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Post-Breeding Migration and Habitat of Unisexual Salamanders in Maine, USA

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ABSTRACT.—**The behavioral phenotypes of hybrids vary in degree of similarity to their parent species. Unisexual salamanders (*Ambystoma laterale* sp.), the result of ancient hybridization, contain nuclear DNA of multiple sperm-host species whose habitat preferences differ from one another. We radio tracked unisexual salamanders from four vernal pools to quantify migration distances and post-breeding habitat selection and compared these to published accounts for Blue-Spotted Salamanders (*A. laterale*) and Jefferson Salamanders (*Ambystoma jeffersonianum*). Unisexual salamanders used sites with higher numbers of small mammal burrows, lower substrate temperatures, and lower cover by forest floor vegetation than available sites, similar to the sperm-hosts. Unisexual salamanders also migrated distances within the range reported for these sperm-hosts. Even so, individual migration distances were context specific. We implore managers to use caution when designating management zones around breeding pools by considering that some populations may move farther than those reported in published accounts.**

Unisexual taxa are almost entirely female and reproduce either without sperm or with sperm contributed by males of bisexual species (with separate males and females; Dawley, 1989). Unisexual teleost fish, unisexual amphibians, and many unisexual lizards are the result of past hybridizations between bisexual species (Neaves and Baumann, 2011). Genetic variation influences habitat selection and can result in some hybrids being less selective than either parent species, easing their fit into hybrid zones between allopatric parent populations, whereas others remain sympatric and compete with parent species (Jaenike and Holt, 1991; Saino, 1992; Wood et al., 2016). Unisexuals, likewise, may use a variety of niches, allowing some to thrive in different habitats, persist in changing environments, and reduce competition with parent species (Bullini, 1994; Mee and Rowe, 2010).

The Blue-Spotted Salamander Complex is the result of a 5-million-year-old hybridization event creating a lineage of modern salamanders carrying combinations of the genomes of Blue-Spotted Salamanders (*Ambystoma laterale*), Jefferson Salamanders (*Ambystoma jeffersonianum*), Tiger Salamanders (*Ambystoma tigrinum*), Small-Mouthed Salamanders (*Ambystoma texanum*), and, rarely, Streamside Salamanders (*Ambystoma barbouri;* Uzzell, 1964; Morris and Brandon, 1984; Bogart et al., 2009; Bi and Bogart, 2010). Unisexual salamanders have nuclear DNA from two or more of these species and are almost always polyploid (Lowcock and Murphy, 1991; Bogart and Klemens, 1997). We use the convention of abbreviating the genetic composition (genomotype rather than genotype) of individuals by how many replicates of each genome they contain (e.g., LL for *A. laterale*, LLJ for *A. (2) laterale–jeffersonianum*, and LLLJ for *A. (3) laterale–jeffersonianum*, Lowcock et al. 1987). Although size and/or mass can give some indication of genomotype and our unpublished data indicate that salamanders over 7 g in our area are unisexuals, they are similar in appearance to sperm-hosts and genetic methods often are needed for identification.

Unisexual salamander habitat studies have been limited to establishing geographic and climatic niche (Greenwald et al., 2016), examining habitat relations to the subcanopy (Belasen et al., 2013), and modeling breeding site characteristics (Hoffmann, 2017). The post-breeding habitat selection and migration distances of unisexual salamanders are critical to informing management decisions but have not been quantified. In Maine, unisexual salamanders contain more *A. laterale* than *A. jeffersonianum* DNA (e.g., are LLJ and LLLJ; Bogart and Klemens, 1997); thus, we hypothesized that their terrestrial habitat preferences and migration distances would be similar to published accounts of *A. laterale*. Both sperm-hosts occupy burrows in forests and migrate to seasonal wetlands to breed (Petranka, 1998); however, other aspects of habitat use vary. They partition habitat by altitude with *A. jeffersonianum* typically in well-drained uplands and *A. laterale* in lowlands (Nyman et al., 1988; Downs, 1989; Klemens, 1993). *Ambystoma jeffersonianum* can migrate farther than *A. laterale* can (Williams, 1973; Douglas and Monroe, 1981; Ryan and Calhoun, 2014). *Ambystoma jeffersonianum* have been documented using forested landscapes with low disturbance (Porej et al., 2004; Rubbo and Kiesecker, 2005; Greenwald et al., 2016), whereas some researchers have documented *A. laterale* in more open habitat that may have more anthropogenic disturbance (Weller et al., 1978; Downs, 1989; Klemens, 1993; Windmiller et al., 2008).

Our goal was to understand the post-breeding habitat selection of unisexual salamanders in comparison to published accounts of sperm-host species. Specifically, we 1) quantified the emigration distances of LLJ and LLLJ, 2) examined microhabitat selection in late-spring and summer, and 3) compared these to published studies of *A. jeffersonianum* and *A. laterale*. We expected the unisexuals to be similar to *A. laterale* by migrating about 70 m and selecting forested habitat with moist soil, deep leaf litter, and woody debris (Ryan and Calhoun, 2014).

MATERIALS AND METHODS

Site Selection and Capture.—We encircled four vernal pools in Penobscot County, Maine, with drift fence for a related study (Hoffmann, 2017). Pools 1 and 2 were located in Old Town on a parcel managed for forestry by the University of Maine and abutting the Stillwater River (>200 m across). Pools 3 and 4 were located on privately owned residential parcels in the town of Orono. Their forest matrix was penetrated by residential neighborhoods and fields. We constructed the drift fences out of silt fence buried 20 cm into the ground with a pair of #10 aluminum cans every 5 m to act as pitfall traps (Shoop, 1965). We

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checked the traps every morning from April to September and alternating mornings in October and November (Hoffmann, 2017).

Surgery and Genetic Testing.—We implanted 14 unisexual salamanders with radio transmitters in 2013 following the methods of Madison et al. (2010) and implanted another 29 in 2014. We monitored only large emigrating unisexual salamanders because *A. laterale* (LL) are generally too small to safely implant (Ryan and Calhoun, 2014), and we were outside the geographic range of *A. jeffersonianum*. We anesthetized salamanders in 3.1 mM tricaine methane sulfonate (MS-222) neutralized to a pH of 7.0 with aqueous NaOH until loss of pain response (toe pinching). We used surgical scissors to remove a 0.5 by 0.3 cm tissue sample (Nöel et al., 2011) from the tip of the tail, which we shipped in 70% ethanol to the University of Guelph to determine genomotype using microsatellite DNA analyses at six loci (AjeD75, AjeD94, AjeD283, AjeD346, AjeD378, and AjeD422; Julian et al., 2003). Our microsatellite DNA methods are described elsewhere (Bogart et al., 2007, 2009). We inserted ATS A2415 transmitters (0.33 g, Advanced Telemetry Systems, Isanti, MN) with the antennas removed and PIT tags (0.09 g, HPT12, 134.2kHz ISO FDXB tag; Biomark, Boise, ID) into coelomic cavities (Ryan and Calhoun, 2014) using 10-mm longitudinal incisions in the left ventrolateral abdominal walls (Ryan and Calhoun, 2014), then closed the wounds with absorbable sutures (Model PDS Plus, RB-1 taper, Size 5-0, Ethicon Inc, Somerville, NJ). Body mass ranged from 7.74–13.38 g, such that the transmitters represented $\leq$4.26% of body mass. The salamanders recovered overnight and were released under wet leaves outside the drift fence in 2013. After realizing that we might bias movement by placing the animals on one side of the drift fence, we released the salamanders back into the vernal pools in 2014. We extended our 2013 telemetry season from 42 days (battery life of one transmitter) to 92 days by replacing transmitters in six animals (after McDonough and Paton, 2007; Titus et al., 2014). Unfortunately, the skin was weak at the site of the original incision, and we found two animals with an open incision 7 and 12 days after the second reimplant surgery. Therefore, in 2014, we tracked each salamander for the life of only one transmitter.

Telemetry.—We relocated 13 salamanders daily in 2013. In 2014, we tracked 27 salamanders and, because of the increase in sample size, we tracked each individual only once every three days. We used a Model R-1000 receiver (Advanced Telemetry Systems) and Model RA-2AK VHF antennae (Telonics, Inc. Mesa, AZ) for direct overhead localization (10-cm accuracy). In 2014 when a transmitter expired, we scanned an ~20 m radius using a Reader 03 PIT tag reader (West Fork Environmental, Turnwater, Washington, USA) with a custom-built antenna (Blomquist et al., 2008) before dismissing a salamander as lost, extending tracking for 11 salamanders for a mean of 15 days (range: 3–36 days). We recorded locations with a handheld GPS (GPSMAP 62stc and eTrex 10, Garmin International, Inc. Olathe, KS). We considered an animal not to have moved if it was within 3 m on subsequent visits in 2013 and within 0.5 m in 2014 attributable to new information in Ryan and Calhoun (2014), who found that *A. laterale* was selecting habitat at a small scale.

Microhabitat Variables.—We measured microhabitat variables at paired used and available plots in succession such that meteorological conditions and vegetation phenology were comparable within pairs. We measured variables at two scales: when the salamanders moved $\geq$3 m (larger scale), we compared 3-m radius used and available plots (Faccio, 2003); and for movements < 3 m (smaller scale), we compared 0.5-m radius used and available plots (2014 only, based on Ryan and Calhoun, 2014).Three available plots evenly surrounded each used plot with one available plot located along a random bearing and the others 120° to either side (Fig. 1). The center of available plots for the smaller movement was always located 6 m from the center of the used plot. Distances between the centers of plots at the larger scale varied by week and were determined by the median distance between sequential locations during the previous two weeks in 2013 (range: 56–6 m), except for during the initial two weeks when we used the first weeks' median distance. We used the distances measured in 2013 to space plots in 2014.

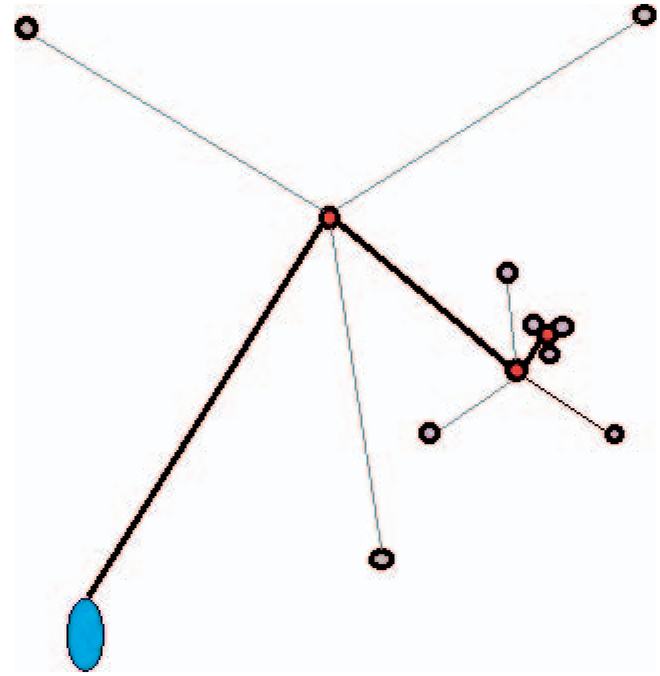

FIG. 1. Schematic of used and random points at our larger scale (3-m plots measured when a salamander moved >3 m). The path (thick black line) of a hypothetical unisexual salamander as it moved from a vernal pool (blue oval). Three random points (gray circles) were spaced 120° apart around each used location (red circles). We used the median distance moved by all salamanders in the previous 2 weeks to determine the distance of random plots from used plots (thin gray lines), such that random plots better represented the scale on which salamanders were making decisions than a constant distance.

We measured 22 microhabitat variables within plots based on studies of *A. jeffersonianum*, *A. laterale*, and other amphibians (Faccio, 2003; Rittenhouse and Semlitsch, 2007; Ryan and Calhoun, 2014; Groff et al., 2017). We recorded land use as forest, yard/field, or wetland. We visually estimated the percent cover of bare soil, all leaf litter, coniferous leaf litter, water, lawn/hay, moss, rock, vegetation < 1 m tall, vegetation between 1 and 3 m tall, and vegetation > 3 m tall but < 10 cm DBH (diameter at breast height), allowing cover amounts to sum to >100%. We counted the number of stumps. We used a spherical convex densitometer (Model-A, Forestry Suppliers Inc. Jackson, MS) to quantify angular canopy cover because we assumed light interception by tree canopy surrounding the plot rather than just directly above it may be biologically important as a cue for cover (Nuttle, 1997). We measured leaf litter depth to the nearest 0.5 cm, soil moisture (FieldScout TDR200; Spectrum Technologies, Inc. Aurora, IL), and soil temperature in °C (Model 9841; Taylor Precision Products, Oak Brook, IL) near the center of each plot. We measured the diameter and length of

TABLE 1. Conditional logistic regression models used to compare each 3-m and 0.5-m plot used by unisexual salamanders to three paired random plots in central Maine. The variables CWD (coarse woody debris) area, CWD decay stage, and forest were not included in models for 0.5-m plots because of lack of field measurements and lack of convergence caused by low variation.

Model		Variables
Land use		
1	LU global	Forest + Yard + Wetland
2	Natural	Forest + Wetland
3	Forest	Forest
4	Yard	Yard
Shelter		
5	Sh global	Horizontal burrows + Vertical burrows + Leaf litter cover + Leaf litter depth + Stumps + Rock + CWD decay stage + CWD area
6	All tunnels	Horizontal burrows + Vertical burrows + Stumps
7	Mammal burrows	Horizontal burrows + Vertical burrows
8	Cover objects	Stumps + Rock + CWD area
9	Rotten wood	CWD decay stage + CWD area + Stumps
Ground cover		
10	GC global	Leaf litter cover + Leaf litter depth + Rock + Moss + Water + Bare soil + Coniferous leaf litter
11	Leaves	Leaf litter cover + Leaf litter depth
12	Bare ground	Rock + Bare soil
13	Moist areas	Moss + Water
14	Needles	Coniferous leaf litter
Microclimate		
15	MC global	Soil moisture + Soil temperature
16	Soil moisture	Soil moisture
17	Soil temp	Soil temperature
Vegetation		
18	Veg global	Veg < 1m + Veg 1 to 3m + Veg > 3m + Canopy density + Lawn/Hay
19	Understory	Veg < 1m + Veg 1 to 3m + Veg > 3m
20	Canopy	Canopy density
21	Low veg	Veg < 1m + Lawn/Hay
22	Shrubs	Veg 1 to 3m
Literature		
23	Lit global	Soil temperature + Leaf litter depth + Soil moisture + Lawn/Hay + Canopy density
24	Ryan 1 m	Soil temperature + Leaf litter depth + Soil moisture
25	Ryan 10 m	Lawn/Hay + Canopy density

coarse woody debris (>10 cm) to calculate the total area covered (cm^2) and recorded the maximum decay stage for 3-m plots only (Monti, 1997). Once a salamander had vacated the plot, we brushed away the leaf litter and recorded the number of horizontal and vertical small mammal burrow openings (after Faccio, 2003).

Analysis.—We plotted locations in ArcGIS 10.3 (ERSI, Redlands, CA) and used the "adehabitatLT" package (Calenge, 2006) in Program R (R Core Team, 2016) to determine step length, cumulative distance, and maximum straight line distance from the vernal pool for each salamander. Unless otherwise noted, summary statistics are reported as mean ± SD. We used a Kruskal–Wallace test to determine whether maximum straight-line distances varied by pool and Spearnman's rank to determine whether distance was correlated with salamander mass (Jehle and Arntzen, 2000). We found the farthest distances from the pool for each unisexual salamander and compared the mean of these distances and 95% life zones for each pool to those calculated from published data for the parent species. Faccio (2003) tracked six *A. jeffersonianum* and followed Semlitsch (1998) in using a 95% confidence interval to determine the radius of a life zone that would include 95% of a study population's distances, suggesting managers keep habitat within this buffer intact to conserve populations. In contrast, we argue the use of confidence intervals to establish 95% life zones is incorrect and that quantiles are more appropriate. Confidence intervals are intended to give precision of estimation of the population mean (μ) such that the maximum of this interval is a possible population mean ($P[\text{lower CI} \leq \mu \leq \text{upper CI}] = 95\%$), not the area that includes 95% of the salamanders. We think Semlitsch may have intended to use quantiles, as we simply use the standard deviation rather than the standard error, such that the distance is not inflated by low sample size. Ryan and Calhoun (2014) sorted the distances traveled by *A. laterale* in ascending order and determined which distance included 95%. We recalculated life zones using the 95% quantile for these published data, the radio-isotope tracked *A. jeffersonianum* of Williams (1973), and our own observations using *t*-scores. Neither of these *A. jeffersonianum* populations has been genomotyped. However, Williams' animals were outside the geographic range of unisexual salamanders (Petranka, 1998; Charney, 2011) and Faccio's salamanders were likely mostly JJ based on sex ratios of the breeding population (S. Faccio, personal communication). Also, half of Faccio's telemetered salamanders were males, and, therefore, almost certainly JJ. Ryan and Calhoun's (2014) *A. laterale* population was known to contain no unisexual salamanders.

We used conditional logistic regression models to examine variables related to microhabitat selection by comparing plots used by individuals to their own available plots at a given time (i.e., study design IV; Erickson et al., 2001). We used the themes of land use, shelter, ground cover, microclimate, and vegetation to develop 22 specific a priori models (Table 1) about how salamanders may be using the landscape (i.e., if salamanders seek rotten wood when choosing where to settle rather than just any cover object, then a model containing just stumps and coarse woody debris would rank better than one also containing rocks) and 3 composite models (literature models in Table 1)

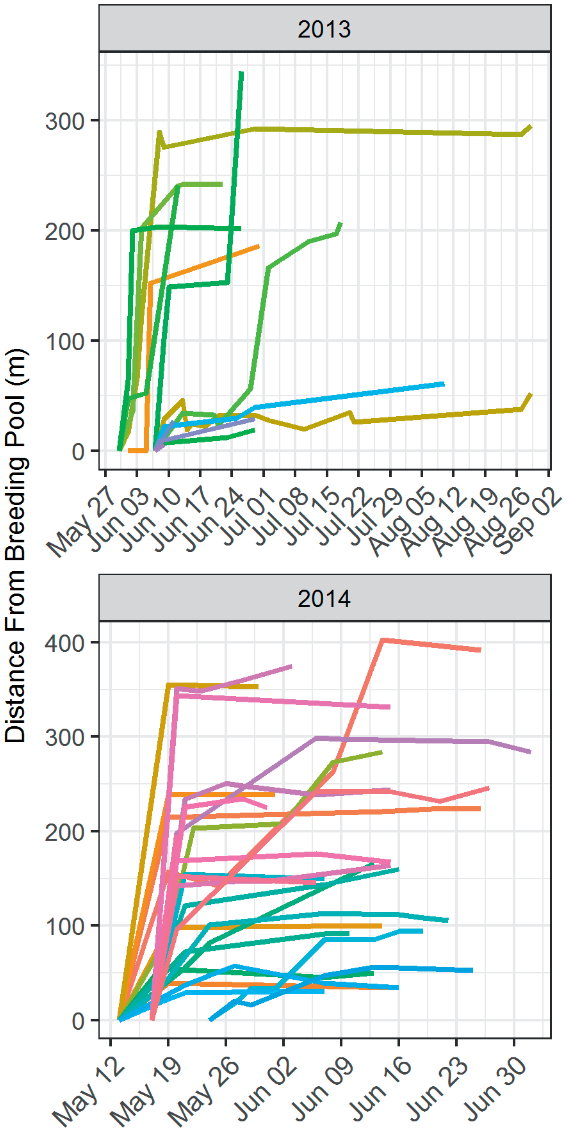

FIG. 2. Distances from the breeding pool for emigrating unisexual salamanders quickly reached asymptotes in central Maine. Each color represents an individual salamander.

based on the top models to predict plots selected by *A. laterale* from Ryan and Calhoun (2014). These models were not exclusive, such that variables in our shelter models may also appear in our ground cover models. We *Z*-standardized continuous variables, checked for collinearity (Pearson $r \geq 0.7$) and ranked all models seperately for the 3-m plot and 0.5-m plot scales. We weighed each plot by the proportion of days the salamander spent there, such that the experimental units were animals rather than relocations (Aebischer et al., 1993; Thomas and Taylor, 2006). We used the "survival" package (Therneau, 2015) in program R to conduct conditional logistic regression to examine selection of microhabitat features. We used Akaike Information Criterion adjusted for small sample size (AICc; Burnham and Anderson, 2002) to rank models separately for each scale with package "AICcmodavg" (Mazerolle, 2016). We used the "support.Ces" package (Aizaki, 2012) to determine McFadden's R^2 (ρ). Rather than make inference based solely on the fit of individual models, we found the model averaged estimates of the odds ratios of the variables from models with a cumulative model weight of ≤ 0.9 and considered these variables important if the confidence intervals of their odds ratios did not include 1.

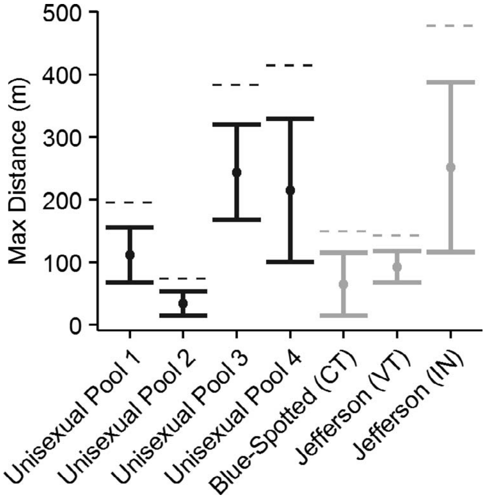

FIG. 3. Maximum distances (mean ± SD) from breeding pools for unisexual salamanders (this study) and their sperm-hosts (based on Williams, 1973; Faccio, 2003; and Ryan and Calhoun, 2014). Dashed lines represent the 95% quantile.

RESULTS

Of the 42 unisexual salamanders sampled in this study, 39 were LLJ, 2 were LLLJ, and 1 was unidentified but greater than the maximum observed mass of local *A. laterale* (LL; unpubl. data). Seven clones were represented in this sample and included 21 salamanders (Appendix 1). Body mass did not vary by pool (Kruskal-Wallace $\chi^2 = 2.91$, df = 3, $P = 0.406$).

Distances.—We tracked unisexual salamanders from 5 to 94 days (mean = 51 days), during which they moved an average straight-line distance of 172 m (range = 6–403 m) from the breeding pool (Table 1, Appendix 1). In 2013, the mean cumulative distance was 191 ± 76 m (range = 6–410 m). The mean cumulative distance in 2014 was 209 ± 140 m (range = 47–463 m). Maximum straight-line distance from the pool was not related to the body mass of the salamander ($r = 0.090$, $P = 0.581$) but varied by pool (Kruskal-Wallis $\chi^2 = 18.45$, df = 3, $P = 0.004$). Salamanders in Old Town remained closer to the pools (mean = 112 ± 44 m and 36 ± 19 m) than did salamanders in Orono (mean = 244 ± 76 and 214 ± 113 m). Distance to the pool generally reached an asymptote within a week, as salamanders made large initial migrations with few short subsequent movements (Fig. 2).

Ninety-five percent life zones for unisexual salamanders in our study also varied by pool (195 m, 74 m, 383 m, 415 m for Pools 1, 2, 3, and 4, respectively) and extended 362 m with all pools combined (Fig. 3). The 95% quantile for distance traveled by *A. jeffersonianum* in Indiana, was 478 m (mean = 252 ±136 m, $N = 86$, based on Williams, 1973), whereas the zone for *A. jeffersonianum*/unisexual salamanders in Vermont, was 143 m (mean = 92 ± 25, $N = 6$, based on Faccio, 2003). The life zone for *A. laterale* was 149 m (mean = 64.9 ± 50.1, $N = 43$, based on Ryan and Calhoun, 2014). These life zones are slightly smaller than those calculated by the authors (e.g., Faccio reported a 157-m zone based on confidence intervals, Ryan and Calhoun reported a 152-m life zone based on sorting distances by size, and Williams did not calculate a zone).

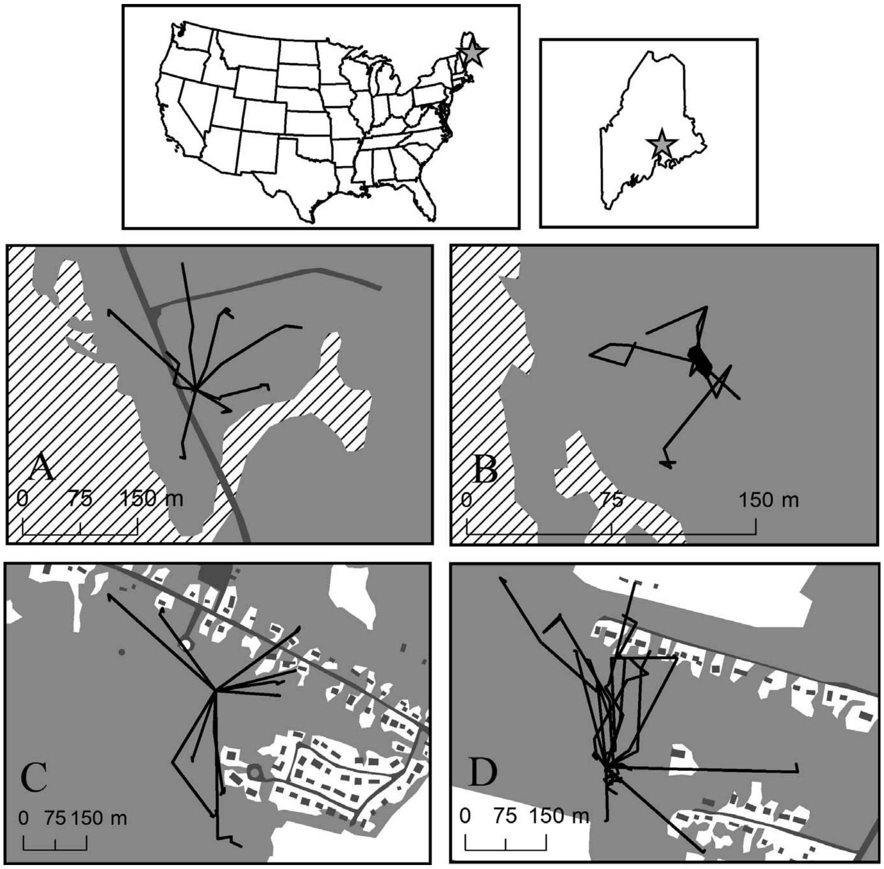

FIG. 4. Paths of emigration unisexual salamanders (black lines) radiating from breeding pools (black polygons) in central Maine. Pool 1 (A) and Pool 2 (B) are in Old Town, and Pool 3 (C) and Pool 4 (D) are in Orono. Lawns and hay fields (white), forest (medium gray), roads and buildings (dark gray), and water (hatched) are shown.

Macrohabitat.—Most unisexual salamanders (36 of 40) remained within the forest matrix for the entire study, although 12 of these emigrated to post-breeding home ranges that were within about 20 m of forest-lawn or forest-hay field edges (Fig. 4). Seven salamanders occupied swamps dominated by Alder (*Alnus incana*) and Highbush Blueberry (*Vaccinium corymbosum*). The remaining four salamanders crossed lawns during emigration and spent the majority of the season underneath buildings (two salamanders under separate sheds with wooden floors and two salamanders under the same garage on a concrete slab).

Microhabitat Selection.—At the larger movement scale ($\geq$3 m movements), only the "All tunnels" model had substantial support (ΔAICc = 0, Table 2). Seven other models related to shelter, vegetation, and microclimate, including important models for *A. laterale* based in Ryan and Calhoun (2014) had some support (ΔAICc < 7), though McFadden's adjusted pseudo R^2 was low for the five models that did not include "Mammal burrows" as a covariate. We model averaged the β estimates and found the 95% confidence intervals for the odds ratio of each variable that appeared in larger movement scale models with a cumulative 0.9 model weight. Selection of these top models

TABLE 2. Top-ranked unisexual salamander paired logistic regression models for used and random locations in central Maine. Only models with ΔAICc < 7 are shown. K is the number of parameters, adjusted ρ^2 is McFadden's adjusted pseudo R^2, and w is the model weight.

Model	K	ΔAICc	w_i	Cum. w	Adjusted ρ^2
3 m plot scale					
All tunnels	3	0.000	0.444	0.444	0.174
Soil temp	1	2.163	0.150	0.594	0.136
Mammal burrows	2	2.266	0.143	0.737	0.176
Veg global	5	3.852	0.065	0.802	0.096
MC global	2	4.065	0.058	0.860	0.080
Ryan 1 m	3	4.175	0.055	0.915	0.043
Lit global	5	4.981	0.037	0.952	-0.005
Low veg	2	6.611	0.016	0.968	0.109
0.5 m plot scale					
All tunnels	3	0	0.443	0.443	0.037
Mammal burrows	2	0.454	0.353	0.797	0.034
Sh global	6	2.104	0.155	0.952	0.016
Soil moisture	1	6.759	0.015	0.967	0.057

TABLE 3. Important model averaged parameter estimates (β), odds ratios, and descriptive statistics for unisexual salamander paired logistic regression models for plots of used and random locations in central Maine. Only covariates from models included in 90% of the cumulative model weight and with 95% confidence intervals or odds ratios that did not include one are shown.

Covariate	β Estimate (SE) of scaled data	Odds ratio of scaled data (95% CI)	Used mean (SD, min, max)	Available mean (SD, min, max)
3-m plot scale				
Horizontal burrows	0.588 (0.246)	1.801 (1.112–2.917)	1.269 (1.351, 0, 6)	0.687 (1.13, 0, 7)
Soil temp	−0.879 (0.425)	0.415 (0.181–0.955)	13.854 (2.78, 8, 27)	14.623 (3.182, 7, 31)
Veg <1 m	−0.681 (0.332)	0.506 (0.264–0.971)	17.234 (19.523, 0, 83)	25.875 (26.366, 0, 100)
0.5-m plot scale				
Horizontal burrows	0.588 (0.246)	1.801 (1.112–2.917)	1.269 (1.351, 0, 6)	0.687 (1.13, 0, 7)

appears to be driven by three important covariates (Table 3), with unisexual salamanders more likely to use plots with more horizontal burrows, lower substrate temperatures, and less vegetation <1 m tall than available plots.

At the smaller movement scale (<3 m), both the "All tunnels" model and "Mammal burrows" model had substantial support, and the global shelter and soil moisture models had some support, although all models had low McFadden's adjusted pseudo R^2. At the small movement scale, only horizontal burrows had an odds ratio with confidence intervals that did not include 1.

DISCUSSION

Unisexual salamander post-breeding movement patterns were similar to other ambystomatids, characterized by long movements during emigration over a few nights followed by infrequent and shorter movements in their post-breeding home range (Fig. 2; Williams, 1973; Madison, 1997; Titus et al., 2014). Unisexual salamanders moved as far as 463 m from the pool. Although individuals moved about five times on average during the study, five salamanders (of those tracked > 20 days) moved only once (from the pool to the summer location) and remained within the same 3-m plot for the season. This stationary behavior has been reported for other ambystomatids and also directly observed in Wood Frogs (*Lithobates sylvaticus*; Douglas and Monroe, 1981; Rittenhouse and Semlitsch, 2007). This may be a "sit-and-wait" predatory strategy.

Mean, median, and 95th percentiles of amphibian migration distances are used to justify the conservation of terrestrial habitat through regulatory or management zones (Semlitsch, 1998); however, these distances have not been widely quantified across and within species, which may be problematic for managers. Managing Orono pools based solely on Old Town Pools could jeopardize the majority of terrestrial habitat. For example, using the 95% life zone from Pool 2 would conserve none of our salamanders at Pool 3 and protect only 12.5% of our salamanders at Pool 4, whereas using Pool 1's life zone would conserve only 25% and 30%.

Unisexual salamanders in our study generally migrated within the range of distances reported for *A. laterale* and *A. jeffersonianum* in other studies (Fig. 3). Mean distances from the pool and 95% life zones for unisexual salamanders at three of our four pools were greater than those of *A. laterale* in Connecticut (Ryan and Calhoun, 2014) and *A. jeffersonianum* in Vermont (Faccio, 2003), but *A. jeffersonianum* in Indiana had a larger mean and life zone distances (Williams, 1973). Other references also list mean distances of unisexual salamanders (presumably LLJ) found under cover objects in Michigan as intermediate (110 m) and radioisotope tagged *A. jeffersonianum* in Kentucky as farther (250 m; Douglas and Monroe, 1981; Belasen et al., 2013). Although we found no relationship between unisexual salamander body mass and distance, many of our populations may have moved farther on average than *A. laterale* because we selected individuals larger than this parent species. This comparison does not consider variation attributable to geographic location, and we recommend that future work directly compare taxa at the same site.

Ninety percent of tracked unisexual salamanders stayed in the forest, but 13 of 22 salamanders from our Orono pools had post-breeding home ranges near or within residential neighborhoods (i.e., within about 20 m of lawns or fields). We are unsure whether salamanders settled in these areas because they interpreted the neighborhoods as less suitable or whether they sought out locations adjacent to open lands. Ambystomatids are known to cross open areas; however, they also avoid forest edges (deMaynadier and Hunter, 1998; Gibbs, 1998; Regosin et al., 2005; Pittman and Semlitsch, 2013). Forest edges are associated with reduced soil moisture, angular canopy cover, and coarse woody debris and increased forest floor disruption, predation, and temperature (reviewed in Lindenmayer and Fischer, 2006). Pesticide and herbicides may contaminate lawns, but these areas also have high primary production and may have high plant and invertebrate diversity (Falk, 1976; Frankie and Ehler, 1978; McKinney, 2008). Buildings may act as large cover objects to reduce fluctuation in temperature and moisture. We cautiously suggest further study to determine whether neighborhoods are filters, whether salamanders in more urban areas behave similarly, and whether salamanders residing near lawns have lower survival than those in forest interior.

Our top unisexual salamander microhabitat selection models included those based on shelter, vegetation, and microclimate, including a model based on microhabitat selection of *A. laterale* (from Ryan and Calhoun, 2014; containing soil temperature, leaf litter depth, and soil moisture). Ground cover and land use covariates were not supported, presumably because of the homogeneity of the landscapes in our study area. Only three variables were important: horizontal burrows; forest floor vegetation (herbaceous and woody plants within a meter of the ground); and soil temperature. The most important feature for predicting use by unisexual salamanders was also important in previous studies of parent species and other ambystomatids (Williams, 1973; Douglas and Monroe, 1981; Madison, 1997; Osbourn et al., 2014). Horizontal small mammal burrows were selected by unisexual salamanders both during large movements (migration) and during shorter movements within their post-breeding home range. Horizontal burrows are particularly important and are selected over vertical by both *A. jeffersonianum* and *Ambystoma maculatum* in Vermont (Faccio, 2003). Our finding that minimal forest floor vegetation and low temperatures are important may be because shaded areas remain moist and, therefore, indicate conditions conducive to thermoregulation and hydroregulation. *Ambystoma jeffersonianum* likewise select areas shaded by shrubs (Faccio, 2003). Salamanders, in general, are thought to behaviorally thermoregulate by selecting cool refugia, but rarely are temperature relations observed in the field (Feder and Pough, 1975; Stebbin and Cohen, 1995; Welsh and Lind, 1995). Stebbin and Cohen (1995) also suggest that selection of low temperatures may aid in recovery from high metabolic demands, such as migration and breeding. Our sites were relatively homogenous; hence, we cannot rule out other variables that may be important. Leaf litter, shrubs, logs, soil moisture, and canopy are important to sperm-hosts (Faccio, 2003; Ryan and Calhoun, 2014) but were consistently high in our area.

Our sample of unisexual salamanders selected microhabitat and migrated distances within the known parameters of both sperm-hosts. The overlap in habitat features may allow unisexual salamanders to colonize landscapes wherever sperm-hosts are present; however, unisexuals may require larger forest patches than sperm-hosts if their life zone is larger than the sperm-host's life zone (Mee and Rowe 2010). We suggest future work to track sperm-hosts and unisexual salamanders from the same breeding pool to directly compare habitat selection for differences that might allow coexistence of the taxa.

Unisexual salamanders are generally more abundant than their sympatric sperm host but are unusual among vertebrates in their reproductive system and, therefore, warrant conservation. We recommend maintaining forest conditions that support small mammal populations to provide burrows, avoiding use of lawn chemicals because some salamanders resided near lawns, and we urge further studies to examine the use of rural and suburban/exurban neighborhoods by ambystomatids. We emphasize that migration distances are context specific, and we caution resource managers to be conservative in designating management zones.

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Appendix 1.—Summary data for 40 unisexual salamanders radio tracked from 4 vernal pools. ID includes the pool of origin followed by the identification number of each animal. Genomotype indicates both ploidy and how many *Ambystoma laterale* and *Ambystoma jeffersonianum* genomes each individual contains. Clone indicates which animals were identical at 3 loci. Body mass and SVL (snout–vent length) were measured under anesthesia prior to transmitter implant surgery. The number of 3-m plots represents the amount of movements $>$ 6 m for which habitat data was recorded, whereas 0.5-m plots represent 1–6 m movements in 2014. Max step indicates the maximum distance moved between successive relocations in 2013 when salamanders were tracked daily, and this distance divided by three in 2014 when salamanders were tracked every 3 days, and estimates the maximum distance traveled in one night. Pool Dist is the maximum Euclidean distance each salamander traveled from the breeding site. The fates of each salamander include mortality events related to the implanted transmitters (MT), mortality events that were unrelated to the transmitters (MU), premature transmitter failure (TF), and battery expiration (BE).

ID	Genomotype	Clone	Mass (g)	SVL (mm)	Release Day	Days tracked	# 3m plots	# 0.5m plots	Max Step	Cumulative Dist	Pool Dist	Fate
P1.763	LLJ		9.5	72	6/7/2013	69	6	0	27	79	61	BE
P1.1	LLLJ		8.2	76	5/13/2014	34	2	3	18	76	54	BE
P1.2	LLJ		8.5	74	5/13/2014	40	3	0	28	167	166	BE
P1.3	LLLJ		9.8	78	5/13/2014	40	2	2	24	98	91	BE
P1.4	LLJ	E	7.8	73	5/13/2014	40	4	1	25	166	160	BE
P1.5	LLJ	F	8.9	74	5/13/2014	82	3	5	22	141	113	BE
P1.6	LLJ	F	10.4	77	5/17/2014	43	1	1	51	161	154	BE
P1.7	LLJ	E	12.2	80	5/24/2014	29	3	3	18	110	95	BE
P2.608	LLJ		11.7	76	6/7/2013	5	0	0	28	28	28	TF
P2.670	LLJ		9.4	73	6/8/2013	23	2	0	37	37	37	MT
P2.692	LLJ		9.9	80	6/7/2013	14	1	0	6	6	6	MU?
P2.1	LLJ		9.0	76	5/13/2014	37	3	1	11	63	31	BE
P2.2	LLJ		10.3	72	5/13/2014	47	5	4	12	91	57	BE
P2.3	LLJ		10.6	71	5/24/2014	71	2	4	18	116	56	BE
P3.1	LLJ	D	10.3	76	5/17/2014	75	2	3	66	392	299	BE
P3.10	LLJ	G	9.5	81	5/17/2014	48	3	4	78	274	251	BE
P3.11	LLJ	D	9.1	78	5/17/2014	48	3	1	117	422	375	BE
P3.12	LLJ		9.6	78	5/17/2014	35	3	2	47	169	164	BE
P3.3	LLJ	G	8.7	77	5/17/2014	75	2	1	114	359	343	BE
P3.5	LLJ		9.8	81	5/17/2014	32	3	2	56	185	176	BE
P3.6	LLJ	D	10.1	80	5/17/2014	41	1	1	75	251	234	BE
P3.7	LLJ	D	9.5	74	5/17/2014	38	1	0	65	196	196	BE
P3.8	LLJ		9.7	81	5/17/2014	35	1	1	50	160	152	BE
P3.9	LLJ	G	10.0	80	5/17/2014	75	4	2	49	274	246	BE
P4.401	Unknown		11.5	83	6/1/2013	45	5	0	152	183	186	BE
P4.629	LLJ	A	10.1	80	6/7/2013	86	14	0	30	229	53	BE
P4.662	LLJ		8.3	70	5/30/2013	91	7	0	178	394	295	BE
P4.718	LLJ	B	12.6	81	5/30/2013	48	4	0	171	342	242	BE
P4.811	LLJ		8.8	71	6/7/2013	64	8	0	126	298	208	MT
P4.871	LLJ		13.4	77	5/30/2013	48	4	0	193	246	241	BE
P4.872	LLJ	A	10.6	82	6/7/2013	53	3	0	15	34	19	MT
P4.899	LLJ	B	12.9	78	5/30/2013	94	4	0	144	218	203	BE
P4.930	LLJ		11.9	73	6/7/2013	87	3	0	194	364	345	MU
P4.1	LLJ		9.6	72	5/13/2014	79	3	1	52	463	403	BE
P4.2	LLJ		9.5	71	5/13/2014	52	2	3	71	225	224	BE
P4.3	LLJ	C	8.6	76	5/13/2014	35	2	2	13	47	39	BE
P4.4	LLJ	C	10.8	83	5/13/2014	50	2	1	80	244	240	BE
P4.5	LLJ	D	7.7	67	5/13/2014	41	2	2	33	102	100	BE
P4.6	LLJ	D	11.2	81	5/13/2014	41	1	1	118	369	355	BE
P4.7	LLJ		8.7	75	5/7/2014	41	4	1	38	404	196	BE