
soilmoist	Volumetric water content (%) of soil measured using FieldScout TDR200 soil moisture probe (Spectrum Technologies, Inc. Aurora, Illinois, USA). Measured for 1-m-diameter plot only.
grndsrftemp	Temperature (°C) at soil surface underneath leaves or other debris using a Kestrel 4100 Pocket Air Flow Tracker (Nielsen-Kellerman). Measured for 1-m-diameter plot only.
grndsrfhum	Relative humidity (%) at soil surface underneath leaves or other debris using a Kestrel 4100 Pocket Air Flow Tracker (Nielsen-Kellerman). Measured for 1-m-diameter plot only.

following data collection on habitat characteristics at a salamander’s actual location. This ensured that the random plots were measured with the same resource availability and weather conditions as for known salamander locations. We did this with our telemetry data only because our method of random point collection depended on knowing an individual salamander’s previous location. We located random plots from a salamander’s location just prior to its current one based on a random compass bearing (0–359°) and the straight-line distance to the animal’s current location. For example, if a salamander moved a straight-line distance of 15 m from point A to point B, the location of a random plot would be determined by taking a random compass bearing at point A and heading 15 m in that direction. If a random plot overlapped with an animal’s current location, a breeding wetland, or the first random plot, a new random location was chosen.

Data Analysis.—For each transmitted salamander, we calculated cumulative minimum total distance traveled (CD), maximum distance between locations (MD), and maximum distance from the breeding wetland (MW). As we did not track all animals for the same number of days, we used linear regression to assess the relationship between length of time tracked and maximum distance observed from the breeding wetland. For normality, we used a Shapiro-Wilk test to examine the straight-line distances that salamanders were detected from the breeding wetland (for both telemetry and PIT tag scanning). If straight-line distance data were not normally distributed, we used a Mann-Whitney *U*-test to compare detection distances between radio telemetry and PIT tag scanning. If no difference was found, data were pooled

prior to calculating the area needed to encompass 95% of the salamanders we detected. We did this by arranging observed MWs in ascending order and determining the distance required to envelop 95% of them.

With salamander locations observed via PIT tag scanning, we compared the number of observations within a cover type to the amount of that cover type relative to the total survey area using the following Resource Selection Function (RSF):

$$RSF = a/b,$$

where *a* = total number of observations in a given cover type/total number of observations and *b* = area of given cover type/total area (Boyce and McDonald, 1999). An RSF of one indicates cover type use in proportion to its availability. RSFs >1 or <1 indicate a cover type being used in greater or lesser proportion than its availability, respectively. We did not calculate an RSF for telemetry locations due to inherent autocorrelation in the data.

For habitat data collected on radio-tracked salamanders, we used conditional logistic regression to compare habitat variables at salamander locations to their paired random locations for both 1-m and 10-m-diameter plots. Prior to fitting conditional logistic regression models, we checked each of the possible variables for correlation with other variables to meet the assumptions of logistic regression (Hosmer et al., 2013). If two or more variables were highly correlated ($r \geq 0.7$), we chose only one in the set for analysis. We also excluded from analysis variables that had a value of zero for >50% of sample locations (e.g., number of logs/stumps and number of rocks). We used an all subsets approach for conditional logistic regression analyses

TABLE 2. Inventory, fate, and movement data of adult Blue-spotted Salamanders radio-tracked in eastern Connecticut, 2009–2010. Listed for each salamander is their ID number, sex, mass at implant surgery, date released after transmitter implantation, number of days tracked, number of unique locations, cumulative minimum total distance traveled (CD), maximum distance traveled between locations (MD), and maximum distance observed from the breeding wetland (MW). The fates include animals whose radio signal was lost (SL), animals whose transmitter was found expelled (EX), animals whose transmitter expired prematurely (TF), animals found dead (FD), and animals whose transmitters expired (TE).

Salamander ID no.	Sex	Mass (g)	Release date	No. days tracked	No. unique locations	CD	MD	MW	Fate
1	F	5.5	7-APR-09	101	7	164	65	100	TE
2	F	6.2	7-APR-09	79	5	79	43	81	TF
3	F	5.7	7-APR-09	19	2	52	40	8	SL
4	M	5.1	7-APR-09	125	6	97	37	77	TE
5	M	5.2	7-APR-09	51	3	23	12	12	EX
6	M	5.8	7-APR-09	17	2	63	49	47	EX
7	F	5.8	16-APR-09	24	2	15	12	23	SL
8	M	5.4	16-APR-09	123	5	119	40	78	EX
9	M	6.7	24-APR-09	54	3	95	52	70	EX
10	M	5.2	30-APR-09	42	4	76	31	28	FD
11	F	5.6	28-MAR-10	126	6	193	70	133	TE
12	F	5.4	28-MAR-10	44	3	281	174	281	TE
13	F	6.1	3-APR-10	54	6	120	56	92	TE
14	M	5.5	3-APR-10	30	2	32	27	37	SL
15	F	8.5	27-APR-10	41	1	7	7	7	TE
16	M	4.9	29-APR-10	6	1	8	8	68	EX
17	M	4.6	5-MAY-10	99	2	27	16	65	EX
18	F	5.5	6-MAY-10	111	9	149	70	98	TF? SL?
19	M	4.3	18-MAY-10	104	7	60	15	62	TE
20	M	Missing	20-MAY-10	83	4	65	24	54	TE
21	M	4.4	9-JUN-10	68	3	78	46	57	EX
22	M	4.9	20-JUL-10	7	1	15	15	122	SL

and constrained models to having a maximum of four variables to ensure a minimum sample-to-variable ratio of 10:1.

We used an information-theoretic approach to assess support for models representing alternative hypotheses of *A. laterale* habitat use (Burnham and Anderson, 2002; Anderson, 2008). We ranked models using Akaike's Information Criterion corrected for small sample size (AIC_c), Akaike's model weights (ω), and Adjusted McFadden's Rho^2 (analogous to r^2 for linear regression, values ≥ 0.2 are considered satisfactory). We considered models < 2 AIC_c units from the top model to be equally supported (Burnham and Anderson, 2002). If no single model comprised $\geq 90\%$ of the AIC weight within the entire candidate model set, then we used model averaging to derive parameter estimates that, when combined, accounted for $\geq 90\%$ of the cumulative model weights (Burnham and Anderson, 2002). Variables were considered to be useful for describing *A. laterale* habitat use if 95% confidence intervals (CI) around odds ratios did not overlap one.

We conducted all statistical analyses using the statistical software R version 2.14.2 (R Development Core Team, 2012). We defined statistical significance as $P \leq 0.05$.

RESULTS

Radio Telemetry.—We tracked 22 *A. laterale* (13 males and 9 females) for a median of 54 days (range 6–126 days). Eight of these individuals were tracked until the transmitter's battery life expired. We lost signals prematurely from five individuals, as we could not get a signal despite searching prior to a transmitter's projected expiration date, and one transmitter failed as was determined by locating the individual using its PIT tag. Seven transmitters were presumably expelled and located, and one salamander was found dead, possibly as a result of transmitter implantation (Table 2).

We located salamanders daily, resulting in 1,408 telemetry fixes. The majority (94%) of relocations indicated that salamanders had not moved since the last telemetry fix. Salamanders spent a median of 10 days (range 1–60 days) at the same location. The distances individual salamanders traveled between successive telemetry fixes ranged from 1 to 174 m, with 35% of movements being ≤ 10 m, 31% between 11 and 19 m, and 34% ≥ 20 m. The median straight-line distance we detected a salamander travelling from the breeding wetland was 67 m (range 7–281 m). There was no relationship between number of days tracked and observed maximum distance from the breeding wetland ($F_{1,20} = 0.75$, $P = 0.40$). Rain events corresponded with 60% of movements.

PIT Telemetry.—The total number of PIT-tagged salamanders released, and hence potentially available for detection during each scanning event, ranged from 290 to 532 individuals. We conducted 34 PIT tag scanning surveys on separate dates between 19 April and 12 August 2009–2011 and recorded 42 detections representing locations of 37 individuals (Fig. 2; Table 3). Thirty-one individuals were located once, four were located twice, and one was located three times. The median straight-line distance between telemetry fixes and the breeding wetland was 69 m (range 21–164 m). We never detected any salamander multiple times at a single location.

Postoperative Condition.—We made 19 and 42 visual contacts of salamanders via telemetry and PIT tag scanning, respectively. Animals inspected more than 30 days postsurgery showed only slight scarring from transmitter and/or PIT tag implantation. Salamanders handled more than 100 days postsurgery generally had no visible scarring. On one occasion a salamander was found lethargic and partially desiccated next to its expelled transmitter.

Migration Distances.—Straight-line distance data were not normally distributed for telemetry ($W = 0.8$, $P = 0.0005$) or PIT Tag scanning ($W = 0.9095$, $P = 0.0028$). We detected no difference between detection distances between radio telemetry and PIT tag

TABLE 3. Detection dates and distance observed from the edge of the breeding wetland for *A. laterale* detected in situ via PIT telemetry.

Salamander PIT tag no.	Date detected	Distance (m) from breeding wetland	Salamander PIT tag no.	Date detected	Distance (m) from breeding wetland
534955	13-MAY-09	86	537489	5-AUG-09	75
644527	21-MAY-09	35	629122	5-MAY-10	78
606503	28-MAY-09	40	087610	11-MAY-10	143
032147	28-MAY-09	24	531270	27-MAY-10	82
629457	1-JUN-09	28	395960	8-JUN-10	37
530138	3-JUN-09	111	421176	10-JUN-10	156
580615	3-JUN-09	43	539569	9-JUN-10	35
541846	4-JUN-09	167	644527	8-JUN-10	38
644527	4-JUN-09	27	530138	24-JUN-10	115
636504	4-JUN-09	35	532039	21-JUL-10	49
531112	10-JUN-09	33	099122	28-JUL-10	79
531326	11-JUN-09	21	360916	28-JUL-10	98
233726	16-JUN-09	45	103866	2-AUG-10	83
201201	17-JUN-09	40	634638	2-AUG-10	68
532039	17-JUN-09	45	089264	5-AUG-10	70
538747	18-JUN-09	139	221396	6-AUG-10	152
233726	26-JUN-09	53	268948	5-AUG-10	56
539569	26-JUN-09	23	458522	6-AUG-10	101
535502	2-JUL-09	77	549568	6-AUG-10	141
636924	10-JUL-09	35	243500	3-MAY-11	99
667731	16-JUL-09	86	365233	27-MAY-11	102

scanning ($W = 435, P = 0.7079$). To encompass 95% of the individuals we tracked (via radio telemetry) or detected (via PIT telemetry), a life zone would have to extend 152 m from the edge of the breeding pool.

Macrohabitat.—Eighteen of the radio-tracked salamanders in our study were tracked to mixed upland forest, three to the wet meadow, and one to a red maple swamp (Fig. 4). *Ambystoma laterale* used upland forest and wet meadow more often than expected whereas hayfield was used less than its availability would suggest (based on RSF's calculated for PIT tag scanning locations; Table 4).

Microhabitat.—Of the radio-implanted individuals that were inspected visually, eleven were found underneath leaf litter, four in horizontal small mammal burrows (one right alongside a Spotted Salamander [*Ambystoma maculatum*]), one in loose, sandy soil of a cut bank, and one underneath a piece of decaying particle board at the bottom of a brush pile. The remaining two individuals were inspected after being captured in pitfall traps. Of the salamanders visually observed via the backpack scanner, 33 were found under leaf litter, four in horizontal small mammal burrows, two just underneath the roots of a grass mat, one in a "tunnel" left by a decaying branch, one in soil next to a tree root, and one in a rotten log.

At the 10-m-diameter scale, salamander locations had a greater percent cover of slash and less percent cover of grass, less basal area of trees, and lower relative humidity than did random locations. The top-ranked logistic regression model included these variables, explained 34% of the deviance in the data, and yielded a McFadden's Rho^2 value of 0.22 (Table 5). Model averaging indicated that none of these variables' odds ratios had 95% CI that overlapped one (Table 6). At the 1-m scale, salamander locations had greater litter depth and soil moisture compared to random locations. The top-ranked logistic regression model included the variables duff temperature, soil moisture, leaf litter depth, and percent cover of slash, explained 36% of the deviance in the data, and yielded a McFadden's Rho^2 value of 0.23 (Table 5). Model averaging

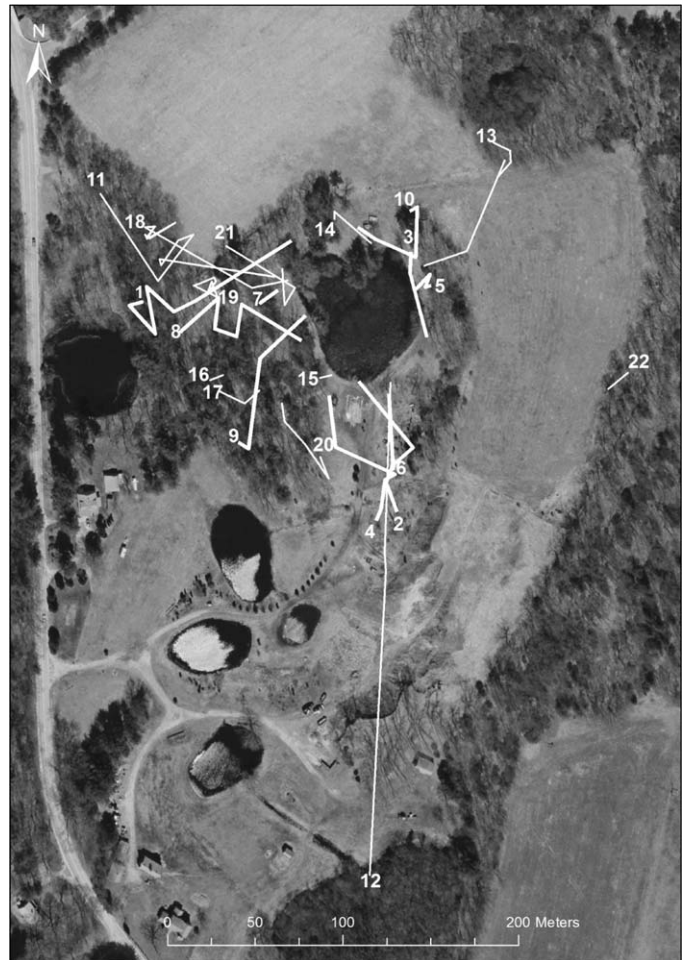


FIG. 4. Movement paths of radio-tracked Blue-spotted Salamanders tracked in 2009 and 2010. Bold and thin lines indicate salamanders tracked in 2009 and 2010, respectively. Numbers are placed at the end of movement paths and reference the salamander ID number in Table 2.

TABLE 4. Resource selection functions (RSF) for PIT-tag implanted salamanders detected in the 127,236-m² survey area. An RSF of 1 indicates habitat use in proportion to its availability. RSF's >1 or <1 indicate habitat being used in greater or lesser proportion than its availability, respectively.

Habitat	No. of observations	Area (m ²)	RSF
Mixed upland forest	38	50,638	2.27
Hayfield	1	52,923	0.06
Wet meadow	2	3,438	1.76
Other	1 ^a	-	-

^a Individual detected under leaf litter alongside pitfall array drift fence at edge of mixed upland forest and hayfield.

results indicated, however, that odds ratios of 95% CI did not overlap one only for litter depth and soil moisture (Table 6).

DISCUSSION

Migration Distances.—Our observed median straight-line distance of *A. laterale* from the breeding wetland (67 m, range 7–281 m) is less than those reported for other ambystomatid species in the Northeast. (We found no relationship between the number of days tracked and observed maximum distance from the breeding wetland.) Empirical estimates of median maximum straight-line distance moved from the breeding wetland for Spotted Salamanders ranges from 76 m (range 12–218 m; Faccio, 2003) to 123 m (range 42–467 m; Montieith and Paton, 2006). An investigation of a population of the Blue-spotted Salamander complex in Maine has documented individuals travelling a median distance of 213 m (range 46–345 m) from a breeding pool (K. Hoffmann, unpubl. data). Regosin et al. (2005) documented 52% of blue-salamander complex individuals wintering >100 m from a breeding pond in Massachusetts. These findings of maximum distance detected from a breeding wetland or release point may be biased downwards. Smith and Green (2005) regressed

maximum distance dispersed as a function of the longest axis of a study area and found a significant positive relationship wherein 72.7% of the observed variance in maximum dispersal distance was explained by having a larger study site.

Nevertheless, our results suggest that existing recommendations for the conservation of vernal pool species are applicable to *A. laterale*. Semlitsch's (1998) classic paper posits that a buffer zone surrounding a breeding pool should extend 164.3 m from the pool's edge in order to encompass 95% of a breeding population of ambystomatid salamanders. Published recommendations of buffer size for ambystomatid salamanders have since increased to 370 m (McDonough and Paton, 2007; anuran life zones may be even larger, see Calhoun et al., 2005 and Rittenhouse and Semlitsch, 2007a). Our combined radio- and PIT-telemetry data suggest that for *A. laterale*, a life zone would need to extend only 152 m from a breeding wetland's high-water mark to encompass the movements of 95% of adult individuals. Note that suitable terrestrial habitat around the breeding pool at our study site was not far from the pool. Migration distances may be greater at other breeding pools where suitable terrestrial habitat is situated farther from the pool. Also, a 152-m life zone at our research site would likely not suffice to encompass the movements of the entire suite of pool-breeding species using the scrub-shrub pool, notably *A. maculatum* and *Lithobates sylvaticus* (formerly *Rana sylvatica*) (Wood Frog). Therefore, a larger life zone may be more effective at conserving the entire suite of vernal pool-breeding amphibians using the wetland. For individual breeding pools, this might be accomplished by assessing the species using them and implementing life zones based on the species known to travel the farthest from the pool.

Note that salamander life zones are based on presumed migration movements, not dispersal movements. Semlitsch (2008) defines amphibian migration as "intrapopulation, round-trip movements toward and away from aquatic breeding sites" and dispersal as "interpopulation, unidirectional movements from natal sites to other breeding sites." Therefore,

TABLE 5. Rankings of logistic regression models of Blue-spotted Salamander habitat use. K is the number of variables included in the model and D² is the proportion of deviance explained by the model. Models were ranked using change in Akaike's Information Criterion corrected for small sample size (Δ AICc), Akaike's model weights (ω), and Adjusted McFadden's Rho². Variable descriptions are given in Table 1.

Rank	Model	K	D ²	AIC _c	Δ AIC _c	ω	Cum. ω	Adjusted Rho ²
1-m-diameter plots								
1	dufftemp+litterdepth+slash+soilmoist	4	0.36	128.85	0.00	0.20	0.20	0.23
2	dufftemp+grndsrflum+litterdepth+soilmoist	4	0.35	129.52	0.67	0.14	0.35	0.23
3	grndsrflum+litterdepth+slash+soilmoist	4	0.35	129.64	0.79	0.14	0.48	0.23
4	litterdepth+slash+soilmoist	3	0.34	129.79	0.94	0.13	0.61	0.23
5	canopy+litterdepth+slash+soilmoist	4	0.34	130.85	2.00	0.07	0.68	0.22
6	grndsrflum+litterdepth+soilmoist	3	0.33	131.42	2.57	0.06	0.74	0.22
7	herbs+litterdepth+slash+soilmoist	4	0.34	131.46	2.61	0.05	0.79	0.22
8	dufftemp+litterdepth+soilmoist	3	0.33	131.48	2.63	0.05	0.84	0.22
9	grndsrflum+herbs+litterdepth+soilmoist	4	0.33	133.39	4.54	0.02	0.87	0.21
10	canopy+grndsrflum+litterdepth+soilmoist	4	0.33	133.39	4.54	0.02	0.89	0.21
10-m-diameter plots								
1	grass+relhum+slash+trees	4	0.34	131.57	0.00	0.38	0.38	0.22
2	grass+relhum+slash	3	0.30	134.39	2.82	0.09	0.47	0.20
3	grass+relhum+trees	3	0.30	134.58	3.01	0.08	0.55	0.20
4	baresoil+grass+relhum+trees	4	0.32	134.82	3.25	0.07	0.63	0.20
5	baresoil+grass+relhum+slash	4	0.31	135.71	4.15	0.05	0.67	0.19
6	canopy+grass+relhum+slash	4	0.31	136.13	4.57	0.04	0.71	0.19
7	grass+herb+relhum+trees	4	0.31	136.39	4.82	0.03	0.74	0.19
8	grass+relhum+shrub+slash	4	0.31	136.40	4.83	0.03	0.78	0.19
9	canopy+grass+relhum+trees	4	0.30	136.45	4.88	0.03	0.81	0.19
10	grass+herbs+relhum+slash	4	0.30	136.45	4.88	0.03	0.84	0.19

TABLE 6. Model-averaged parameter estimates (β), standard error, odds ratios, 95% CI, and descriptive statistics from logistic regression models comprising >90% of the weight of the candidate model set (Table 3) explaining Blue-spotted Salamander habitat use. Variables are defined in Table 1; SE = unconditional standard error, SD = standard deviation, Min. = minimum, Max. = maximum. Variables in bold are those whose 95% CI for odds ratios did not overlap one.

	Estimate	SE	Odds ratio	95% CI		Animal locations				Random locations			
				Lower	Upper	Mean	SD	Min.	Max.	Mean	SD	Min.	Max.
1-m-diameter plots													
canopy	-0.009	0.02	0.991	0.960	1.024	30	18	9	85	33	22	10	85
dufftemp	-0.269	0.15	0.764	0.567	1.031	15	4	7	23	16	5	7	31
grndsrflhum	0.052	0.03	1.053	0.990	1.120	82	11	45	100	79	15	32	100
herbs	0.006	0.01	1.006	0.983	1.028	7	22	0	100	6	16	0	98
litterdepth	0.374	0.10	1.454	1.184	1.786	4	3	0	15	2	2	0	9
slash	0.034	0.02	1.035	0.995	1.077	9	22	0	100	3	5	0	33
soilmoist	0.100	0.03	1.105	1.033	1.183	13	11	1	50	11	8	0	50
10-m-diameter plots													
baresoil	-0.020	0.021	0.980	0.941	1.020	2	5	0	33	3	11	0	90
canopy	0.007	0.018	1.007	0.972	1.043	30	18	9	85	33	22	10	85
grass	-0.027	0.009	0.973	0.956	0.991	13	20	0	98	29	36	0	100
herb	-0.003	0.015	0.997	0.969	1.026	9	19	0	98	9	16	0	90
relhum	-0.173	0.049	0.841	0.764	0.926	58	20	19	100	62	21	23	100
shrub	0.002	0.012	1.002	0.979	1.025	16	19	0	90	12	16	0	68
slash	0.032	0.016	1.032	1.001	1.064	13	20	0	98	8	11	0	68
trees	-0.019	0.009	0.982	0.965	0.999	25	23	0	78	25	26	0	100

maintaining connectivity among populations at a larger scale, >1–10 km (Semlitsch, 2008), may be important for long-term persistence of a species in a particular landscape because it may promote connectivity and, hence, gene flow between natal pools, promote recolonization of formerly inhabited areas, and perhaps colonization of entirely new ones.

Habitat Use.—The majority of *A. laterale* radio tracked or detected via PIT telemetry were tracked to, or found in, upland forest (Figs. 3, 4); this finding was expected because all ambystomatids in the Northeast are known to be associated with forested habitat (Klemens, 1993). Of particular interest is that Blue-spotted Salamanders also utilized the wet meadow as nonbreeding habitat. We could not find any other accounts of the use of open-canopy habitats by ambystomatids in the Northeast with which to compare our results. However, this finding is consistent with our personal observations of *A. laterale*—*jeffersonianum* being detected in relatively open-canopy habitats with saturated soil during visual-encounter surveys at other locations.

At the 10-m scale, *A. laterale* presence was positively correlated with percent cover of slash and negatively correlated with percent cover of grass, total basal area of trees within the plot, and relative humidity. The literature contains contrary results with regard to slash (also referred to as “coarse woody debris”) for other ambystomatid species. Our finding of a positive association with percent cover of slash is consistent with results from studies on *A. maculatum* (e.g., Windmiller, 1996; Faccio, 2003; Montieth and Paton, 2006; but see deMaynadier and Hunter, 1998). Windmiller (1996) radio-implanted *A. maculatum* in Massachusetts and typically detected them directly under or within 0.5 m of coarse woody material. However, Montieth and Paton (2006) reported that only two of 44 individuals visually detected were underneath coarse woody debris objects. Despite our finding of a positive correlation with slash, during the course of our study we never directly observed *A. laterale* under woody material. The role of coarse woody material therefore remains an important question.

The negative association with percent grass cover is consistent with the findings of Rittenhouse and Semlitsch (2006) who

report that Spotted Salamanders avoid grassland, although they will apparently move across it, as was evidenced by two of our radio-tracked salamanders (Fig. 4, salamander ID numbers 12 and 13). The negative association with total basal area of trees and relative humidity is counterintuitive. The former is a very weak relationship and may be partially the result of much of our tacking occurring primarily in mature forest; additionally, we typically did not observe salamanders near the base of trees, which may have caused nearby trees not to be encompassed within the 10-m plot.

The relationship of salamander presence to humidity may exhibit a threshold pattern. The relationship of ambient relative humidity to animal locations has not been reported as part of ambystomatid telemetry studies, and studies on anurans have reported conflicting results. Rittenhouse and Semlitsch (2007b) found that wood frog locations had lower humidity levels than did the paired random locations, but Baldwin et al. (2006) reported that the microclimate of wood frog upland retreats was moister than ambient conditions.

Microhabitat use of *A. laterale* documented during this study was not entirely consistent with what we originally hypothesized. At the 1-m scale, salamander locations had deeper leaf litter and moister soil than did random locations, but they were seldom found under cover objects (e.g., rocks, logs; Table 6). This may be particularly counterintuitive given that the density of cover objects, woody material in particular, within our study forest may be relatively low. The landowner mentioned that the majority of downed wood is collected for firewood. If cover objects were highly selected for by *A. laterale*, then one would expect to find them under the few suitable cover objects on site.

We feel that our method of locating random plots from a salamander’s location just prior to its current one, based on a random compass bearing and the straight-line distance to the animal’s current location, is an improvement over methods that sampled points randomly within an entire study area (e.g., Faccio, 2003) or at various distances from animals’ current locations (e.g., Montieth and Paton, 2006). Our method likely more accurately reflects locations to which individuals could have actually moved. Even though we do not compare models

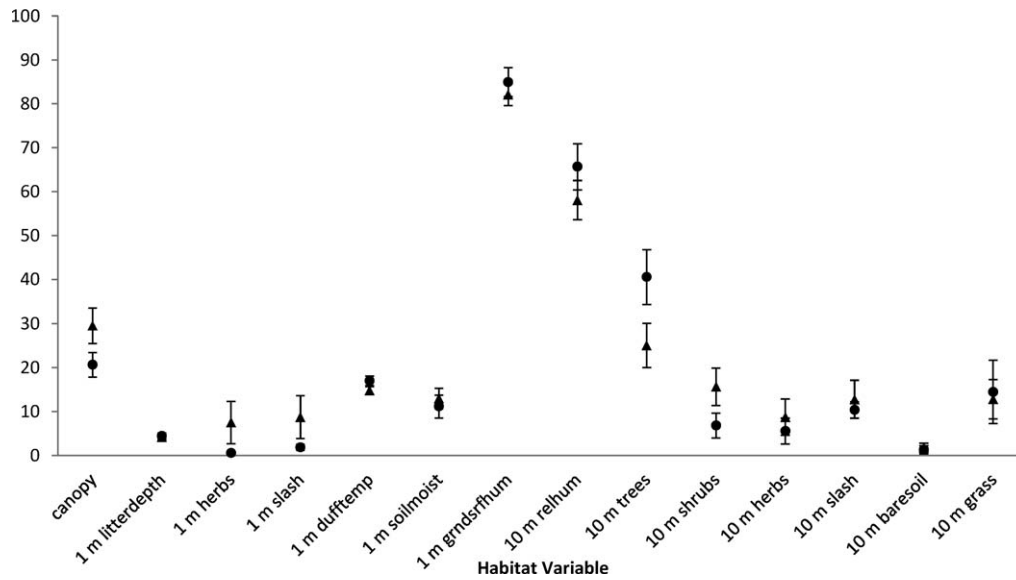


FIG. 5. Comparison of mean habitat variables ($\pm 95\%$ CI) at animal locations for telemetry (triangles) and PIT tag scanning (circles) data for both 1-m and 10-m-diameter plots.

derived from telemetry and scanning, we did compare the methods in terms of habitat variables at both the 1-m and 10-m scales, and nine of 14 variables were not statistically different (95% CI overlapped) (Fig. 5). Of the five statistically different variables, only one (trees) was considered useful for describing *A. laterale* habitat use (Table 6).

Of 61 visual contacts, only eight (13%) were of salamanders in small mammal burrows. Based on their enclosure experiments, Regosin et al. (2003) suggest that small mammal burrow availability and distribution of conspecific individuals might affect the density of Spotted Salamanders within terrestrial habitats. As we did not assess small mammal abundance at either known salamander or random locations, we are unable to assess this relationship. However, *A. laterale* may not exhibit the same relationship with small mammal burrows, as we located the vast majority (44 out of 59 visual contacts) of salamanders directly underneath leaf litter, in the duff layer in particular. Finding *A. laterale* primarily near the surface is consistent with the observations of Klemens (1993) and Gibbs et al. (2007).

Ambystoma laterale are considerably smaller than their congeners in the Northeast. The average adult SVL and mass for salamanders captured in pitfall arrays at our research site was 54.5 mm and 3.7 g, respectively. Average SVL of Spotted Salamanders in the Veysey et al. (2009) study is 82.0 mm. Average mass reported for Spotted Salamanders ranges from 17.9 g (Veysey et al., 2009) to 22.4 g (Madison, 1997). Average mass of polyploid Jefferson Salamanders in Faccio's (2003) study was 22.4 g. Observed difference in microhabitat use may be, in part, because of this size difference, as *A. laterale* perhaps do not rely on other organisms to provide suitable refuge. That is, more refuge locations that meet thermal and hydric requirements are available to them due to their small size.

Conservation Implications.—Conservation of *A. laterale* is an important issue. Calhoun and Klemens (2002) and Calhoun et al. (2005) set forth habitat protection guidelines of a 230-m life zone to encompass foraging, summering, and overwintering habitat for salamanders. The data presented here describe a range of terrestrial habitat use for *A. laterale* that would be protected under these guidelines.

As *A. laterale* appears to be more surficial than are their close relatives, disturbances to the forest floor of the life zone could potentially have negative impacts on salamander populations. If activities such as tree harvesting, trail building, or construction are to take place, measures to minimize impacts to salamanders might include avoiding the use of heavy machinery and conducting operations during frozen soil conditions when the salamanders are hibernating.

If conservationists and land managers wish to ensure the regional persistence of this species, maintaining connectivity between individual breeding populations might prove more important than maintaining any single local population (Semlitsch, 2008). Maintenance of undeveloped, preferably forested areas connecting individual breeding populations might be most effective. Further study examining the permeability of different cover types for different life stages (e.g., Popescu and Hunter, 2011; Cline and Hunter, 2014) will be useful in informing management decisions.

Acknowledgments.—We thank T. Mahard and T. Mammone for their help in the field and lab. Fieldwork was sanctioned by the Connecticut Department of Energy and Environmental Protection, of which we thank J. Dickson, K. Moran, and J. Victoria for their guidance and support. Handling of animals was conducted under University of Maine Institutional Animal Care and Use Committee Permits A2008-02-06 and A2011-02-01. We thank K. Capps, W. Halteman, D. Harrison, and B. Timm for conceptual and statistical guidance and M. Hunter, D. Harrison, B. Timm, and J. Zydlewski for helpful comments on previous drafts of this manuscript. Special recognition goes to the Shinkiewicz family for very generously providing study sites and housing; to the Hicks/O'Neill family for providing housing and project advice and support; to M. Klemens for initiating the overall project, lending his invaluable experience with Blue-spotted Salamanders, and for contributing essential data to assist with this research; and to D. Quinn of CTHerpConsultant, LLC for partnering with the project and providing much useful research advice. Funding was provided by Lowe's Home Centers, Inc., Connecticut State Wildlife Grants, the Connecticut Endangered Species/Wildlife Income Tax Check-off Fund, the

University of Maine's Sustainability Solutions Initiative, and the University of Maine Department of Wildlife Ecology. We thank I. Broadwater for serving as a liaison between Lowe's and the University of Maine. This is Maine Agriculture and Forest Experiment Station Paper 3367.

LITERATURE CITED

- ANDERSON, D. R. 2008. Model based inference in the life sciences: a primer on evidence. Springer Science+Business Media, LLC, New York, New York, USA.
- BALDWIN, R. F., A. J. K. CALHOUN, AND P. G. DEMAYNADIER. 2006. Conservation planning for amphibian species with complex habitat requirements: a case study using movements and habitat selection of the wood frog *Rana sylvatica*. *Journal of Herpetology* 40:442–453.
- BI, K., AND J. P. BOGART. 2010. Time and time again: unisexual salamanders (genus *Ambystoma*) are the oldest unisexual vertebrates. *BMC Evolutionary Biology* 10:238–251.
- BOGART, J. P., J. BARTOSZEK, D. W. A. NOBLE, AND K. BI. 2009. Sex in unisexual salamanders: discovery of a new sperm donor with ancient affinities. *Heredity* 103:483–493.
- BOGART, J. P., AND M. W. KLEMENS. 1997. Hybrids and genetic interactions of mole salamanders (*Ambystoma jeffersonianum* and *A. laterale*) (Amphibia, Caudata) in New York and New England. *American Museum Novitates* No. 3218.
- . 2008. Additional distributional records of *Ambystoma laterale*, *A. jeffersonianum* (Amphibia: Caudata) and their unisexual kleptogens in northeastern North America. *American Museum Novitates* No. 3627.
- BOYCE, M. S., AND L. L. McDONALD. 1999. Relating populations to habitats using resource selection functions. *Trends in Ecology & Evolution* 14: 268–272.
- BURNE, M. R., AND C. R. GRIFFIN. 2005. Habitat associations of pool-breeding amphibians in eastern Massachusetts, USA. *Wetlands Ecology and Management* 13:247–259.
- BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model Selection and Multi-Model Inference: A Practical Information-Theoretic Approach. Springer-Verlag, New York, USA.
- CALHOUN, A. J. K., AND M. W. KLEMENS. 2002. Best development practices: conserving pool-breeding amphibians in residential and commercial developments in the northeastern United States. MCA Technical Paper No. 5, Metropolitan Conservation Alliance, Wildlife Conservation Society, Bronx, New York, USA.
- CALHOUN, A. J. K., N. A. MILLER, AND M. W. KLEMENS. 2005. Conserving pool-breeding amphibians in human-dominated landscapes through local implementation of best development practices. *Wetlands Ecology and Management* 13:291–304.
- CLINE, B. B., AND M. L. HUNTER. 2014. Different open-canopy vegetation types affect matrix permeability for a dispersing forest amphibian. *Journal of Applied Ecology*. In press.
- DAUBENMIRE, R., AND J. B. DAUBENMIRE. 1968. Forest Vegetation of Eastern Washington and Northern Idaho. Washington Agricultural Experiment Station Technical Bulletin No. 60, Washington State University, Pullman, Washington, USA.
- DEMAYNADIER, P. G., AND M. L. HUNTER. 1998. Effects of silvicultural edges on the distribution and abundance of amphibians in Maine. *Conservation Biology* 12:340–352.
- FACCIO, S. D. 2003. Postbreeding emigration and habitat use by Jefferson and spotted salamanders in Vermont. *Journal of Herpetology* 37:479–489.
- GAMBLE, L. R., K. MCGARIGAL, C. L. JENKINS, AND B. C. TIMM. 2006. Limitations of regulated "buffer zones" for the conservation of marbled salamanders. *Wetlands* 26:298–306.
- GIBBS, J. P., A. R. BREISCH, P. K. DUCEY, G. JOHNSON, J. L. BEHLER, AND R. C. BOTHNER. 2007. The Amphibians and Reptiles of New York State: Identification, Natural History, and Conservation. Oxford University Press, New York, USA.
- GREENWALD, K. R., AND H. L. GIBBS. 2012. A single nucleotide polymorphism assay for the identification of unisexual *Ambystoma* salamanders. *Molecular Ecology Resources* 12:354–362.
- HOSMER, D. W., JR., S. LEMESHOW, AND R. X. STURDIVANT. 2013. Applied Logistic Regression. John Wiley & Sons, Inc., Hoboken, New Jersey, USA.
- JOHNSON, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65–71.
- KLEMENS, M. W. 1993. Amphibians and reptiles of Connecticut and adjacent regions. State Geological and Natural History Survey of Connecticut, Bulletin No. 112. Connecticut Department of Environmental Protection, USA.
- LANNOO, M. (ed.). 2005. Amphibian Declines: The Conservation Status of United States Species. University of California Press, Berkeley, California, USA.
- MADISON, D. M. 1997. The emigration of radio-implanted spotted salamanders, *Ambystoma maculatum*. *Journal of Herpetology* 31: 542–551.
- MADISON, D., V. R. TITUS, AND V. S. LAMOUREUX. 2010. Movement patterns and radiotelemetry. In C. K. Dodd (ed.), *Amphibian Ecology and Conservation*, pp. 185–201. Oxford University Press Inc., New York, New York, USA.
- MCDONOUGH, C., AND P. W. C. PATON. 2007. Salamander dispersal across a forested landscape fragmented by a golf course. *Journal of Wildlife Management* 71:1163–1169.
- MINTON, S. A., JR. 1972. Amphibians and reptiles of Indiana. Monograph No. 3, Indiana Academy of Science, Indianapolis, Indiana, USA.
- . 2001. Amphibians and reptiles of Indiana, 2nd edition. Indiana Academy of Science, Indianapolis, Indiana, USA.
- MONTIETH, K. E., AND P. W. C. PATON. 2006. Emigration behavior of spotted salamanders on golf courses in southern Rhode Island. *Journal of Herpetology* 40:195–205.
- POPESCU, V. D., AND M. L. HUNTER. 2011. Clear-cutting affects habitat connectivity for a forest amphibian by decreasing permeability to juvenile movements. *Ecological Applications* 21:1283–1295.
- R DEVELOPMENT CORE TEAM. 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at <http://www.R-project.org/>. Archived by WebCite at <http://www.webcitation.org/6OnvPnN4C> on 13 April 2014.
- REGOSIN, J. V., B. S. WINDMILLER, AND J. M. REED. 2003. Influence of abundance of small-mammal burrows and conspecifics on the density and distribution of spotted salamanders (*Ambystoma maculatum*) in terrestrial habitats. *Canadian Journal of Zoology—Revue Canadienne De Zoologie* 81:596–605.
- REGOSIN, J. V., B. S. WINDMILLER, R. N. HOMAN, AND J. M. REED. 2005. Variation in terrestrial habitat use by four pool-breeding amphibian species. *Journal of Wildlife Management* 69:1481–1493.
- RITTENHOUSE, T. A. G., AND R. D. SEMLITSCH. 2006. Grasslands as movement barriers for a forest-associated salamander: migration behavior of adult and juvenile salamanders at a distinct habitat edge. *Biological Conservation* 131:14–22.
- . 2007a. Distribution of amphibians in terrestrial habitat surrounding wetlands. *Wetlands* 27:153–161.
- . 2007b. Postbreeding habitat use of wood frogs in a Missouri oak-hickory forest. *Journal of Herpetology* 41:645–653.
- RYAN, K., A. CALHOUN, AND J. ZYDLEWSKI. 2014. Using passive integrated transponder (PIT) systems for terrestrial detection of blue-spotted salamanders (*Ambystoma laterale*) in situ. *Herpetological Conservation and Biology*. In press.
- SEMLITSCH, R. D. 1998. Biological delineation of terrestrial buffer zones for pond-breeding salamanders. *Conservation Biology* 12:1113–1119.
- . 2008. Differentiating migration and dispersal processes for pond-breeding amphibians. *Journal of Wildlife Management* 72:260–267.
- SKIDDS, D. E., F. C. GOLET, P. W. C. PATON, AND J. C. MITCHELL. 2007. Habitat correlates of reproductive effort in wood frogs and spotted salamanders in an urbanizing watershed. *Journal of Herpetology* 41: 439–450.
- SMITH, M. A., AND D. M. GREEN. 2005. Dispersal and the metapopulation paradigm in amphibian ecology and conservation: are all amphibian populations metapopulations? *Ecography* 28:110–128.
- TINER, R. W. 1997. Wetland Indicators: A Guide to Wetland Identification, Delineation, Classification, and Mapping. Lewis Publishers, New York, New York, USA.

- VEYSEY, J. S., K. J. BABBITT, AND A. COOPER. 2009. An experimental assessment of buffer width: implications for salamander migratory behavior. *Biological Conservation* 142:2227–2239.
- VOGHT, R. C. 1981. *Natural History of Amphibians and Reptiles in Wisconsin*. Milwaukee Public Museum, Milwaukee, Wisconsin, USA.
- WINDMILLER, B. S. 1996. *The Pond, the Forest, and the City: Spotted Salamander Ecology and Conservation in a Human-dominated Landscape*. Unpubl. Ph.D. diss., Tufts University, Medford, Massachusetts, USA.

Accepted: 17 February 2014.