

Moving beyond the plane: measuring 3D home ranges of juvenile salamanders with passive integrated transponder (PIT) tags

Brittany H. Ousterhout^{1,2} · Jacob J. Burkhart¹

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Abstract

An individual's home range, or how much space it requires to obtain resources and meet its needs for survival and reproduction, affects the scale of many fundamental processes in ecology and can inform the management of species. Although home range size has been described for many taxa in two dimensions (2D), for species that also have a strong vertical component to their movement, such representations can miss core components of their ecology, including the size of their home ranges and the amount of overlap, and thus competition, between individuals. Measuring three-dimensional (3D) home ranges for small-bodied life history stages and species can be particularly difficult, as they cannot tolerate high resolution tracking technologies like GPS collars. In this study, we used Passive Integrated Transponder (PIT) tags to measure the 2D and 3D home ranges of two species of fossorial juvenile salamander: the ringed salamander (*Ambystoma annulatum*) and the spotted salamander (*A. maculatum*). We also tested whether individuals modified their habitat selection or movement behavior in response to environmental variation.

Brittany H. Ousterhout and Jacob J. Burkhart contributed equally to this work

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✉ Brittany H. Ousterhout
bousterhout@gmail.com

¹ Division of Biological Sciences, University of Missouri, Columbia, MO 65211, USA

² Present address: Department of Biological Sciences, University of Arkansas, Fayetteville, AR 72701, USA

Salamanders in our study frequently used subterranean habitats. However, we rarely detected them more than 5 cm below ground. Additionally, the overlap among 2D and 3D home ranges, respectively, were similar. These findings indicate that these salamanders may move vertically through their habitat less than previously thought. Alternatively, salamanders may have moved into soil strata beyond the detection range of PIT telemetry. We conclude that PIT telemetry can be a suitable technique for determining the 3D home range of fossorial life-stages or species for which other tracking technologies are unsuitable.

Significance statement

When animal behavior includes movements with a vertical component, simplifying assumptions of 2D home ranges can affect ecological inferences by overestimating competition between individuals and underestimating home range size. We used Passive Integrated Transponder (PIT) tags to describe the home range of fossorial juvenile salamanders in 3D. The juvenile salamanders in this study modulated their habitat selection in response to weather, but in general remained close to the soil surface. As a result, juveniles may be more susceptible than previously thought to habitat management practices that alter the local microclimate. Because individuals moved vertically less than predicted, 2D and 3D home ranges had similar patterns. We demonstrate that PIT telemetry can facilitate subterranean tracking of a cryptic life stage. However, this technology is limited in its subterranean detection depth, and until antenna strength is improved, the resolution of 3D home ranges may be limited.

Keywords *Ambystoma* spp. · Core area · Kernel density estimation · Minimum convex polygon · Ringed salamander · Spotted salamander

Introduction

Patterns of space use by individual animals reflect many fundamental ecological processes, including habitat use and selection (Marzluff et al. 2004), population demography (Morales et al. 2010), predator-prey relationships, intra- and interspecific competition (Amarasekare 2003; Börger et al. 2008), nutrient flow (Earl and Zollner 2014), dispersal (Pittman et al. 2014), and niche partitioning (Cunha and Vieira 2004). One measure of space use is the home range, or the space used by an individual to obtain resources and meet its requirements for survival and reproduction (Burt 1943; Börger et al. 2008; Powell and Mitchell 2012). Home range size can be used to model several other processes, including an animal's cognitive map of its environment (Powell and Mitchell 2012), species' extinction risks (Cardillo et al. 2008), the scale of movement behavior including homing and dispersal, and ultimately buffer size required to conserve essential habitat (Semlitsch and Bodie 1998; Powell and Mitchell 2012).

Two-dimensional (2D) home ranges have been described for many taxa. However, in addition to horizontal space (x , y), most animals also utilize space in a third dimension (3D; z) representing depth, altitude, or elevation (flying, burrowing, aquatic, and arboreal animals). 2D analyses systematically misrepresent space use in animals that occupy habitats with a strong vertical component, such as arboreal and marine habitats, by not capturing vertical stratification. By assuming individuals utilize the same vertical space, 2D analyses can also overestimate the overlap between individuals which stratify vertically (Simpfendorfer et al. 2012; Tracey et al. 2014). In a comparison of 2D and 3D estimates, Simpfendorfer et al. (2012) found that 2D analyses overestimated the amount of overlap between eels by 13–20%. A high degree of overlap would imply potential associations or competition for resources, leading to a very different picture of a population or community than if individuals were not overlapping. Moreover, 2D representations can underestimate the surface area of a home range for animals that occupy habitat with a strong vertical component. Tracey et al. (2014) reported that 2D movement-based kernel density estimates underestimate the space use of giant pandas, a montane species, by 13–16% relative to 3D estimates. Given that vulnerability to extinction increases with home range size (Cardillo et al. 2008), use of 2D home range estimates when 3D estimates are more behaviorally relevant may misguide conservation efforts.

In addition to more accurately capturing the size and overlap of home ranges, 3D representations of home ranges also allow the relationship between movement and environmental gradients to be explicitly studied. Although environmental variation can be considered a 2D process (e.g., latitude), research in alpine, marine, and lentic ecosystems has found strong effects of depth, altitude, and elevation on several

environmental factors, including temperature, wind, and photosynthetic active radiation (PAR). These vertical environmental gradients can exert strong effects on movement behavior and space utilization. For example, many species of plankton migrate diurnally through the water column in response to PAR (Tilzer 1973). Phytoplankton complete similar vertical seasonal migrations to moderate the temperature of their microhabitat (Banse and English 1999). Likewise, many alpine mammals complete seasonal migrations which track seasonal food resources that vary with elevation (Middleton et al. 2013; Tracey et al. 2014). Although the importance of depth, elevation or altitude, and corresponding environmental gradients have long been recognized in marine, aquatic, and alpine systems, whether similar gradients affect movement of fossorial species remains poorly understood.

Global Positioning System (GPS) biologgers and other technologies have dramatically increased the availability of 3D location data (Hebblewhite and Haydon 2010; Bouten et al. 2013); however, z -coordinates are still not frequently integrated into studies of space use (Belant et al. 2012; Tracey et al. 2014). Additionally, many life-stages and animals are prohibitively small for such transmitters. As such, the ecology of animals that utilize 3D space remains rarely studied for many taxa and potentially misunderstood for other taxa if 2D representations lead to different inferences. In this study, we use Passive Integrated Transponder (PIT) tags to measure 2D and 3D space utilization in two species of pond-breeding salamanders. Many amphibians, including salamanders of the genus *Ambystoma*, are fossorial during the terrestrial juvenile and adult life stages. Home range size has been estimated for many amphibian species in 2D (Semlitsch 1981; Kleeberger and Werner 1982; Johnson et al. 2008; Heemeyer et al. 2012; O'Donnell et al. 2016), and other studies have quantified the depth below ground selected by amphibians (Semlitsch and Pechmann 1985; Schabetsberger et al. 2004; Badje et al. 2016). However, these data have not been simultaneously considered. If these amphibians have a strong vertical component to their movement, then inferences drawn from 2D home range estimates may be very different from those following from 3D home range estimates (e.g., overlap between home ranges; Tracey et al. 2014).

For amphibian species that are frequently surface active, capture-mark-recapture approaches have been a successful alternative to radio telemetry for identifying 2D home ranges (Liebgold and Jaeger 2007; Ousterhout and Liebgold 2010; Valenzuela-Sánchez et al. 2014). However, such approaches are not readily applied to fossorial species, which are rarely available for recapture (O'Donnell et al. 2015). In such cases, telemetry with Passive Integrated Transponders (PIT) tags has been used to identify 2D space utilization (Connette and Semlitsch 2012; Ousterhout and Semlitsch 2014; Ryan and Calhoun 2014). PIT telemetry also presents an alternative approach for obtaining 3D location data for fossorial, small-

bodied animals. When activated by a low-energy field produced by a PIT tag reader, PIT tags broadcast a unique code. PIT tags are small (<0.033 g) because they do not require a battery, making them suitable for use in small animals (Gibbons and Andrews 2004; Connette and Semlitsch 2012; Ousterhout and Semlitsch 2014). Additionally, because there is a limited maximum distance from which PIT tags can be detected (30 cm; Ousterhout and Semlitsch 2014), the depth of an individual can be approximated by calculating the difference between the maximum detection distance and the distance from the antenna to the ground surface.

In this study, we investigated the home range of fossorial juveniles of two species of pond-breeding salamanders in two habitat types. We tracked individually marked juveniles over a 6-month period (October–March) and used relocation data to quantify the size of 2D and 3D home ranges and to determine if the overlap between home ranges, and predicted competition, differed when vertical space use was incorporated. We also tested whether individuals modified their habitat selection (depth below ground) or movement in response to environmental variation in soil temperature, air temperature, humidity, or precipitation. We predicted that overlap between 2D home ranges would be larger than the overlap between 3D home range estimates, because these species are thought to utilize small mammal burrows, and thus may stratify vertically, in addition to horizontally, reducing competition between individuals (Semlitsch 1983; Petranka 1998). Because amphibians are ectotherms and have skin that is highly permeable to water (Spotila and Berman 1976), we predicted that salamander habitat selection and movement would respond to soil and air temperature, humidity, and precipitation. We expected salamanders to move more and select habitat at the soil surface as temperature, precipitation, and humidity increased (Spotila and Berman 1976; Kane et al. 2001). Here, we present our findings and discuss the efficacy of using PIT tags to measure movement behavior in 3D.

Methods

Study area and species Our study was conducted at Fort Leonard Wood, Missouri, USA (37.92° N, 92.17° W), which is a 24,852-ha active military training facility in the northern Ozark Highland. Fort Leonard Wood is primarily forested; 80% of its landscape is characterized by oak-hickory forests (canopy: *Quercus* spp., *Q. stellata*, *Carya* spp., and *C. texana*; understory: *Rhus aromatic* and *Cornus florida*) or short leaf pine plantations (*Pinus echinata*).

In this field experiment, we examined the habitat use of juveniles of two co-occurring species of pond-breeding salamander, ringed salamanders (*Ambystoma annulatum* Cope 1886) and spotted salamanders (*A. maculatum* Shaw 1802). Ringed salamanders are endemic to the Ozark Highlands and

Ouachita Mountains of Missouri, Arkansas, and Oklahoma, whereas spotted salamanders are distributed throughout much of the eastern USA and portions of southeastern Canada (Petranka 1998). Ringed and spotted salamander adults oviposit eggs in ponds August–October and February–March, respectively. Ringed salamander juveniles metamorphose from their natal ponds and enter the terrestrial environment in late April–early June. Spotted salamander juveniles metamorphose early June–August, although larvae will occasionally metamorphose through November and in some cases overwinter and metamorphose the following spring (Petranka 1998; Hocking et al. 2008; Semlitsch et al. 2014). Upon metamorphosis, juveniles of both species will disperse into the terrestrial landscape and settle in burrows made by small mammals and insects (Semlitsch 1981; Trenham 2001), preferentially selecting closed canopy forest over open canopy habitats (Petranka 1998; Rothermel and Semlitsch 2006; Osbourn et al. 2014).

Larval mesocosms All animals used in this experiment were reared in pond mesocosms (1000 L, 1.52 m diameter, polyethylene cattle watering tanks). We established mesocosms on September 09, 2012 and March 01, 2013 for ringed salamanders ($N = 18$ mesocosm) and spotted salamanders ($N = 16$ mesocosms), respectively, by adding dechlorinated tap water, leaves, and zooplankton (Ousterhout and Semlitsch 2016). We collected eggs from several clutches at two ponds at Fort Leonard Wood. Because space utilization is expected to vary with body size (Lindstedt et al. 1986; Wells 2007), we generated juveniles that varied in size by rearing larvae at one of the three larval densities: low density (6 larvae/mesocosm), medium density (18 larvae/mesocosm), and high density (36 larvae/mesocosm). On October 30, 2012 and April 23, 2013 for ringed and spotted salamanders, respectively, we randomly assigned larval densities to mesocosms and hatchlings to pond mesocosms. Beginning April 15, 2013, we checked mesocosms with a light for metamorphosed salamanders at least every other night. Animals were considered to have metamorphosed if their gills were <2 mm in length. We measured wet mass (± 0.001 g, Mettler AT-100 electronic balance, Mettler Toledo, Columbus, OH, USA) and snout vent length (SVL; ± 1 mm) of all metamorphosed individuals. Animals were individually housed in containers on wet sphagnum moss and fed fruit flies (*Drosophila melanogaster*) and red wiggler worms (*Eisenia fetida*) ad libitum until their release.

Experimental enclosures We used replicated experimental enclosures to test the effects of species, seasonality, and habitat on overwintering movement and home range size in juvenile salamanders. Although tracking free moving salamanders would have been ideal, transmitters that are small enough to be used in small animals and can be detected from several meters away have not yet been developed. When confronted

with this technological limitation, previous studies have successfully used long, rectangular enclosures to test amphibian movement (Rosenberg et al. 1998; Rothermel and Semlitsch 2002; Osbourn et al. 2014). Our enclosures ($N = 7$, $2 \text{ m} \times 50 \text{ m}$) were composed of plastic weave silt fencing (90 cm tall) buried 15 cm into the ground with the top 10 cm of fencing folded inwards to create a baffle. The silt fence was supported by wooden stakes pounded into the ground at a 90° angle. We constructed replicate enclosures in both closed canopy forest and mixed grassland habitat at two sites (site 1: $N = 3$ enclosures in forest, $N = 2$ in mixed grassland; site 2: $N = 2$ in forest). Our selected sites were level and within 100 m of ringed and spotted salamander breeding ponds to increase the probability that our enclosures mimic habitat that would be encountered by metamorphs in the wild. See the supplementary material for additional information about enclosure design (Fig. S1).

Marking procedure We individually marked salamanders with PIT tags as in Ousterhout and Semlitsch (2014). Using PIT tags in concert with a portable antenna system allows for re-detection of small bodied animals from a distance of 30 cm or less underground (Connette and Semlitsch 2012; Ousterhout and Semlitsch 2014). We anesthetized each juvenile by immersion in a 1% solution of neutral buffered tricaine methanesulfonate (MS-222) until it could not right itself and did not respond to toe pinching. Animals were rinsed in spring water, patted dry, and weighed (Mettler Toledo, LLC, Columbus, OH, USA; $\pm 0.01 \text{ g}$). We assigned juveniles to one of the three PIT tag (full duplex, Biomark, Boise, ID, USA) sizes based on individual's weight. In situations where half the torso length of a juvenile was equal to or less than that of the length of the assigned PIT tag, we implanted the next smallest PIT tag size into that individual. We chose to use the largest appropriate tag size for each individual, because PIT tag detection distance increases with tag size (Ousterhout and Semlitsch 2014). Tag sizes and the range of salamander masses that were used for each are as follows: 12-mm PIT tag (HPT12 $12 \text{ mm} \times 2.12 \text{ mm}$, 0.115 g), 3.07–1.51 g; 9-mm PIT tag (HPT9 $9 \times 2.12 \text{ mm}$, 0.08 g), 2.25–0.68 g; and 8-mm PIT tag (HPT8 $8.5 \times 1.4 \text{ mm}$, 0.033 g), 0.43–1.28 g. To implant a PIT tag, we made a 3-mm incision to the muscle and skin anterior to a hind limb and inserted the tag into the body cavity. All animals were PIT tagged on September 27, 2013 or September 30, 2013. Post implantation, we monitored salamanders until they recovered, and returned them to their individually occupied plastic container until released in the field.

Experimental procedure We released 140 juvenile salamanders ($N = 80$ spotted salamanders and 60 ringed salamanders) into enclosures after sunset on October 5, 2013, which was within 24 h of a rain event that saturated the leaf litter. We

randomly assigned a species to each enclosure ($N = 4$ spotted: 3 forest, 1 grassland; $N = 3$ ringed: 2 forest, 1 grassland). Given previous experimental work showing higher survival rates in forested habitats (Rothermel and Semlitsch 2006; Osbourn et al. 2014) and a limited number of available juvenile salamanders, we chose to have a higher number of replicates for each species within forested habitat rather than grassland habitat. We released 20 randomly selected juveniles of the same species within each enclosure, with each individual being released at a randomly assigned location. We marked each release site with a flag and designated that as the individual's starting location.

We searched the enclosures 24 h after release and then every 1 to 2 weeks until March 29, 2014 ($N = 19$ tracking days) using a portable RFID system (FS-2001F-ISO reader and BP portable antenna, Biomark, Boise, ID, USA). Our searches consisted of passing the antenna close to the ground over the entirety of the enclosure. Every time we detected an individual, we measured their location ($\pm 5 \text{ cm}$). If an individual did not move more than 10 cm, we marked it as not moving. At each relocation, we approximated the vertical location of the juvenile by lifting the antenna until the salamander could no longer be detected. We measured the height of the antenna above the ground and subtracted this distance from the maximum detection ranges for each PIT tag with this antenna system (HPT8 = 16 cm, HPT9 = 24 cm, HPT12 = 30 cm; Ousterhout and Semlitsch 2014), to approximate depth of each individual in the soil column. We had intended to track animals through the summer; however, we were forced to conclude the experiment after a fire destroyed the enclosures at one site on February 26, 2014. We continued to search for animals post-burn to capture vertical migrations of individuals as soil temperatures warmed, recognizing that surface active salamanders could emigrate from our search area. To minimize bias, observers were blind to the species of individuals, but because measurements occurred in the field, it was not possible to record data blind to habitat type or weather.

Environmental measures At each habitat type at each site, we deployed two sets of HOBO Loggers and iButtons, one set on each side of the enclosure array. We measured soil temperature at 0, 5, 15, and 20 cm below the surface every 4 h for the duration of the experiment (accuracy $\pm 1^\circ \text{C}$; iButton model DS1921G, Maxim Integrated Products, San Jose, CA USA). We measured air temperature and relative humidity (RH) at 30-min intervals with data loggers (HOBO U10–003, Onset Computer Corp., Bourne, Massachusetts, USA). However, some of the air temperature and RH data loggers failed during the first week of the experiment and during the fire. To impute these values, we regressed daily average temperature, minimum temperature, maximum temperature, average RH, minimum RH, and maximum RH observed at our sites against observations from a weather station 4.03 km away from site

1 and 4.22 km away from site 2 (Waynesville Regional Airport at Forney Field, Weather Underground, <http://www.wunderground.com>). We then used the regression equations to impute missing site-specific weather data. We also used the weather station data to calculate the amount of precipitation (cm) since the last tracking occasion.

Statistical analyses We conducted all analyses with R (R Core Team 2016). We tested whether the spatial distribution of salamanders was random ($R = 1$), uniform ($R > 1$), or clumped ($R < 1$) using the Clark and Evans test (“clarkevans.test” in package spatstat; Baddeley and Turner 2005). To achieve unbiased estimates of aggregation, the location of all possible neighbors must be known. However, we searched a confined area, and as a result, the nearest neighbor for individuals at the edge of an enclosure may have been outside of the search area. In cases like ours where the location

of all nearest neighbors is not known, observed nearest neighbor distances are generally larger than true nearest neighbor distances. To correct for this, we applied a Donnelly edge correction (Table S1). For this test, we considered the mean location of individuals during three periods—fall (October 12, 2013–November 18, 2014), winter (January 01, 2014–February 21, 2014), and spring (March 01, 2014–April 03, 2014). We analyzed animals in enclosures in the same site and habitat type together (e.g., all forest enclosures at site 1).

For each individual, we calculated both 50 and 95% kernel density estimate (KDE) in both 2D and 3D space. The 50% KDE (hereafter, core area) represented an individual’s core area or home range, whereas the 95% KDE (hereafter, extent) described the extent of its movements excluding sallies (Burt 1943; Simpfendorfer et al. 2012). We conducted a bootstrap analysis to determine the effect of the number of the relocations per individual on 2D and 3D KDEs. For each

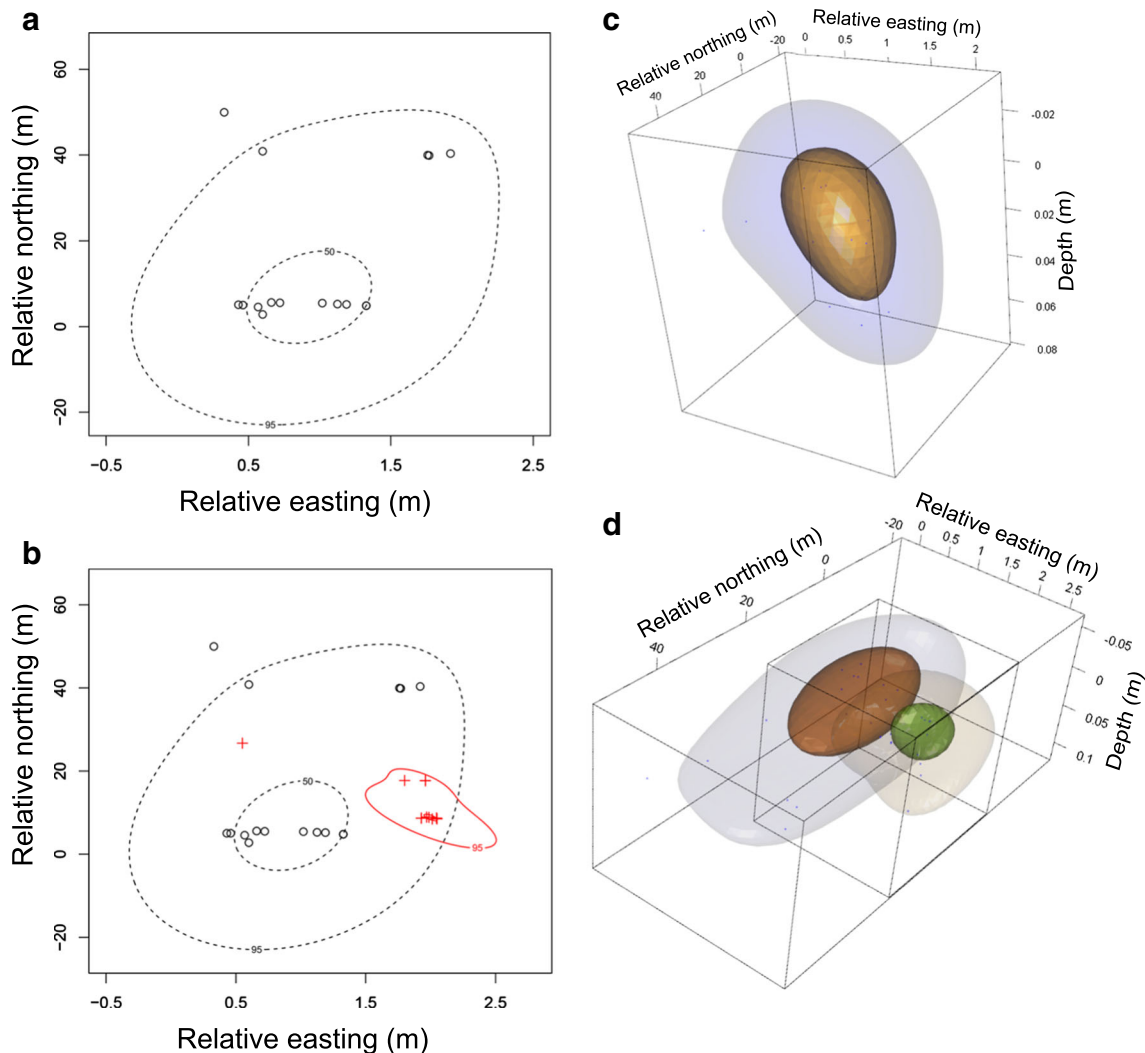


Fig. 1 A representative **a** 2D kernel density estimate (KDE), **b** the overlap between two 2D KDEs, **c** 3D KDE, and **d** the overlap between two 3D KDEs. The same individuals were used in 2D and 3D examples. Note, axes are scaled differently

salamander with at least 14 relocations ($N = 14$), we randomly drew 4–14 locations and calculated a KDE. For each individual and number of relocations combination, we ran 500 simulations (Fig. S2). To minimize bias in KDE due to a low number of relocations, we included individuals in the analysis that had at least six unique locations and moved at least 10 cm between new relocations (detection accuracy threshold, 140 salamanders released; 2D analyses $N = 51$; 3D analyses $N = 55$), resulting in 6–17 relocations per individual (median = 11.00 locations). We used a plug-in bandwidths selector to estimate the smoothing factor matrix for kernel estimation, and after testing a range of multipliers to identify the optimal value, we applied a multiplier of six to reduce the complexity of kernels and increase smoothing, thereby more accurately representing the uncertainty in our relocation estimates. We used the “kde” function from the ks package (Duong 2007) to estimate core area and extent as well as the overlap between core areas and extents, respectively. We calculated an intraspecific overlap index (hereafter overlap index) by summing the total area or volume of overlap between an individual and all other salamanders at a site and then dividing by the individual’s core area or extent. An overlap index of 0 would indicate that an individual had exclusive use of its core area or extent.

We assessed if the number of times an individual was relocated or how far it moved affected KDE with a generalized linear model (GLM), assuming a gamma distribution.

We tested whether species, habitat, and the interaction between species and habitat had an effect on KDE and intraspecific KDE overlap index with a generalized linear mixed effects model (GLMM) assuming a gamma and a negative binomial distribution, respectively. We included the covariates tag size and the number of relocations to control for differences in detection between individuals, and the random effect of enclosure crossed with site. Because mass was highly collinear with tag size (Pearson’s correlation coefficient $r = 0.74$), we opted to analyze the tag size as it affected detection depth, and did not retain mass in models. For all assessments of KDE, we modeled the response of core area and extent KDEs for 2D and 3D estimates.

We tested if salamanders modified their habitat selection (i.e., depth below ground), probability of moving, or distance moved in response to weather conditions with GLMMs. We assessed if mean temperature, total precipitation, mean soil surface temperature, or mean RH in the week preceding tracking had an effect on whether a salamander moved, assuming a Bernoulli distribution. We also tested if these independent variables had an effect on salamander depth or distance moved with a negative binomial distribution. In all three GLMMs, we included in the variables species, habitat, and their interaction (as above). We also included covariates site, PIT tag size, number of relocations, as well as the random effect of individual to account for repeated measures. The residuals of all models met assumptions of homoscedacity. GLMs and

Table 1 Summary of 2D and 3D kernel density estimates (KDE) and KDE overlap index, the amount of overlap between home ranges

Dim	Space	Species	Habitat	N	Size			Overlap index		
					Median	IQR	Range	Median	IQR	Range
2D	Core	Ringed	Forest	9	1.60	5.96	0.46–12.36	0.43	0.29	0–2.96
			Grassland	4	7.40	34.95	0.36–117.23	8.95	2.99	3.01–10.01
		Spotted	Forest	30	5.09	13.42	0.12–117.8	2.77	2.38	0–13.71
			Grassland	8	15.65	19.92	3.14–51.32	5.44	1.42	1.67–8.80
	Extent	Ringed	Forest	9	18.26	26.52	1.56–45.01	1.35	0.66	0.49–4.60
			Grassland	4	39.00	73.68	18.52–301.57	20.13	2.81	17.54–25.18
		Spotted	Forest	30	31.29	46.02	6.25–300.78	7.14	7.89	1.23–25.35
			Grassland	8	101.08	49.19	26.23–242.79	12.79	1.71	9.58–20.31
3D	Core	Ringed	Forest	11	0.16	0.44	0–3.02	0.49	0.58	0.03–2.19
			Grassland	5	0.44	0.41	0–34.24	7.55	5.70	0–13.34
		Spotted	Forest	31	0.30	0.94	0.02–6.54	3.40	3.16	0–13.62
			Grassland	8	1.54	3.36	0.14–5.74	4.57	2.40	2.43–6.33
	Extent	Ringed	Forest	11	1.62	3.43	0–6.37	1.31	0.65	0.20–3.38
			Grassland	5	2.78	3.44	0.03–73.93	14.72	3.56	6.16–19.23
		Spotted	Forest	31	4.03	7.29	0.12–65.01	6.45	5.68	1.35–16.82
			Grassland	8	5.51	11.06	3.10–47.86	7.87	2.60	4.86–13.91

Dim refers to dimensions in KDE, space refers to size of KDE (Core = 50%; Extent = 95%), N is the number of salamanders, IQR is the interquartile range, and range is described by the minimum and maximum values

GLMMs were built using “glmmadmb” in package glmmADMB (Fournier et al. 2012; Skaug et al. 2016). We considered findings to be statistically significant if $P < 0.05$ and a trend if $P < 0.10$.

Results

Home range size In the forest habitat, KDEs were based on 9.8 ± 2.6 (mean \pm SD) relocations for each ringed

salamander and 12.1 ± 3.8 relocations for each spotted salamander. In the grassland, ringed salamanders KDEs had 11.2 ± 4.4 relocations, and spotted salamander KDEs had 10.3 ± 2.6 relocations. There was a positive correlation between KDE and the distance moved by a salamander (Table S2). However, 50% KDEs had a negative relationship with the number of relocations (Table S2).

Juvenile ringed salamanders had a median 2D core area of 3.58 m^2 and extent of 28.68 m^2 (Fig. 1, Table 1). Spotted

Table 2 Effects of species (ringed or spotted salamander), habitat (forest or grassland), and their interaction on KDEs

Predictor		Estimate	χ^2	DF	<i>P</i>
2D core area					
Intercept	Ringed, forest, small	2.18 (0.86, 3.50)	10.42	1	0.001
Species	Spotted	1.01 (−0.15, 2.17)	<i>2.90</i>	<i>1</i>	<i>0.089</i>
Habitat	Grassland	1.72 (0.10, 3.34)	4.31	1	0.038
Species x habitat	Spotted, grassland	0.18 (−3.56, 0.49)	2.20	1	0.138
Relocations		−0.09 (−0.18, 0.004)	3.50	<i>1</i>	<i>0.061</i>
Tag size			0.75	2	0.687
	Medium	0.40 (−0.75, 1.54)			
	Large	0.66 (−0.87, 2.19)			
2D extent					
Intercept	Ringed, forest, small	2.58 (1.57, 3.59)	25.04	1	<0.001
Species	Spotted	0.59 (−0.14, 1.32)	2.48	1	0.115
Habitat	Grassland	1.40 (0.32, 2.49)	6.40	1	0.011
Species x habitat	Spotted, grassland	−0.88 (−2.31, 0.55)	1.44	1	0.230
Relocations		0.05 (−0.02, 0.12)	1.95	1	0.162
Tag size			1.94	2	0.380
	Medium	0.14 (−0.55, 0.84)			
	Large	0.71 (−0.31, 1.72)			
3D core volume					
Intercept	Ringed, forest, small	−1.60 (−3.05, −0.15)	4.69	1	0.030
Species	Spotted	0.30 (−0.80, 1.40)	0.29	1	0.590
Habitat	Grassland	2.00 (0.40, 3.60)	6.01	1	0.014
Species x habitat	Spotted, grassland	−2.01 (−4.15, 0.13)	3.38	<i>1</i>	<i>0.066</i>
Relocations		0.03 (−0.13, 0.08)	0.25	1	0.614
Tag size			13.79	2	0.001
	Medium	1.81 (0.76, 2.86)			
	Large	2.59 (0.92, 4.25)			
3D extent					
Intercept	Ringed, forest, small	−0.51 (−1.82, 0.80)	0.58	1	0.446
Species	Spotted	0.46 (−0.45, 1.37)	0.97	1	0.325
Habitat	Grassland	1.58 (0.24, 2.92)	5.33	1	0.021
Species x habitat	Spotted, grassland	−1.47 (−3.29, 0.34)	2.53	1	0.111
Relocations		0.07 (−0.03, 0.17)	1.96	1	0.162
Tag size			14.30	2	<0.001
	Medium	1.11 (0.25, 1.97)			
	Large	2.38 (1.10, 3.66)			

Core and extent refer to 50 and 95% KDEs, respectively. x indicates an interaction. Estimate refers to predicted effects and 95% confidence interval. χ^2 is Wald’s chi squared. $P < 0.05$ are bolded, and $P < 0.10$ are in italics

salamanders utilized approximately twice as much space as ringed salamanders (Table 1), with a median 2D core area of 7.81 m² and extent of 41.43 m². A similar pattern emerged with 3D space utilization—spotted salamanders had greater core volumes (median = 0.45 m³) and extents (4.03 m³) than ringed salamanders (core volume = 0.24 m³; extent = 2.45 m³) (Table 1). All estimates of home-range size were predicted by habitat (Table 2). Salamanders had smaller home ranges in the forest than the grassland (Figs. 2 and S3). However, in all instances, the relationship between habitat and home range was strongly affected by one influential observation and were not significant if the outlier was censored. 2D kernel density estimates were not affected by PIT tag size, whereas 3D KDEs were (Table 2).

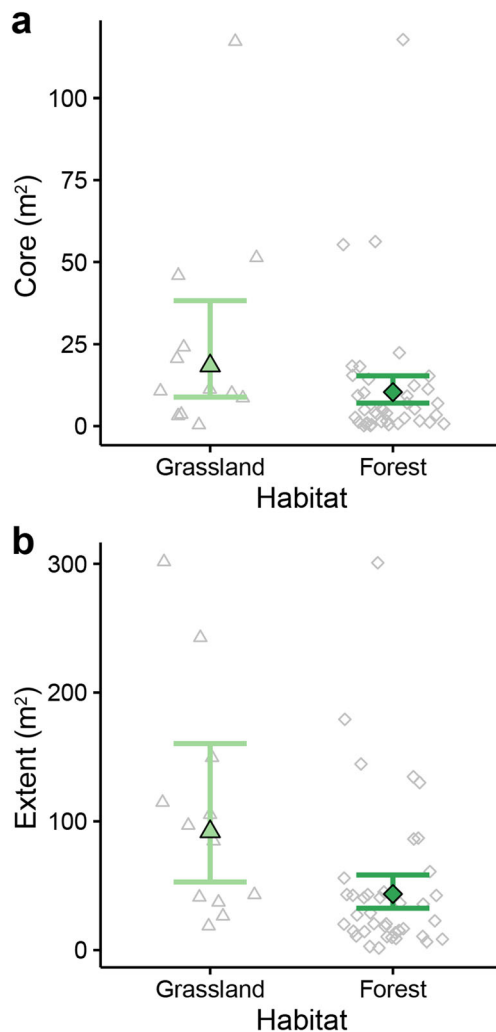


Fig. 2 2D and 3D KDEs were predicted by habitat type. There was a similar relationship between KDE and habitat type in all instances, so here we display only 2D **a** core area and **b** extent. *Open symbols* are individual observations. *Filled symbols* represent predicted mean values and error bars represent 95% confidence intervals. 3D core area and extent are presented in the supplemental information (Fig. S3)

Home range overlap Juvenile ringed and spotted salamanders were randomly spaced during the fall and spring sampling periods (Table S3). During the winter sampling period, salamanders were uniformly spaced in the grassland and clustered at one forest site (Table S3). Few salamanders had exclusive use of their core area/volume (2D 7.8%, 3D 3.6%), and no salamanders had exclusive use of their extent. In addition to affecting the KDE of salamanders, habitat also affected the overlap between home ranges (Table 3). The overlap index was 42–60% smaller in the forest than in the grassland (Figs. 3 and S4; Table 1). Species also affected KDE overlap (Figs. 3 and S4; Table 3); spotted salamanders had three to six times greater overlap than ringed salamanders. Additionally, the home range overlap index was predicted by an interaction between habitat and species (Table 3). The overlap between spotted salamander home ranges (2D and 3D core areas and extents) did not differ between the grassland and the forest, whereas ringed salamanders overlapped more in the grassland than the forest (Figs. 3 and S4).

Lateral movement and weather Unsurprisingly, salamanders that moved farther had larger core areas and extents (Table S2; Spearman's rank correlation ρ 0.62–0.84, $P < 0.001$). The probability of an animal moving between tracking sessions was affected by weather. Salamanders were more likely to move when the surface soil temperature was higher (Fig. 4; $\chi^2 = 7.54$, $P = 0.006$). During this study, soil surface temperature ranged between -2.9 and 16.0 °C (mean = 5.03 °C). Salamander movement probability decreased with RH (Fig. 4; $\chi^2 = 4.45$, $P = 0.035$). Additionally, there was a trend for the probability of salamanders moving to increase with precipitation ($\chi^2 = 3.80$, $P = 0.051$). Between tracking sessions, 1.12 cm of rain fell (mean, range 0–5.54 cm), and the RH was 60.52% (range 38.23–76.08%).

The distance moved by salamanders between relocations increased with air temperature (Fig. 5; $\chi^2 = 8.92$, $P = 0.003$) and soil surface temperature (Fig. 5; $\chi^2 = 5.10$, $P = 0.024$). Mean weekly air temperature during the study ranged between -2 and 20 °C (mean = 10.48 °C). The distance moved by salamanders was also affected by species ($\chi^2 = 7.58$, $P = 0.006$). Spotted salamanders moved 19% farther between relocations than ringed salamanders (Fig. 5).

Vertical movement and weather Unlike the probability of moving and distance moved, surface soil temperature, RH, and precipitation did not affect vertical movement by salamanders ($P > 0.83$). PIT tag size also did not affect our ability to detect vertical movements ($\chi^2 = 3.80$, $P = 0.150$). Additionally, ringed and spotted salamanders were generally detected near the soil

Table 3 Effects of species (ringed or spotted salamander), habitat (forest or grassland), and their interaction on the overlap of KDEs

Predictor		Estimate	χ^2	DF	<i>P</i>
2D core area overlap					
Intercept	Ringed, forest, small	0.13 (−1.07, 1.33)	0.05	1	0.828
Species	Spotted	1.76 (0.73, 2.78)	11.30	1	<0.001
Habitat	Grassland	2.20 (0.97, 3.44)	12.18	1	<0.001
Species x habitat	Spotted, grassland	−1.89 (−3.31, −0.47)	6.77	1	0.009
Relocations		−0.10 (−0.14, −0.05)	17.52	1	<0.001
Tag size			2.39	2	0.303
	Medium	0.34 (−0.19, 0.87)			
	Large	0.04 (−0.61, 0.69)			
2D extent overlap					
Intercept	Ringed, forest, small	0.85 (0.08, 1.62)	4.70	1	0.030
Species	Spotted	1.74 (0.92, 2.56)	17.39	1	<0.001
Habitat	Grassland	2.51 (1.50, 3.52)	23.64	1	<0.001
Species x habitat	Spotted, grassland	−2.13 (−3.44, −0.82)	10.14	1	<0.001
Relocations		−0.05 (−0.07, −0.02)	11.18	1	<0.001
Tag size			0.63	2	0.729
	Medium	0.12 (−0.19, 0.43)			
	Large	0.05 (−0.33, 0.43)			
3D core volume overlap					
Intercept	Ringed, forest, small	0.06 (−0.90, 1.01)	0.014	1	0.906
Species	Spotted	1.83 (0.88, 2.79)	14.08	1	<0.001
Habitat	Grassland	2.35 (1.22, 3.48)	16.61	1	<0.001
Species x habitat	Spotted, grassland	−2.28 (−3.71, −0.85)	9.73	1	0.002
Relocations		−0.06 (−0.10, −0.02)	8.39	1	0.004
Tag size			0.79	2	0.675
	Medium	0.19 (−0.23, 0.62)			
	Large	0.16 (−0.41, 0.73)			
3D extent overlap					
Intercept	Ringed, forest, small	0.70 (−0.02, 1.42)	3.59	<i>1</i>	<i>0.058</i>
Species	Spotted	1.59 (0.84, 2.34)	17.30	1	<0.001
Habitat	Grassland	2.25 (1.34, 3.16)	23.58	1	<0.001
Species x habitat	Spotted, grassland	−2.07 (−3.25, −0.88)	11.73	1	<0.001
Relocations		−0.05 (−0.08, −0.02)	10.09	1	0.001
Tag size			1.90	2	0.388
	Medium	0.22 (−0.10, 0.54)			
	Large	0.14 (−0.29, 0.58)			

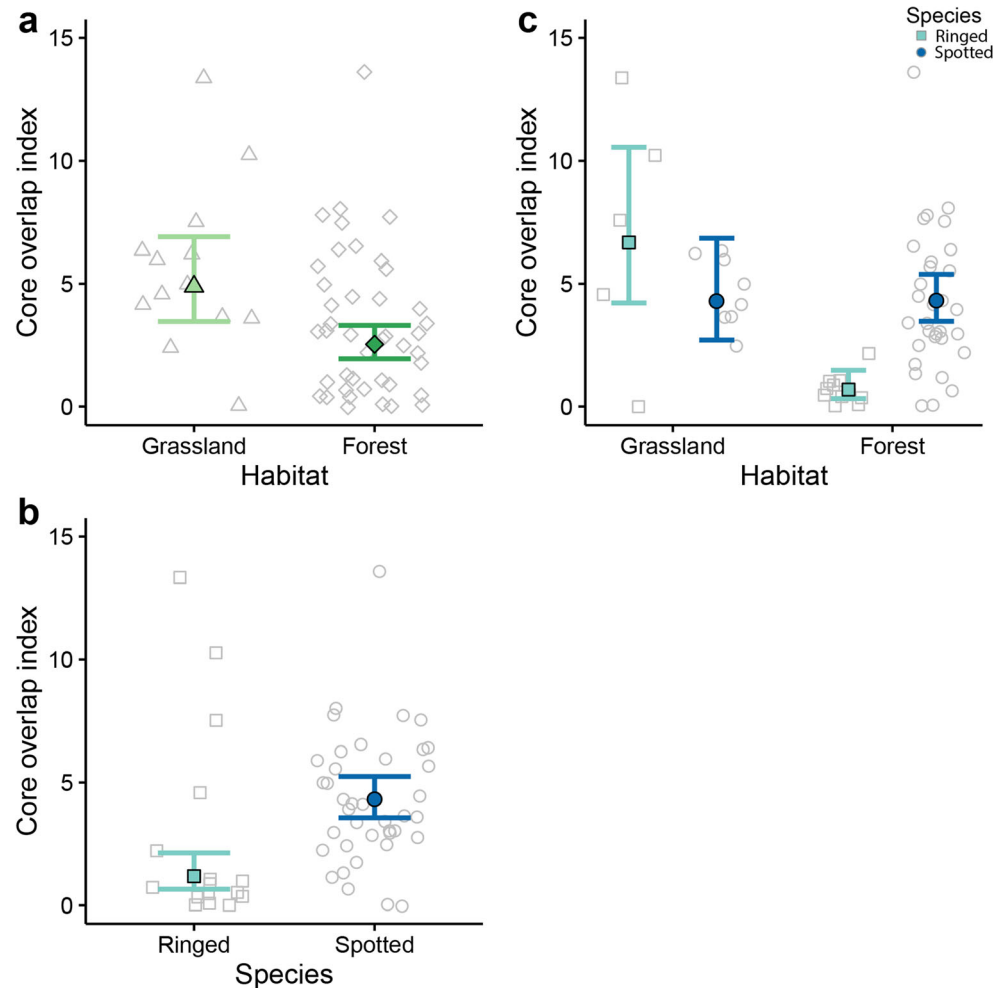
Core and extent refer to 50% and 95% KDEs, respectively. x indicates an interaction. Estimate refers to predicted effects and 95% confidence interval. χ^2 is Wald's chi squared. *P* < 0.05 are bolded and *P* < 0.10 are in italics

surface (mean \pm 1 SD = 2 \pm 3 cm); however, they utilized a range of depths (Fig. 6; 0–22 cm) with a range of temperatures (Fig. 6; temperatures at depths used by salamanders—range 2.17–12.46 °C, mean \pm 1 SD 7.71 \pm 2.99 °C). The temperature range of habitats selected by salamanders was narrower than the variation measured in soil temperature and always exceeded freezing (Fig. 6; range of soil temperatures observed: −2.92–16.00 °C).

Discussion

The amount of space used by animals reflects many ecological processes, including habitat use and selection (Marzluff et al. 2004), competition and exclusion (Amarasekare 2003; Börger et al. 2008), nutrient flow (Earl and Zollner 2014), and even extinction risk (Cardillo et al. 2008). Despite the importance of space use to the ecology and conservation of species, historically, vertical components of animal movements have been

Fig. 3 The overlap index of intraspecific core areas and extents was affected by **a** habitat, **b** species, and **c** the interaction between species and habitat. In all instances, there was a similar relationship between intraspecific KDE overlap index and predictor variables, so here we display only the 3D core volumes. *Open symbols* are individual observations, *filled symbols* represent predicted mean values, and *error bars* are 95% confidence intervals



considered separately, if at all, from the more often analyzed space utilization along a single plane (e.g., x, y). Vertical movements have been particularly ignored for small-bodied animals such as the pond-breeding salamanders in this study, which are too small to wear high-resolution tags for tracking movement (e.g., GPS collars). Here, we estimated the 2D and 3D home range size of juveniles of two species of pond-breeding salamanders by tracking them over a 6-month period. In addition to computing and analyzing predictors of both 2D and 3D space utilization, we also report on the movement of juvenile amphibians well beyond the 24 h–1 week following metamorphosis generally considered.

Although comparison of home range size between studies must be done cautiously due to methodological differences in which animals were tracked and how calculations were made, overwintering 2D home range sizes in our study (ringed salamander median core area [50% KDE] = 1.56 m², extent [95% KDE] = 18.39 m²; spotted salamander core area = 7.02 m², extent = 40.58 m²) were small, similar to those measured during the summer months in other studies of juveniles and

adults of *Ambystoma*. In Michigan, post-breeding adult spotted salamanders had an extent of 9.83 m² (Kleeberger and Werner 1983), whereas in South Carolina, mole salamanders (*A. talpoideum*) had smaller median extents (juveniles 0.25 m², adults 3.61 m²; Semlitsch 1981). Adult marbled salamanders (*A. opacum*) in Indiana had larger extents, using 14.5 m² (Williams 1973). Collectively, these studies indicate that both juveniles and adults of *Ambystoma* have small 2D home ranges, with adults generally using more space than juveniles.

Although 2D home ranges have been quantified for amphibians, to our knowledge, this is the first time that a depth profile has been simultaneously tracked, allowing the estimation of 3D home ranges. Patterns of 3D space use in our study were similar to the patterns of 2D space use. Spotted salamanders had larger home ranges than ringed salamanders, and for both species, core volumes were substantially smaller than extents. The small volume of space used by salamanders was strongly affected by depth. Most of the salamanders in our study stayed near the surface, and if habitat deeper than

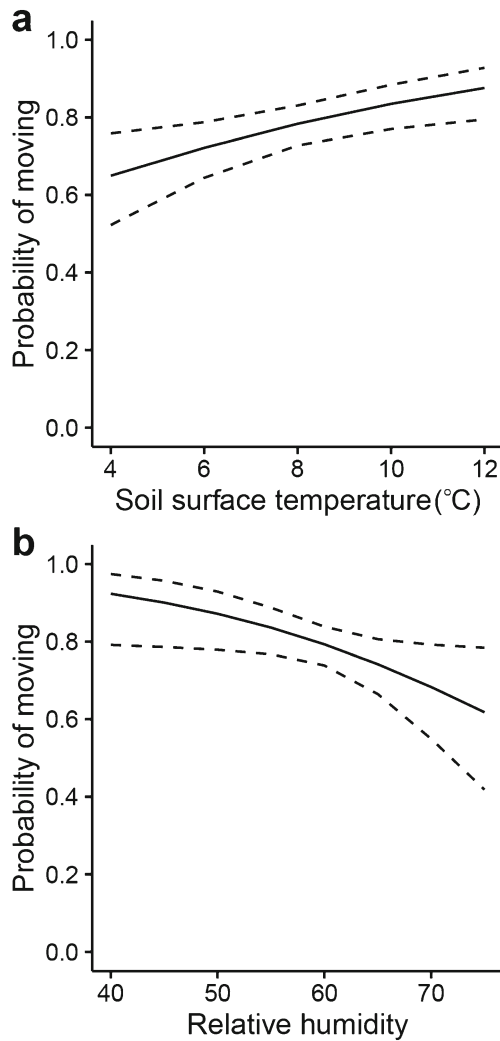


Fig. 4 The probability of an individual moving was affected by **a** soil surface temperature (°C) and **b** relative humidity. *Solid lines* represent predicted values and *dashed lines* represent 95% confidence intervals

22 cm was selected, we did not detect it. Both the 2D and 3D KDEs presented here must be interpreted with caution due to the small number of spatial relocations per individual. Kernel estimates of home range size are affected by sample size, and sample sizes less than 30–50 will bias results (Seaman et al. 1999; Laver and Kelly 2008). Bias from small sample size undoubtedly affected our estimates of home range size (Fig. S2) and home range overlap. However, because relocations across species and habitat types were similar, any bias in KDEs should not affect analyses of predictors of home range size or overlap.

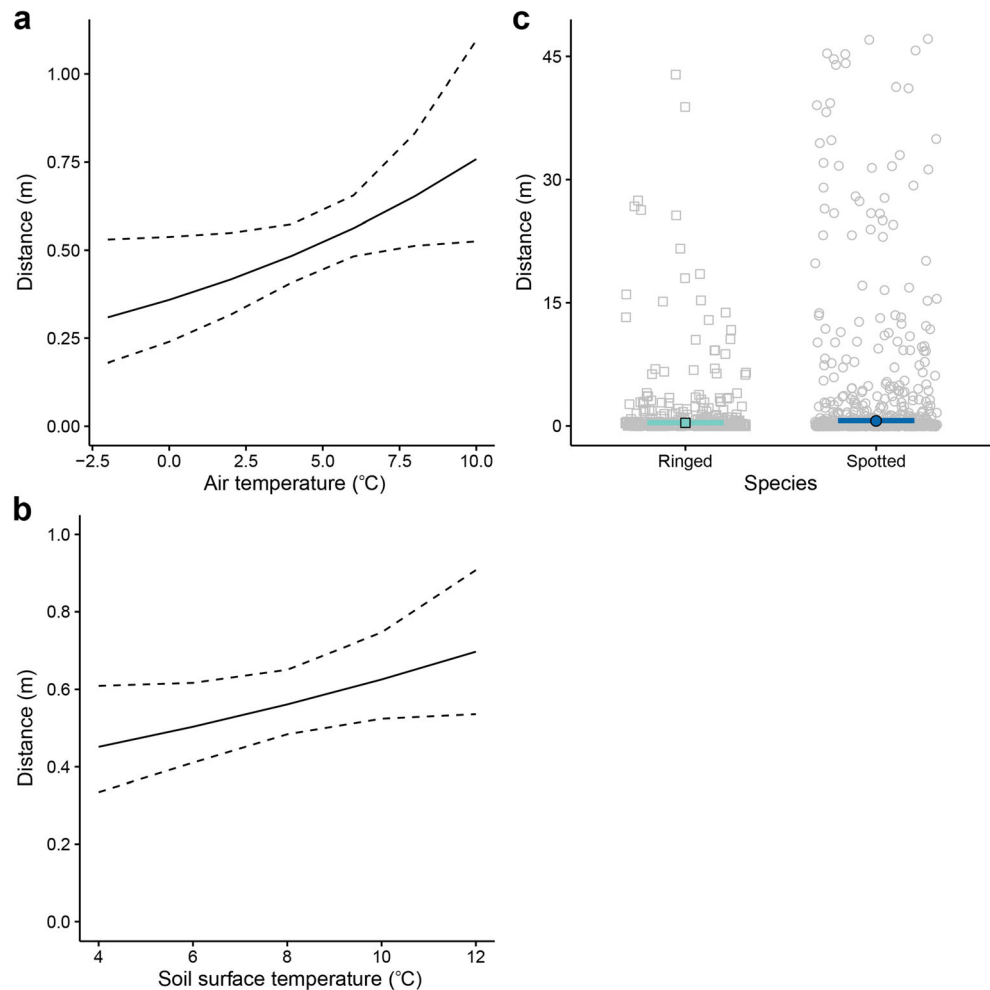
The two species examined in this study altered their space utilization depending on the habitat type they occupied, and had greater KDEs in the grassland than the forest. A major constraint for amphibians is desiccation, and risk of desiccation is highest for salamanders in habitats such as grasslands

(Loredo et al. 1996; Rothermel and Luhring 2005; Rothermel and Semlitsch 2006) which have high solar radiation, lower soil moisture, and a lower density of burrows which salamanders use as refuges (JJB unpublished data). Salamanders may move farther in grasslands in search of burrows, resulting in larger KDEs. Alternatively, salamanders may have larger home ranges in grasslands in order to meet their energetic requirements, because soil invertebrates are less abundant in the leaf litter of grasslands than forests (Curry 1994).

Ringed salamanders had greater intraspecific overlap of home ranges in the grassland. The effect of habitat type on overlap index is unlikely to reflect variation in the strength of competition between the two habitat types. We would expect advantages from exclusive space use, such as burrow refuges, to be stronger in the grassland where there is a lower density of burrows (JJB unpublished data), lower prey density (Curry 1994), and more extreme weather conditions (this study). Additionally, exclusive space used due to resource limitation seems unlikely, as there is no evidence of territorial behavior in either salamander species used in this study (Nussbaum et al. 2016), and spotted salamanders display conspecific attraction (Greene et al. 2016). Instead, we suggest that overlap reflects differences in the distribution of resources between habitat types which are limiting to ringed salamanders. Ringed salamanders may have moved more in the grassland in search of burrows because desiccation risk is higher in grasslands (Rothermel and Luhring 2005), and particularly for species such as ringed salamanders with larger surface-area-to-volume ratios (Grover 2000; Peterman et al. 2013). Differences in prey abundances between habitat types (Curry 1994) and energetic requirements between species could also drive the interaction between species and habitat. However, future studies will be required to test these hypotheses.

Whereas the home range overlap index differed between habitat types and species, there was not a strong difference in the overlap index when comparing 2D and 3D home ranges. The lack of a difference in overlap between estimate types indicates that salamanders were not partitioning space vertically. Indeed, although salamanders in this study frequently used burrows and selected habitats that had less variation in temperature than the ambient air temperature, vertical movements were generally limited to 5 cm below ground. The limited vertical movement and the lack of statistical relationship between surface soil temperature and the depth selected by salamanders could be attributed to several non-exclusive factors. The shallow depth profiles of the salamanders we tracked may reflect limitations of PIT tag detection. The vertical movements we measured were generally restricted to <0.05 m and never exceeded 0.22 m, approximately the maximum detection depth of the PIT tags used in this study (Ousterhout and Semlitsch 2014). Additionally, some individuals were only detected in the fall and spring, but not during the colder winter months. It seems unlikely that salamanders

Fig. 5 Distance moved by individuals was affected by **a** air temperature (°C), **b** soil surface temperature (°C), and **c** species. *Solid lines and symbols* represent predicted values, *dashed lines and error bars* represent 95% confidence intervals, and *open symbols* are individual observations



moved laterally out of enclosures, because we had a low trespassing rate (7%, $N = 6$ salamanders pre-fire, $N = 3$ salamanders post-fire). Instead, we suggest that these salamanders may have moved vertically beyond the detection limit of PIT tags (30 cm for largest PIT tags; Ousterhout and Semlitsch 2014) and were unavailable for surveying (Connette and Semlitsch 2012; O'Donnell and Semlitsch 2015).

The structure and availability of burrows may have also affected the vertical movements, or lack thereof, of salamanders. *Ambystoma* salamanders, with the exception of *A. tigrinum*, cannot create their own burrows and must use burrows made available by small mammals or widen out spaces along root tunnels (Semlitsch 1983). The characteristics of available burrows depend on both behavioral differences between species of small mammals and site specific-soil traits (Reichman and Smith 1990; Laundré and Reynolds 1993; Connor et al. 2010). Replication of this study in other regions or under experimental manipulations of temperature is necessary to determine whether the vertical position selected by salamanders is indeed an artifact of the structure of available burrows.

Alternatively, the narrow range of depths used by salamanders in our study could reflect the vertical distribution of prey. *Ambystoma* salamanders are sit and wait predators that feed primarily on terrestrial macroinvertebrates (Petranka 1998 and references therein). In temperate forests, macroinvertebrate abundance and species richness are higher in the leaf litter than the soil of the forest floor ecosystem (Jacobs et al. 2015). Some species of salamanders are limited by the availability of prey, and in some cases, this effect is stronger than that of burrow availability. In an experimental comparison of the effects of prey availability and burrow availability, Kleeberger (1985) found that *Desmognathus monticola* increased their home range size in response to lower prey density, but not decreased burrow density. Therefore, the selection of shallower burrows may indicate that salamanders are more limited by prey availability than temperature or moisture. Finally, and most simply, the narrow range of depths selected could reflect the temperature preference of salamanders. Although soil surface temperatures ranged over 23.5 °C during this study, the temperatures on days we tracked on had a 10.6 °C range, and the lowest temperature on a tracking day

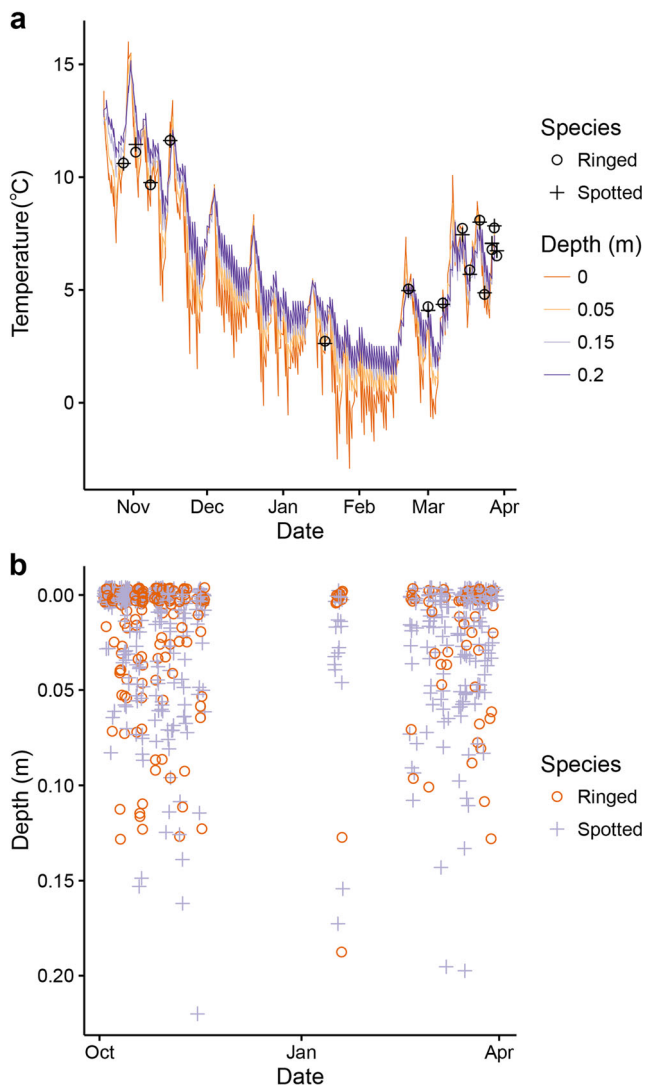


Fig. 6 **a** The profile of soil temperatures at 0, 5, 15, and 20 cm below ground and the mean depth selected by salamanders on that date. **b** The depth (cm) used by salamanders. Each symbol is an individual observation and symbols are horizontally jittered to minimize overlap

was 2.2 °C. Therefore, the use of shallow burrows by salamanders may simply reflect the low variation in temperature on days that salamander positions were measured. We encourage future studies to consider a sampling regime that deliberately tracks over a wide range of temperature to test this hypothesis.

Conclusions By calculating 2D and 3D KDEs, we were able to compare the space use of two salamander species in two habitat types, and concluded that individuals may not partition space vertically. The salamanders in this study were detected using a narrower depth profile than expected, and were most frequently found near the ground surface. Because salamanders selected habitat near the surface, they may be particularly susceptible to management practices that alter local microhabitats, such as prescribed burns and timber harvest when air

temperatures are above freezing. We expect that salamanders also used deeper soil strata beyond the detection range of PIT telemetry (>30 cm below ground). However, future work examining 3D space use by amphibians will be required to further elucidate whether habitat selection, and specifically depth, is a behavioral response to the environment or limited entirely by available refuges.

Future studies of habitat selection for fossorial species should consider collecting data so 3D KDEs can be calculated and compared to 2D KDEs. In this manner, the degree of vertical movement can be rigorously tested rather than assumed not to affect ecological inferences. PIT telemetry may be a useful tool for collecting 3D data, particularly for animals that are too small for radio transmitters or GPS collars. However, the resolution of depth profiles generated by PIT telemetry may be limited to 20–30 cm below the ground surface until antennas with larger detection fields are created.

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Compliance with ethical standards This research complies with the current laws of the USA and was conducted under Missouri Department of Conservation Permits 14922 and 15186 and approved by the University of Missouri Animal Care and Use Committee (7403).

References

- Amarasekare P (2003) Competitive coexistence in spatially structured environments: a synthesis. *Ecol Lett* 6:1109–1122
- Baddeley A, Turner R (2005) Spatstat: an R package for analyzing spatial point patterns. *J Stat Softw* 12:1–42
- Badje AF, Brandt TJ, Bergeson TL, Paloski RA, Kapfer JM, Shuurman GW (2016) Blanchard's cricket frog *Acris blanchardi* overwintering ecology in southwestern Wisconsin. *Herpetol Conserv Biol* 11:101–111
- Banse K, English DC (1999) Comparing phytoplankton seasonality in the eastern and western subarctic Pacific and the western Bering Sea. *Prog Oceanogr* 43:235–288
- Belant JL, Millspaugh JJ, Martin JA, Gitzen RA (2012) Multi-dimensional space use: the final frontier. *Front Ecol Environ* 10:11–12
- Börger L, Dalziel BD, Fryxell JM (2008) Are there general mechanisms of animal home range behaviour? A review and prospects for future research. *Ecol Lett* 11:637–650
- Bouten W, Baaij EW, Shamoun-Baranes J, Camphuysen KCJ (2013) A flexible GPS tracking system for studying bird behaviour at multiple scales. *J Ornithol* 154:571–580
- Burt WH (1943) Territoriality and home range concepts as applied to mammals. *J Mammal* 24:346–352
- Cardillo M, Mace GM, Gittleman JL, Jones KE, Bielby J, Purvis A (2008) The predictability of extinction: biological and external correlates of decline in mammals. *Proc R Soc Lond B* 275:1441–1448
- Connette GM, Semlitsch RD (2012) Successful use of a passive integrated transponder (PIT) system for below-ground detection of plethodontid salamanders. *Wildlife Res* 39:1–6

- Connior MB, Kershner AA, Medlin RE, Elrod DA, Sasse DB, Risch TS (2010) Distribution and habitat attributes of an endemic subspecies of pocket gopher. *Am Midl Nat* 164:217–229
- Cunha AA, Vieira MV (2004) Two bodies cannot occupy the same place at the same time, or the importance of space in the ecological niche. *Bull Ecol Soc Am* 85:25–26
- Curry JP (1994) Grassland invertebrates: ecology, influence on soil fertility and effects on plant growth. Chapman and Hall, London
- Duong T (2007) Ks: kernel density estimation and kernel discriminant analysis for multivariate data in R. *J Stat Softw* 21:1–16
- Earl JE, Zollner PA (2014) Effects of animal movement strategies and costs on the distribution of active subsidies across simple landscapes. *Ecol Model* 283:45–52
- Fournier D, Skaug H, Ancheta J, Ianelli J, Magnusson A, Maunder M, Nielsen A, Sibert J (2012) AD model builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. *Optim Methods Softw* 27:233–249
- Gibbons JW, Andrews KM (2004) PIT tagging: simple technology at its best. *Bioscience* 54:447–454
- Greene KM, Pittman SE, Dorcas ME (2016) The effects of conspecifics on burrow selection in juvenile spotted salamanders (*Ambystoma maculatum*). *J Ethol* 34:309–314
- Grover MC (2000) Determinants of salamander distributions along moisture gradients. *Copeia* 2000:156–168
- Hebblewhite M, Haydon DT (2010) Distinguishing technology from biology: a critical review of the use of GPS telemetry data in ecology. *Philos T Roy Soc B* 365:2303–2312
- Heemeyer JL, Williams PJ, Lannoo MJ (2012) Obligate crayfish burrow use and core habitat requirements of crawfish frogs. *J Wildlife Manage* 76:1081–1091
- Hocking DJ, Rittenhouse TAG, Rothermel BB, Johnson JR, Conner CA, Harper EB, Semlitsch RD (2008) Breeding and recruitment phenology of amphibians in Missouri oak-hickory forests. *Am Midl Nat* 160:41–60
- Jacobs KA, Nix B, Scharenbroch BC (2015) The effects of prescribed burning on soil and litter invertebrate diversity and abundance in an Illinois oak woodland. *Nat Area J* 36:318–327
- Johnson JR, Mahan RD, Semlitsch RD (2008) Seasonal terrestrial microhabitat use by gray treefrogs (*Hyla versicolor*) in Missouri oak-hickory forests. *Herpetologica* 64:259–269
- Kane DL, Hinkel KM, Goering DJ, Hinzman LD, Outcalt SI (2001) Non-conductive heat transfer associated with frozen soils. *Glob Planet Chang* 29:275–292
- Kleeberger SR (1985) Influence of intraspecific density and cover on home range of a plethodontid salamander. *Oecologia* 66:404–410
- Kleeberger SR, Werner JK (1982) Home range and homing behavior in *Plethodon cinereus* in northern Michigan. *Copeia* 1982:409–415
- Kleeberger SR, Werner JK (1983) Post-breeding migration and summer movement of *Ambystoma maculatum*. *J Herpetol* 17:176–177
- Laundré JW, Reynolds TD (1993) Effects of soil structure on burrow characteristics of five small mammal species. *West N Am Naturalist* 53:358–366
- Laver PN, Kelly MJ (2008) A critical review of home range studies. *J Wildlife Manage* 72:290–298
- Liebgold EB, Jaeger RG (2007) Juvenile movements and potential inter-age class associations of red-backed salamanders. *Herpetologica* 63: 51–55
- Lindstedt SL, Miller BJ, Buskirk SW (1986) Home range, time, and body size in mammals. *Ecology* 67:413–418
- Loredo I, Van Vuren D, Morrison ML (1996) Habitat use and migration behavior of the California tiger salamander. *J Herpetol* 30:282–285
- Marzluff JM, Millspaugh JJ, Hurvitz P, Handcock MS (2004) Relating resources to a probabilistic measure of space use: forest fragments and Steller's jays. *Ecology* 85:1411–1427
- Middleton AD, Kauffman MJ, McWhirter DE, Cook JG, Cook RC, Nelson AA, Jimenez MD, Klaver RW (2013) Animal migration amid shifting patterns of phenology and predation: lessons from a Yellowstone elk herd. *Ecology* 94:1245–1256
- Morales JM, Moorcroft PR, Matthiopoulos J, Frair JL, Kie JG, Powell RA, Merrill EH, Haydon DT (2010) Building the bridge between animal movement and population dynamics. *Philos T Roy Soc B* 365:2289–2301
- Nussbaum SE, Ousterhout BH, Semlitsch RD (2016) Agonistic behavior and resource defense among sympatric juvenile pond-breeding salamanders. *J Herpetol* 50:388–393
- O'Donnell KM, Semlitsch RD (2015) Advancing terrestrial salamander population ecology: the central role of imperfect detection. *J Herpetol* 49:533–540
- O'Donnell KM, Thompson FR, Semlitsch RD (2015) Partitioning detectability components in populations subject to within-season temporary emigration using binomial mixture models. *PLoS One* 10: e0117216
- O'Donnell KM, Thompson FR, Semlitsch RD (2016) Prescribed fire alters surface activity and movement behavior of a terrestrial salamander. *J Zool* 298:303–309
- Osborn MS, Connette GM, Semlitsch RD (2014) Effects of fine-scale forest habitat quality on movement and settling decisions in juvenile pond-breeding salamanders. *Ecol Appl* 24:1719–1729
- Ousterhout BH, Liebgold EB (2010) Dispersal versus site tenacity of adult and juvenile red-backed salamanders (*Plethodon cinereus*). *Herpetologica* 66:269–275
- Ousterhout BH, Semlitsch RD (2014) Measuring terrestrial movement behavior using passive integrated transponder (PIT) tags: effects of tag size on detection, movement, survival, and growth. *Behav Ecol Sociobiol* 68:343–350
- Ousterhout BH, Semlitsch RD (2016) Non-additive response of larval ringed salamanders to intraspecific density. *Oecologia* 180:1137–1145
- Peterman WE, Locke JL, Semlitsch RD (2013) Spatial and temporal patterns of water loss in heterogeneous landscapes: using plaster models as amphibian analogues. *Can J Zool* 140:135–140
- Petranka JW (1998) Salamanders of the United States and Canada. Smithsonian Institution Press, Washington, DC
- Pittman SE, Osborn MS, Semlitsch RD (2014) Movement ecology of amphibians: a missing component for understanding population declines. *Biol Conserv* 169:44–53
- Powell RA, Mitchell MS (2012) What is a home range? *J Mammal* 93: 948–958
- R Core Team (2016) R: a language and environment for statistical computing, version 3.3.0. R Foundation for Statistical Computing, Vienna <http://www.R-project.org>
- Reichman OJ, Smith SC (1990) Burrows and burrowing behavior by mammals. In: Genoways HH (ed) *Current Mammology*. Plenum Press, New York, pp 197–244
- Rosenberg DK, Noon BR, Megahan JW, Meslow EC (1998) Compensatory behavior of *Ensatina eschscholtzii* in biological corridors: a field experiment. *Can J Zool* 76:117–133
- Rothermel BB, Luhring TM (2005) Burrow availability and desiccation risk of mole salamanders (*Ambystoma talpoideum*) in harvested versus unharvested forest stands. *J Herpetol* 39:619–626
- Rothermel BB, Semlitsch RD (2002) An experimental investigation of landscape resistance of forest versus old-field habitats to emigrating juvenile amphibians. *Conserv Biol* 16:1324–1332
- Rothermel BB, Semlitsch RD (2006) Consequences of forest fragmentation for juvenile survival in spotted (*Ambystoma maculatum*) and marbled (*Ambystoma opacum*) salamanders. *Can J Zool* 84:797–807
- Ryan KJ, Calhoun AJK (2014) Postbreeding habitat use of the rare, pure-diploid blue-spotted salamander (*Ambystoma laterale*). *J Herpetol* 48:556–566
- Schabetsberger R, Jehle R, Maletzky A, Pesta J, Sztatecsny M (2004) Delineation of terrestrial reserves for amphibians: post-breeding

- migrations of Italian crested newts (*Triturus C. carnifex*) at high altitude. *Biol Conserv* 117:95–104
- Seaman DE, Millspaugh JJ, Kernohan BJ, Brundige GC, Raedeke KJ, Gitzen RA (1999) Effects of sample size on kernel home range estimates. *J Wildlife Manage* 63:739–747
- Semlitsch RD (1981) Terrestrial activity and summer home range of the mole salamander (*Ambystoma talpoideum*). *Can J Zool* 59:315–322
- Semlitsch RD (1983) Burrowing ability and behavior of salamanders of the genus *Ambystoma*. *Can J Zool* 61:616–620
- Semlitsch RD, Bodie JR (1998) Are small, isolated wetlands expendable? *Conserv Biol* 12:1129–1133
- Semlitsch RD, Pechmann JHK (1985) Diel pattern of migratory activity for several species of pond-breeding salamanders. *Copeia* 1985:86–91
- Semlitsch RD, Anderson TL, Osbourn MS, Ousterhout BH (2014) Structure and dynamics of ringed salamander (*Ambystoma annulatum*) populations in Missouri. *Herpetologica* 7:14–22
- Simpfendorfer CA, Olsen EM, Heupel MR, Moland E (2012) Three-dimensional kernel utilization distributions improve estimates of space use in aquatic animals. *Can J Fish Aquat Sci* 69:565–572
- Skaug H, Fournier D, Bolker BM, Magnusson A, Nielsen A (2016) Generalized linear mixed models using AD Model Builder. R package version 0.8.3.3, <http://glmmadmb.r-forge.r-project.org/>
- Spotila JR, Berman EN (1976) Determination of skin resistance and the role of the skin in controlling water loss in amphibians and reptiles. *Comp Biochem Physiol* 55:407–411
- Tilzer MM (1973) Diurnal periodicity in the phytoplankton assemblage of a high mountain lake. *Limnol Oceanogr* 18:15–30
- Tracey JA, Sheppard J, Zhu J, Wei F, Swaisgood RR, Fisher RN (2014) Movement-based estimation and visualization of space use in 3D for wildlife ecology and conservation. *PLoS One* 9:e101205
- Trenham PC (2001) Terrestrial habitat use by adult California tiger salamanders. *J Herpetol* 35:343–346
- Valenzuela-Sánchez A, Harding G, Cunningham AA, Chirgwin C, Soto-Azat C (2014) Home range and social analyses in a mouth brooding frog: testing the coexistence of paternal care and male territoriality. *J Zool* 294:215–223
- Wells KD (2007) *The ecology and behavior of amphibians*. University of Chicago Press, Chicago
- Williams PK (1973) Seasonal movements and population dynamics of four sympatric mole salamanders, genus *Ambystoma*. PhD-thesis. Indiana University, Bloomington