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METHODS

Measuring terrestrial movement behavior using passive integrated transponder (PIT) tags: effects of tag size on detection, movement, survival, and growth

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Abstract Movement behaviors have broad ecological and evolutionary implications, affecting individual fitness, metapopulation dynamics, the distribution and abundance of species, as well as gene flow and thus adaptation and speciation. However, movement behaviors such as dispersal, station keeping, and ranging are poorly understood in many taxa due to the incompatibility of traditional tracking methods with long-term observations. This is particularly true for small-bodied life history stages and species. While the introduction of smaller passive integrated transponder (PIT) tags and the development of PIT telemetry have removed some barriers, the trade-offs between different tag sizes are unknown. Through a series of experiments, we tested for effects of PIT tag size on detection, movement, tag retention, growth, and survival of a juvenile amphibian. We found no effect of PIT tag size on initial movement distance, survival, or growth; and all individuals retained their tag for the course of the experiment. Detection and recapture rates, however, were increased with PIT tag size. The orientation of the tag relative to the vertical axis of the antenna also affected the size of the detection field, which was 15.78–43.90 % smaller when the antenna was moved perpendicular rather than parallel to the long axis of the tag. We conclude that PIT telemetry is a suitable technique for marking previously untraceable species or life history stages and may offer insight into the behaviors of these individuals. Investigations using multiple PIT tag sizes should include this in statistical analyses to account for tag size biased detection differences.

Keywords *Ambystoma annulatum* · Detection depth · Mark–recapture · PIT telemetry · Subterranean tracking

Introduction

Movement behavior is a critical component of ecology, affecting how individuals interact spatially with other organisms and their environment (Nathan et al. 2008). Animals may move to avoid predators, acquire resources (i.e., station keeping and ranging), find mates (i.e., breeding migration), or to escape high conspecific density (i.e., dispersal; Fahrig 2007). Individual movement has broad ecological and evolutionary consequences, including individual fitness, population demography and persistence, metapopulation dynamics, the flow of nutrients through an ecosystem, and the distribution and abundance of species. Movements such as dispersal drive gene flow and thus adaptation and speciation (Hanski et al. 1994; Hanski 1999; Conradt et al. 2003; Bowler and Benton 2005; Clobert et al. 2009; Templeton et al. 2011). Movement studies are unique in their capacity to investigate processes at a variety of levels including individual, population, and community (Clobert et al. 2009). Despite the importance of movement for determining ecological and evolutionary patterns and processes, these behaviors remain poorly understood in many systems. This is particularly true for juvenile life history stages, the dispersing class in many taxa (Bowler and Benton 2005; Semlitsch 2008; Clobert et al. 2009). Until recently, these gaps in knowledge could be attributed to technological limitations. Methodologies were (1) prohibitively expensive, (2) too heavy to use on many species and life history stages, and/or (3) limited to initial movements following release (<1 day).

Some direct tracking methods, such as radio transmitters and satellite telemetry, facilitate detection from a distance for extended time periods in medium- and large-bodied animals.

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Radiotelemetry is ideal for measuring short to moderate movements while satellite telemetry allows researchers to acquire real-time location data for animals during long distance movements (e.g., migration; reviewed in Webster et al. 2002). However, both approaches are expensive and batteries in transmitters sized for small life history stages or taxa such as insects, small bats, or amphibians, are active for less than 3 weeks. Furthermore, satellite radio cannot penetrate water, requiring alternative location calculations (e.g., light levels and Doppler shifts) to make this approach compatible with marine and aquatic species (Hammerschlag et al. 2011). Low-cost techniques like spool tracking and fluorescent powder tracking, are compatible with small individuals and provide detailed measures of fine-scale movements such as perceptual abilities (Zollner and Lima 1997; Pittman 2013), homing (Ousterhout and Liebgold 2010), and resource selection (Roe and Grayson 2008; White and Geluso 2012). However, these approaches are limited by (1) the amount of powder or string attached to the individual and (2) the ability of the researchers to follow tracks, and are best suited to provide detailed data on movement immediately following release for species that move primarily on the surface of the ground.

Indirect approaches to studying movement, such as molecular techniques and biogeochemical markers, provide insight into the landscape level patterns of movement. Recent advances in the development of highly variable genetic markers and high throughput technologies allow researchers to screen many samples and discriminate between individuals within populations (Planes and Lemer 2011). Biogeochemical markers use stable isotope and trace element concentrations in tissues to infer geographical origins and differentiate populations. Stable isotopes are ideal for studying populations which move over distances that have biogeochemical structure, and have been successfully applied to studies of migrations and natal dispersal patterns in marine reptiles, mammals, birds, and fish (Webster et al. 2002; Rubenstein and Hobson 2004). A key limitation of indirect approaches such as parentage analysis and stable isotope markers is that they can only identify patterns, not ecological processes and their underlying behavioral mechanisms.

With the development of portable antenna systems, passive integrated transponder (PIT) telemetry has become a reliable and nondestructive approach to relocate individuals at biologically meaningful spatial and temporal scales (Gibbons and Andrews 2004; Cucherousset et al. 2008; Charney et al. 2009; Connette and Semlitsch 2012). PIT tags, also known as radio-frequency identification (RFID) tags, are electronic microchips encased in biocompatible glass. When activated by a low-energy field produced by a RFID reader, they broadcast a unique code. The battery-less design allows PIT tags to be small (>0.033 g), inexpensive relative to radio transmitters (USD $4–5), and long lasting (>10 years). Monitoring movement with PIT tags is ideal for species with seasonal site fidelity or low vagility. The small size of PIT tags may allow for the detailed and long-term observation of movement behavior in species and juvenile life history stages previously considered too small for tracking (Roussel et al. 2000; Gibbons and Andrews 2004).

While hand-held PIT tag readers (e.g., Biomark Pocket Reader) initially used for mark–recapture studies (e.g., Cunjak et al. 2005) required close proximity to individuals being scanned (<5 cm), PIT tag antennas can detect individuals c.a. 30 cm away (Cucherousset et al. 2005; Cabarle et al. 2007). Fixed location antennas can be installed at locations used daily (e.g., cavity nest [Garroway et al. 2012] or burrow entrance [Rehmeier et al. 2006]) or seasonally (e.g., river stretch used in migration [Drenner et al. 2012]) and remotely monitored using data loggers. An alternative to fixed location antennas are portable antennas. While more labor intensive, PIT telemetry can be conducted through the use of portable antennas, allowing fine-scale movement to be measured on a continuous spatial scale. Although this approach has been predominately used in freshwater ecosystems (Roussel et al. 2000, 2004; Cucherousset et al. 2008; Breen et al. 2009), it has recently been applied to ground-dwelling species, including those which utilize subterranean habitats (Hamed et al. 2008; Steele et al. 2011; Connette and Semlitsch 2012; Suselbeek et al. 2013).

Despite the widespread use of PIT telemetry, there are still basic unknowns in the methodology. Several studies have noted that detection distance will increase with tag size (Bateman and Gresswell 2006; Cucherousset et al. 2010; Connette and Semlitsch 2012; Suselbeek et al. 2013); however, the relationship between PIT tag size and detection distance has yet to be systematically quantified. Furthermore, some authors have noted that tag orientation affects detection range (Baras et al. 2000; Cucherousset et al. 2005, 2008; Connette and Semlitsch 2012), but this has not been tested in a subterranean context.

To inform future studies, we assayed the effects of PIT tag size on survival, growth, and detection of juvenile ringed salamanders (*Ambystoma annulatum* Cope). The ringed salamander is a pond-breeding salamander endemic to the Ozark Plateau (Southern Missouri, Western Arkansas, and Eastern Oklahoma; Petranka 1998). As in other pond-breeding amphibians, the larval stage and reproductive behavior have been well documented. However, aside from components of adult breeding migrations (e.g., timing, orientation, and environmental cues (Madison and Shoop 1970; Semlitsch 1981, 1983; Rittenhouse and Semlitsch 2006; Johnson et al. 2008)), movements and the terrestrial behavior of ambystomatid salamanders have been largely unexplored (Semlitsch 2008). This holds particularly true for recently metamorphosed juveniles, which are too small to support radiotransmitters. Field studies to date have been limited to powder tracking the initial movements of juveniles over short distances (Pittman 2013) and recapturing marked individuals (Osbourn 2012).

We hypothesized that PIT tag implantation would not affect the survival, growth, or initial movement of individuals, and that detection would decrease as depth increased or tag size decreased, and would vary with PIT tag orientation relative to the antenna. In a laboratory experiment, we tested for effects of PIT tag implantation on growth and survival of juvenile salamanders. To determine factors that affect PIT tag detection, we conducted two field experiments. In the first field experiment, we buried tags of different sizes and measured the detection depth at two different antenna orientations. In the second field experiment, we quantified whether the probability of detecting juvenile salamanders varied with tag size or habitat. In this experiment, we also measured the initial movement of individuals to determine if tag size affected movement behavior.

Materials and methods

Retention of PIT tags and survival We selected 27 juvenile salamanders weighing 1.170–1.846 g, which metamorphosed over a 9-day period from a concurrent experiment. These masses are within 1 SD of the mean of all metamorphosed juveniles from that experiment (1.537±0.479 g, mean±1 SD; Ousterhout unpublished data). Salamanders were weighed (Mettler Toledo, LLC, Columbus, OH, USA; ±0.01 g) and immersed in a 1 % solution of tricaine methanesulfonate (MS-222) until they failed to right themselves or respond to stimuli (toe pinching, 7–15 min). After rinsing individuals in deionized water, we measured their snout–vent length (SVL; ±0.01 mm) using digital calipers (Mitutoyo America Corporation, Aurora, IL, USA) and randomly assigned them to a treatment: control ($n=9$), 8 mm PIT tag (8.5×1.4 mm, 0.033 g, full duplex, HPT8, Biomark, Boise, ID, USA; $n=9$) or 12 mm PIT tag (12.5×2.12 mm, 0.115 g, full duplex, HPT12, Biomark, $n=9$). Control individuals underwent the same surgical procedure as the 12 mm group, except the tag was immediately removed following insertion using forceps.

To implant the tag, we used a sterile scalpel blade to make a 3 mm incision to the skin and muscle anterior to the left hind limb, and then used the blade to make a 5 mm subcutaneous incision along the anteroposterior axis, away from the hind limb. We then inserted the assigned tag size and pushed it into the body cavity away from the incision. The implant procedure took <1 min. Following PIT tag implantation, we placed the salamanders on wet sphagnum moss and monitored them until they recovered from the anesthesia and righted themselves (15–59 min). We held all salamanders in the laboratory for 6 weeks in individual plastic containers (17×12×9 cm) on moist sphagnum moss, and fed them cut-up nightcrawler worms (*Lumbricus terrestris*) ad libitum (~2.42 g every other day). Every 6 days, we weighed the salamanders, inspected the incision site, and checked whether PIT tags were retained. We tested the hypothesis that PIT tag size does not negatively affect juvenile growth or survival by conducting a one-way analysis of variance (ANOVA) and a Freeman–Halton exact test, an extension of the Fischer's exact test, respectively. To ensure that treatment groups did not systematically differ in initial size (mass or SVL), we conducted two one-way ANOVAs. Finally, to test the hypothesis that the probability of surviving varied with size, we conducted a Freeman–Halton exact test.

In situ detection and movement To determine if recapture rates of juvenile salamanders varied with PIT tag size, we conducted a field experiment. We implanted individuals with PIT tags as described above, assigning juveniles a 12 mm ($n=109$), 9 mm ($n=14$), or 8 mm ($n=54$) tag based on their mass (12 mm, >1.5 g; 9 mm, 1.5–1 g; 8 mm, <1 g). Twenty-four to 48 h following surgery, salamanders were randomly assigned to a habitat type (forest or grassland), and released into a 50×2 m silt fence enclosure. As groups of approximately 60 animals were available, we conducted releases at night following rain (30 juveniles in forest enclosure and 30 in grassland enclosure). We attempted to relocate salamanders for seven consecutive days using a portable RFID system (FS-2001 F-ISO reader and BP portable antenna; Biomark). The antenna was moved over the entirety of the enclosure twice; with the antenna rotated 90° around its vertical axis for the second pass. The number of individuals recaptured each day in each habitat was recorded.

To test the hypothesis that detection would increase with tag size, we used a generalized mixed model to examine the effect of tag size on the proportion of times an individual was recaptured (recaptures/searches). Generalized mixed models utilize Laplace approximation for maximum likelihood estimation of parameters and are robust to designs with uneven sample sizes such as the one in this experiment (Pinheiro and Bates 2000). To account for environmental differences between forest and grassland enclosures and between release groups, we included the factor of habitat and its interaction with tag size and random effect of release group. To test whether tag size affected initial movement distance, we conducted a mixed effects model. Mixed effects models are also robust to uneven sample sizes (Pinheiro and Bates 2000). We included the factor tag size, the covariate habitat, and random effect of release group. To capture initial movement, we used movement over 24 h following release as the response variable and included only individuals that were captured during the first day of tracking for each release group. We fitted both models using the "lme4" package in program R (Bates et al. 2011; R Development Core Team 2012).

PIT tag detection distance To determine whether PIT tag detection varied by tag size, antenna orientation, or distance from antenna, we buried three sizes of tags (HPT8, HPT12, and HPT9: 9×2.12 mm, 0.08 g, full duplex; Biomark) horizontally to the surface, 0–30 cm underground, in 5 cm increments. We then used an RFID system (FS-2001 F-ISO reader and BP portable antenna; Biomark) to detect the tags. To determine the maximum detection field by PIT tag size and depth, we held the antenna facing a constant direction and moved it systematically right to left (parallel to the long axis of the buried PIT tag) through a 40×30 cm grid. At the end of each row, we moved the antenna forward 1 cm (perpendicular to the long axis of the PIT tag) and repeated the process. We moved the antenna through the entire grid for each depth, recording the location of the center of the antenna each time the tag was detected. Maximum detection depth was determined by increasing the depth a PIT tag was buried by increments of 1 cm from last detection depth until a threshold was identified.

We determined the average detection field by moving the antenna towards the buried PIT tag and recording the distance between the antenna and tag at the first detection. The antenna was moved both parallel and perpendicular to the long axis of the PIT tag 10 times at each depth. All trials were conducted with a constant antenna power and current (100 % power, 3.3–3.6 amp). To test whether PIT tag size or orientation relative to the antenna affected detection field size, we conducted an ANOVA. For this test, we used only measurements taken when tags were buried 0–10 cm so that the HPT8 tag was detected at all depths analyzed.

Results

Retention of PIT tags and survival Mean salamander mass and SVL prior to implantation was 1.418±0.175 g and 43.51 ±3.64 mm for the control group, 1.573±0.163 g and 42.86± 0.70 mm for individuals receiving an 8 mm tag, and 1.579± 0.138 g and 43.48±1.89 mm for individuals implanted with a 12 mm tag. There were no statistical differences between groups in initial mass ($F_{2,24}$=0.86, P=0.47) or SVL ($F_{2,24}$= 0.21, P=0.81). Six days following surgery, all but one salamander had healed entirely, with only a small scar apparent. At the conclusion of the 6-week experiment, we observed 100 % tag retention. On average, salamanders from all treatments exhibited an increase in mass (Fig. 1): 46.4±53.17 % (mean±1SD) for the control group, 35.1±47.88 % for the 8 mm group, and 69.5±8.83 % for the 12 mm group. PIT tag implantation had no statistical effect on percent mass gain between treatment groups after the first week ($F_{2,24}$=0.50, P=0.61) or at the conclusion of the experiment ($F_{2,16}$=0.76, P=0.48). While individuals implanted with 12 mm tags had lower survival than other groups (12 mm, 44.4 %; 9 mm, 88.9 %; control, 77.8 %), treatment did not have a statistical effect on likelihood of mortality (P=0.17; Freeman–Halton), nor did initial mass (χ^2=2.31, P=0.41) or SVL (χ^2=0.13, P=0.55).

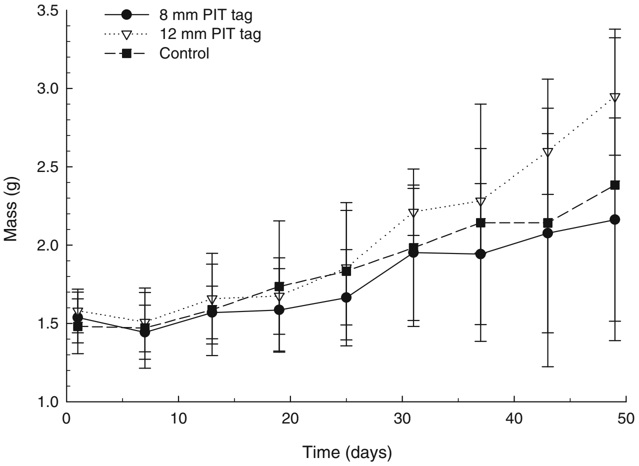

Fig. 1 Comparison of mean salamander body mass (in gram) by PIT tag treatment over time (days). Data points represent treatment means with *error bars* (±1 SD)

In situ detection and movement We released 177 salamanders (group 1, n=59; group 2, n=58; group 3, n=59). Sixty-two percent of these individuals were implanted with a 12 mm tag (n=109), 8 % were implanted with a 9 mm tag (n=14), and 31 % were implanted with an 8 mm tag (n=54). We detected 110 animals 24 h after release. Initial movement distance was not affected by tag size (t=−0.028, P=0.978), habitat (t= −0.246, P=0.807), or their interaction (t=−0.209, P=0.835).

Over a 7-day period, there was a significant increase in individual recapture rate as PIT tag size increased (Fig. 2; GLMM; χ^2=13.63, P=0.001). In seven searches, juveniles with 12 mm tags were detected at a mean of 4.7±2.6 times, individuals with 9 mm tags were detected 4.2±2.9 times, and animals with 8 mm tags were detected 2.9±2.5 times. Habitat type was a significant predictor of detection probability

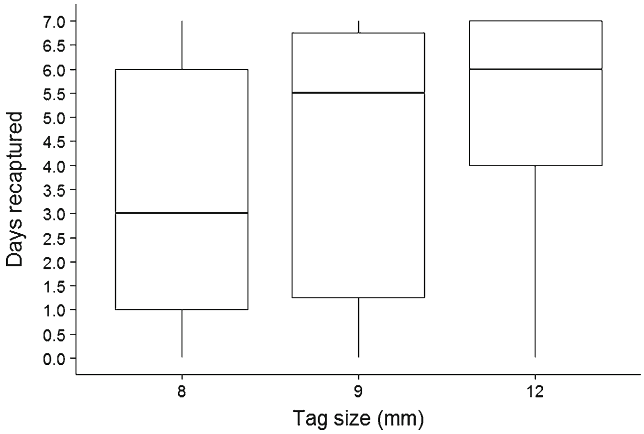

Fig. 2 Number of days individuals were detected (maximum of seven) by PIT tag size. *Center line* treatment medians with *box* equaling mean± 1 quartile. *Whiskers* extend to maximum and minimum values for each treatment

(Fig. 2; χ^2=229.02, P<0.001). On average, we recaptured 81.9±24.7 % of individuals in the forest enclosure each day and 36.4±36.4 % of individuals per day in the grassland. We found no interaction between habitat and tag size (χ^2=2.88, P=0.24).

PIT tag detection distance Both tag size ($F_{2,176}$=98.16, P< 0.001) and orientation ($F_{1,176}$=326.22, P<0.001) affected detection distance. The 12 mm tags had the greatest maximum detection depth (30 cm), but the detection field of 9 mm tags was largest (0.245±0.009 m^2; Table 1 and Fig. 3). Detection distance decreased 15.78–43.90 % when the antenna was perpendicular rather than parallel to the long axis of the tag (Fig. 3).

Discussion

As noted by Nathan et al. (2008), a critical shortcoming in movement research has been the practical limitation in quantifying individual movement and testing underlying mechanisms. This shortcoming has resulted in a bias in movement studies towards adult life history stages at the detriment of understanding processes unique to larval and juvenile stages (e.g., natal dispersal). Previous studies have validated the use of PIT tags in animals (Acolas et al. 2007; Connette and Semlitsch 2012; Garroway et al. 2012), compared the detection range of different antennas (Cucherousset et al. 2005), and measured the detection range of a single tag size (Roussel et al. 2000; Cucherousset et al. 2005; Hamed et al. 2008). Here, we describe the successful use of PIT telemetry to relocate juvenile salamanders and quantify the effect of tag size on relocation probability. In doing so, we demonstrate how PIT telemetry can be used to determine important movement processes in the small-bodied juvenile stage critical to amphibian population persistence (Semlitsch 2008).

During the laboratory experiment, 100 % of PIT tags were retained and all treatment groups gained body mass. In addition to the rapid healing of the incision site, this indicates there may not be long-lasting effects of PIT tag implantation on the growth of juvenile-ringed salamanders. Although there was no statistical difference in likelihood of mortality between treatments, this test had low statistical power, and thus the high mortality in the 12 mm group is of concern. The high mortality could be due complications from being implanted with a larger PIT tag or due to other processes. Given that the 12 mm tag has a much greater volume than the 8 mm tag (44.12 versus 13.08 mm^3), the mortalities may reflect effects of being implanted with a larger tag size. Alternatively, the deaths may be unrelated to the implantation procedure as indicated by the lack of statistical difference between experimental treatments in mortality likelihood.

A heuristic for determining appropriate tag mass has often been <10 % of the animal's body mass (Richards et al. 1994; Murray and Fuller 2000), and this was the standard that we applied in the in situ movement experiment. We found that initial movement distance did not vary with tag size, suggesting that 10 % may be an appropriate rule for juvenile salamanders. By this standard, all individuals in the laboratory experiment were candidates for both tag size treatments. However, Mougey (2009) found that lizards assigned transmitters that were 10 % of their body mass experienced a 28 % reduction in stamina, with a 13 % reduction in stamina when transmitters weighing 5 % of individual mass were used. In fisheries, an even smaller percent of the individual's body mass is suggested (≤3.4 %; Acolas et al. 2007). Although limiting tag mass to 10 % of body mass is the standard for terrestrial vertebrates, we suggest that there may still be subtle effects of tag mass below this threshold.

This is the first experiment to quantitatively test the effects of PIT tag size and orientation on detection range and recapture probability. We detected 80 % of PIT tagged individuals in at least one survey. This rate was comparable to other field studies with salamanders (e.g., 100 % in Connette and Semlitsch 2012, 63 % in Connette and Semlitsch 2013), and notably better than studies which relied entirely on direct observations of marked individuals (e.g., 4–15 % in Osbourn et al. in review (Effects of fine-scale forest habitat quality on movement behavior and settling decisions in juvenile pond-breeding salamanders); 15 % in Marsh et al. 2004). We found noticeable differences in detection field due to both tag size and antenna orientation. Furthermore, our study demonstrates a significant relationship between PIT tag size and the probability of recapturing an individual. To maximize detection in field studies where individual distance from antenna will vary,

Table 1 Mean and maximum detection distance and area by tag size. Maximum depth (in centimeter) at which the PIT tag was detected is in parentheses. Parallel and perpendicular refer to the location of the antenna along the long axis of the PIT tag

		Parallel distance (cm)			Perpendicular distance (cm)			Detection area (cm^2)		
Tag size (mm)	Max depth	Mean	SD	Max	Mean	SD	Max	Mean	SD	Max
8	16	23.4	7.0	24 (10)	3.7	7.9	18 (10)	1,666.1	39.0	1,722 (0)
9	24	24.3	10.8	33 (10)	10.6	12.5	20 (10)	2,449.0	90.5	2,597 (10)
12	30	24.5	15.6	36 (15)	10.0	9.9	25 (0)	2,025.1	475.1	2,380 (0)

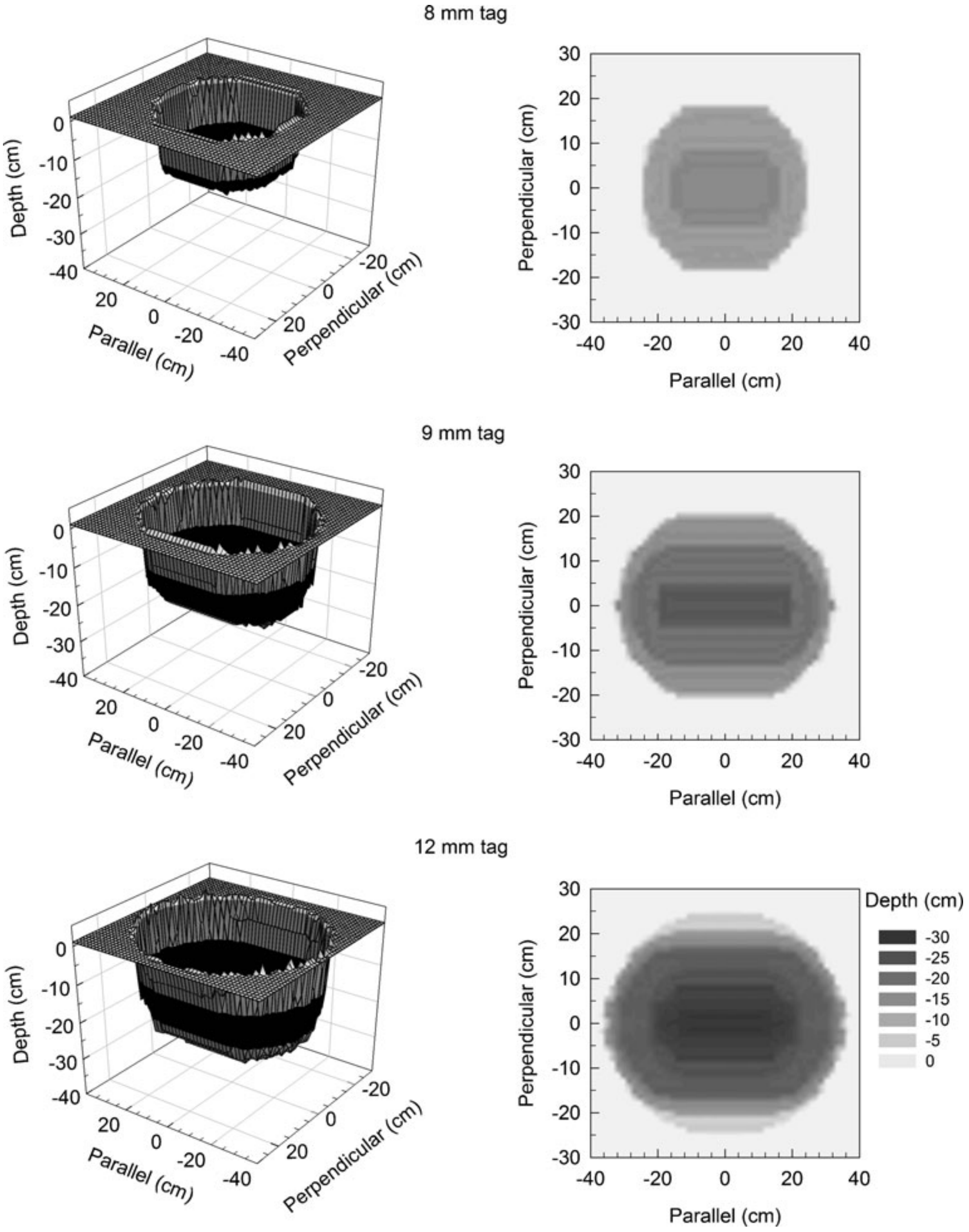

Fig. 3 Three-dimensional representation of maximum detection range by PIT tag size. Perpendicular and parallel refer to movement of the antenna relative to the long axis of the PIT tag, and depth (in centimeter) is the distance underground the tag was buried. Mesh plots (*left*) highlight difference in detection volume and contour plots (*right*) demonstrate differences in detection area

we suggest that the largest appropriate PIT tag size be used. If multiple tag sizes are used within a study, the differences in detection probability stemming from this variation must be accounted for in analyses. In all cases, detection distance, and therefore recapture probability, can be increased by checking all areas with the antenna oriented in both possible directions (i.e., antenna rotated 90° around its vertical axis). These limitations in detection distance may account for the lower recapture probability in field habitats as compared to forests. Ambystomatid salamanders are fossorial and will often use small mammal burrows underground (Petranka 1998). While the forests have limited understory, allowing the antenna to be moved immediately next to the surface of the ground, the fields are thick with grass, often forcing the antenna >10 cm above the surface, limiting the detection of subterranean individuals. Alternatively, forests may have a preferable microclimate, allowing salamanders to remain near the surface rather than using deep burrows for cooler temperatures and increased moisture.

Despite the availability of increasingly small tags, tracking using PIT tags remains a novel approach in terrestrial field ecology. Disciplines such as herpetology and mammalogy, which have historically relied upon methods that interrupt movement behavior in the process of assaying it (e.g., pitfall traps, drift fences, and trap lines), may benefit from PIT tracking. Whether using fixed or portable antennas, tracking using PIT tags allows movement to be measured without interference. Although fixed location antennas provide continuous temporal monitoring, data can be collected on a continuous spatial scale with portable antennas. By allowing the detection of individuals at a distance, PIT tracking may facilitate advances in our understanding of long-term movement behavior, fitness consequences, and population processes of previously unobservable life history stages or species.

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Ethical standards This research complies with the current laws of the United States of America and was conducted under Missouri Department of Conservation collection permit 14922 and University of Missouri IACUC protocol 7403.

References

Acolas ML, Roussel JM, Lebel JM, Baglinière JL (2007) Laboratory experiment on survival, growth and tag retention following PIT injection into the body cavity of juvenile brown trout (*Salmo trutta*). Fish Res 86:280–284

Baras E, Malbrouck C, Houbart M, Kestemont P, Melard C (2000) The effect of PIT tags on growth and physiology of age-0 cultured Eurasian perch *Perca fluviatilis* of variable size. Aquaculture 185: 159–173

Bateman DS, Gresswell RE (2006) Survival and growth of age-0 steelhead after surgical implantation of 23-mm passive integrated transponders. N Am J Fish Manag 26:545–550

Bates DM, Maechler M, Bolker BM (2012) lme4: Linear mixed-effects models using S4 classes. R package version 0.999999-0. http://cran.r-project.org/package=lme4. Accessed 16 May 2013

Bowler DE, Benton TG (2005) Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. Biol Rev 80:205–25

Breen MJ, Ruetz CR, Thompson KJ, Kohler SL (2009) Movements of mottled sculpins (*Cottus bairdii*) in a Michigan stream: how restricted are they? Can J Fish Aquat Sci 66:31–41

Cabarle KC, Henry FD, Entzel JE (2007) Experimental analysis of RFID antennas for use in herpetological studies using PIT tagged salamanders (*Amybstoma tigrinum*). Herpetol Rev 38:406–409

Charney ND, Letcher BH, Haro A, Warren PS (2009) Terrestrial passive integrated transponder antennae for tracking small animal movements. J Wildl Manag 73:1245–1250

Clobert J, Le Galliard J-F, Cote J, Meylan S, Massot M (2009) Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. Ecol Lett 12:197–209

Connette GM, Semlitsch RD (2012) Successful use of a passive integrated transponder (PIT) system for below-ground detection of plethodontid salamanders. Wildl Res 39:1–6

Connette GM, Semlitsch RD (2013) Context-dependent movement behavior of woodland salamanders (*Plethodon*) in two habitat types. Zoology 116:325–330

Conradt L, Zollner PA, Roper TJ, Frank K, Thomas CD (2003) Foray search: an effective systematic dispersal strategy in a fragmented landscape. Am Nat 161:905–915

Cucherousset J, Roussel J-M, Keeler R, Cunjak RA, Stump R (2005) The use of two new portable 12-mm PIT tag detectors to track small fish in shallow streams. N Am J Fish Manag 25:270–274

Cucherousset J, Marty P, Pelozuelo L, Roussel J-M (2008) Portable PIT detector as a new tool for non-disruptively locating individually tagged amphibians in the field: a case study with Pyrenean brook salamanders (*Calotriton asper*). Wildl Res 35:780–787

Cucherousset J, Britton JR, Beaumont WRC, Nyqvist M, Sievers K, Gozlan RE (2010) Determining the effects of species, environmental conditions and tracking method on the detection efficiency of portable PIT telemetry. J Fish Biol 76:1039–1045

Cunjak RA, Roussel J-M, Gray MA, Dietrich JP, Cartwright DF, Munkittrick KR, Jardine TD (2005) Using stable isotope analysis with telemetry or mark–recapture data to identify fish movement and foraging. Oecologia 144:636–46

Drenner SM, Clark TD, Whitney CK, Martins EG, Cooke SJ, Hinch SG (2012) A synthesis of tagging studies examining the behaviour and survival of anadromous salmonids in marine environments. PLoS ONE 7:e31311

Fahrig L (2007) Non-optimal animal movement in human-altered landscapes. Funct Ecol 21:1003–1015

Garroway CJ, Bowman J, Wilson PJ (2012) Complex social structure of southern flying squirrels is related to spatial proximity but not kinship. Behav Ecol Sociobiol 67:113–122

Gibbons JW, Andrews KM (2004) PIT tagging: simple technology at its best. Bioscience 54:447–454

Hamed MK, Leford DP, Laughlin TF (2008) Monitoring non-breeding habitat activity by subterranean detection of ambystomatid salamanders with implanted passive integrated transponder (PIT) tags and radio frequency identification (RFID) antenna system. Herpetol Rev 39:303–306

Hammerschlag N, Gallagher AJ, Lazarre DM (2011) A review of shark satellite tagging studies. J Exp Mar Biol Ecol 398:1–8

Hanski I (1999) Habitat connectivity, habitat continuity, and metapopulations in dynamic landscapes. Oikos 87:209–219

Hanski I, Kuussaari M, Nieminen M (1994) Metapopulation structure and migration in the butterfly *Melitaea cinxia*. Ecology 75:747–762

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

Madison DM, Shoop CR (1970) Homing behavior, orientation, and home range of salamanders tagged with tantalum-182. Science 168:1484–1487

Marsh DM, Thakur KA, Bulka KC, Clarke LB (2004) Dispersal and colonization through open fields by a terrestrial, woodland salamander. Ecology 85:3396–3405

Mougey K (2009) Radio transmitter mass: impacts on home range, daily displacement, and endurance in Texas horned lizards and bearded dragons. Dissertation, Texas Tech

Murray DL, Fuller MR (2000) A critical review of the effects of marking on the biology of vertebrates. In: Boitani L, Fuller TK (eds) Research techniques in animal ecology: controversies and consequences, 2nd edn. Columbia University Press, New York, pp 15–64

Nathan R, Getz WM, Revilla E, Holyoak M, Kadmon R, Saltz D, Smouse PE (2008) A movement ecology paradigm for unifying organismal movement research. Proc Natl Acad Sci USA 105: 19052–19059

Osbourn MS (2012) Initial juvenile movement of pond-breeding amphibians in an altered forest habitat. Dissertation, University of Missouri

Ousterhout BH, Liebgold EB (2010) Dispersal versus site tenacity of adult and juvenile red-backed salamanders (*Plethodon cinereus*). Herpetologica 66:269–275

Petranka JW (1998) Salamanders of the United States and Canada. Smithsonian Institution Press, Wasington

Pinheiro JC, Bates DM (2000) Mixed-effects models in S and S-PLUS. Springer, New York

Pittman SE (2013) The role of juvenile movement behavior in the conservation and management of pond-breeding amphibian populations. Dissertation, University of Missouri

Planes S, Lemer S (2011) Individual-based analysis opens new insights into understanding population structure and animal behaviour. Mol Ecol 20:187–9

R Core Team (2012) R: A language and environment for statistical computing R Foundation for Statistical Computing. Vienna, Austria. http://www.R-project.org/. Accessed 16 May 2013

Rehmeier RL, Kaufman GA, Kaufman DW (2006) An automatic activity-monitoring system for small mammals under natural conditions. J Mammal 87:628–634

Richards SJ, Sinsch U, Alford RA (1994) Radio tracking. In: Heyer WR, Donnelly MA, McDiarmid RW, Hayek LC, Foster MS (eds) Measuring and monitoring biological diversity standard methods for amphibians. Smithsonian Institute Press, Wasington, pp 155–158

Rittenhouse TAG, Semlitsch RD (2006) Grasslands as movement barriers for a forest-associated salamander: migration behavior of adult and juvenile salamanders at a distinct habitat edge. Biol Conserv 131: 14–22

Roe AW, Grayson KL (2008) Terrestrial movements and habitat use of juvenile and emigrating adult eastern red-spotted newts, *Notophthalmus viridescens*. J Herpetol 42:22–30

Roussel J-M, Haro A, Cunjak RA (2000) Field test of a new method for tracking small fishes in shallow rivers using passive integrated transponder (PIT) technology. Can J Fish Aquat Sci 57:1326–1329

Roussel J-M, Cunjak RA, Newbury R, Caissie D, Haro A (2004) Movements and habitat use by PIT-tagged Atlantic salmon parr in early winter: the influence of anchor ice. Freshw Biol 49:1026–1035

Rubenstein DR, Hobson KA (2004) From birds to butterflies: animal movement patterns and stable isotopes. Trends Ecol Evol 19:256–263

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 (2008) Differentiating migration and dispersal processes for pond-breeding amphibians. J Wildl Manag 72:260–267

Steele MA, Bugdal M, Yuan A, Bartlow A, Buzalewski J, Lichti N, Swihart R (2011) Cache placement, pilfering, and a recovery advantage in a seed-dispersing rodent: could predation of scatter hoarders contribute to seedling establishment? Acta Oecol 37:554–560

Suselbeek L, Jansen PA, Prins HHT, Steele MA (2013) Tracking rodent-dispersed large seeds with passive integrated transponder (PIT) tags. Methods Ecol Evol 4:513–519

Templeton AR, Brazeal H, Neuwald JL (2011) The transition from isolated patches to a metapopulation in the eastern collared lizard in response to prescribed fires. Ecology 92:1736–1747

Webster MS, Marra PP, Haig SM, Bensch S, Holmes RT (2002) Links between worlds: unraveling migratory connectivity. Trends Ecol Evol 17:76–83

White JA, Geluso K (2012) Seasonal link between food hoarding and burrow use in a nonhibernating rodent. J Mammal 93:149–160

Zollner PA, Lima SL (1997) Landscape-level perceptual abilities in white-footed mice: perceptual range and the detection of forested habitat. Oikos 80:51–60