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# Efficacy and Uses of PIT Tag Telemetry in Salamanders From the Western USA: *Aneides vagrans*, *Ensatina eschscholtzii*, and *Ambystoma mavortium*

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*Abstract*.—**Mark-recapture studies make use of uniquely marked individuals to answer fine-scale questions about population dynamics, movement patterns, and longevity. Passive integrated transponder (PIT) tags are a popular way to achieve uniquely marked individuals in mark-recapture studies. Additionally, PIT tags may be used for short-range telemetry, to find hidden animals, and to identify animals without capture, facilitating studies of individual movement patterns and longevity. We examined three species that occupy different ecological niches and show the efficacy of PIT telemetry for salamanders in a variety of habitats: Wandering Salamanders (*Aneides vagrans*) occupying a Redwood Forest canopy, Ensatinas (*Ensatina eschscholtzii*) occupying a Redwood Forest floor, and Arizona Tiger Salamanders (*Ambystoma mavortium nebulosum*) occupying sub-alpine ponds in the Colorado Rocky Mountains. We found three advantages to PIT telemetry shared by all three species and habitats: it (1) minimizes destructive sampling; (2) reveals in-situ salamander locations away from cover-objects and traps; and (3) increases possibility of confirming death of individuals in the field. We identified other advantages and some drawbacks of PIT telemetry specific to each population monitored.**

*Key Words*.—canopy, cover object, mark-recapture, plethodontid, Wandering Salamander, Tiger Salamander

## Introduction

Passive integrated transponder (PIT) tags have become common tools in animal research, allowing researchers to mark individuals with a unique, decipherable, and long-lasting identification code (Smyth and Nebel 2013). In addition, PIT tags allow for short-range telemetry to find hidden individuals, and identification of individuals without the need to capture them. PIT telemetry has been used successfully to track tortoises (Boarman et al. 1999) and, more recently, applied to studies of aquatic systems involving fishes (Roussel et al. 2000; Aarestrup et al. 2003; Cucherousset et al. 2005; Skov et al. 2005; Teixeira and Cortes 2007), larval lamprey (Quintella et al. 2005), crayfish (Bubb et al. 2002, 2006), and salamanders (Cucherousset et al. 2009). PIT telemetry was quickly adopted for terrestrial herpetofauna with the origination of portable tag readers and antennae (Lee et al. 2009; Leuenberger et al. 2019; Ryan et al. 2015; Oldham et al. 2016; Ousterhout and Burkhart 2017).

Approaches to studying salamanders via mark-recapture methods have historically used toe clipping (Clarke 1972; Corn and Bury 1991; Donnelly et al. 1994) and, more recently, visual implant elastomer and visible implant alphanumeric tags (Davis and Ovaska 2001; Spickler et al. 2006; Osbourn et al. 2011). Both toe clipping and visual implants have drawbacks that can make long-term identification difficult, such as regeneration of the toes and migration of visual implants; furthermore, neither of these methods allow for remote detection of individuals. By contrast, salamander telemetry has traditionally involved radio-tracking (e.g., Madison 1997; Rittenhouse and Semlitsch 2006; Peterman et al. 2008), limiting its use to relatively large-bodied species. PIT tags, however, have been used successfully both for mark-recapture studies and telemetry in small-bodied plethodontids and juvenile ambystomatids from the eastern U.S. (Connette and Semlitsch 2013, 2015; Ousterhout and Semlitsch 2014; O'Donnell et al. 2016; Ousterhout and Burkhart 2017); importantly, all of these focal species occupy forest floor or aquatic niches, or some combination of the two.

Because of their small size, ease of implantation, longevity, and low cost, PIT tags are a potentially valuable addition to conventional mark-recapture and telemetry approaches for salamanders, but some salamanders, especially plethodontids, inhabit a broad range of habitats (Petranka 1998), each with unique features that could influence the efficacy of PIT telemetry. Although > 200 species of plethodontids are known to climb or occupy elevated niches (McEntire 2016), the use of PIT telemetry in arboreal settings is unknown. Furthermore, different niches feature different substrates and depths of salamander burrowing, but usefulness of PIT telemetry in rocky, montane niches remains undetermined. Exploring these gaps in PIT telemetry facilitates inferences about ecologically distinct salamander species.

We sought to test the efficacy of PIT telemetry for studying movement and survival patterns in salamanders across three distinct ecological niches from the western U.S., with the goal of expanding the application of PIT telemetry in small-bodied herpetofauna with complex niches. We studied the Wandering Salamander (*Aneides vagrans*), an arboreal plethodontid, in the canopy of an old-growth Redwood Forest, the Arizona Tiger Salamander (*Ambystoma mavortium nebulosum*), a facultatively-paedomorphic ambystomatid, in the sub-alpine Rocky Mountains, and Ensatina (*Ensatina eschscholtzii*), a terrestrial plethodontid, in a more stereotypical salamander niche, the floor of an old-growth Redwood Forest. Our objective was to assess the efficacy of PIT telemetry in salamanders from three distinct niches as a complementary approach to traditional mark-recapture methods and radio-tracking, providing information not readily available with other methods. Specifically, we sought to test if PIT tags were safe for small salamanders, and if PIT telemetry would: (1) minimize destructive sampling; (2) reveal in-situ salamander locations away from obvious cover-objects and traps; and (3) confirm death of individuals in the field. Having validated the method, we then explored some of the possible uses of PIT telemetry in expanding our knowledge of movement patterns and survival and making interesting inferences about ecologically distinct species.

## Methods

We previously established the safety of implanting PIT tags into ambystomatids (Whiteman et al. 2016). To confirm the safety of PIT tags for small-bodied plethodontid salamanders, we first conducted a laboratory study using *Ensatina eschscholtzii.* We then deployed PIT tags in wild populations of *E. eschscholtzii*, *Aneides vagrans*, and *Ambystoma mavortium nebulosum*, and tracked their movements and survival over several years.

**Ensatina eschscholtzii: *laboratory test*.**—We captured 30 *E. eschscholtzii* (> 2 g each) from the Arcata Community Forest, Humboldt County, California, USA, in April and May of 2016. We housed animals in individual plastic boxes (23 × 18 × 15 cm) with fitted lids, lined with 3–4 cm of moist EcoEarth (Zoo Med Inc., San Louis Obispo, California, USA). We provided animals with cover objects and maintained under controlled conditions (13°–14° C, 12:12 h light/dark cycle). We fed each salamander two small House Crickets (*Acheta domesticus*) twice weekly and gave them at least two weeks to adjust to captivity before starting the experiment.

We randomly assigned salamanders to control (n = 15) or experimental (n = 15) groups and anesthetized them by immersion in 0.02% benzocaine (Crook and Whiteman 2006). We injected experimental animals intraperitoneally near the 7$^{th}$ costal groove with a 0.05 g, 8-mm long PIT tag using a MK25 implanter (Biomark, Boise, Idaho, USA); we applied a drop of Bactine antibiotic (Bayer, Leverkusen, Germany) to a cotton swab and rubbed it on the incision to prevent infection. We allowed the animals to recover from the anesthetics on a wet paper towel before returning them to their container.

We observed all animals every 1 h for the first 12 h after a tagging event, and then daily for 90 days. We measured mass (in g) weekly and measured snout-vent length (SVL) at the beginning and end of the experiment. After the initial 12 h period, we checked the tag incision sites daily for signs of infection and monitored animals daily for mortality or abnormal behavior, such as lethargy, thrashing, impaired locomotion, or impaired feeding.

**Ensatina eschscholtzii: *field study*.**—We established a 60 × 30 m plot in the Redwood Experimental Forest in Klamath, California, USA, and deployed 20 flat, redwood cover objects (45 × 45 cm) to capture *E. eschscholtzii.* Cover objects were comprised of two boards separated by redwood spacers to create a 1 cm gap between the top and bottom of the cover object (Spickler et al. 2006). From July 2015 to June 2016, we searched for salamanders under cover objects. We scanned all salamanders with a Global Pocket Reader Plus handheld PIT tag reader (Biomark, Boise, Idaho, USA) to determine if they had been marked previously. We measured, weighed, and released previously captured salamanders immediately at the point of capture. We anesthetized, measured, weighed, determined the sex, and injected newly captured individuals with an 8-mm PIT tag (as described above) and visual implant elastomer (VIE; Northwest Marine Technology, Shaw Island, Washington, USA), the latter of which indicated a marked animal in the event of PIT tag loss. We injected a VIE subcutaneously on the lateral side of the base of the tail, using a 0.3 cc insulin syringe with a 9-gauge needle. After recovery on a moist paper towel, we released each animal at the point of capture. We


**Figure 1.** (A) Researcher scanning the forest floor for Ensatina (*Ensatina eschscholtzii*) in the angiosperm understory of the Redwood Experimental Forest near Klamath, California, USA (Photographed by Jim Campbell-Spickler). (B) Researcher scanning the edge of a pond for Arizona Tiger Salamanders (*Ambystoma mavoritum nebulosum*) at the Mexican Cut Nature Preserve, Colorado, USA. (Photographed by Pamela Brown).

captured, PIT tagged, and released 51 Ensatinas.

From July 2016 to January 2017, we sampled in the plot with a Biomark HPR Plus PIT tag reader connected to a Biomark BP Plus portable antenna (Fig. 1). Individual PIT tagged salamanders can be detected up to 30 cm away (Ousterhout and Semlitsch 2014). When an individual was remotely detected, we flagged the capture site. After the first sampling event, we rescanned these flagged locations in the subsequent sampling event. If an individual was not redetected at the flagged location, we scanned the forest floor in 3 m long radiating lines from that point until a full rotation had been made. After surveys for previously detected salamanders were complete, we scanned four random transects in 30 × 4 m belts from north to south across the plot to look for new remote detections, using a random number generator to select the E–W start of the transect (Fig. 2; limitations of battery life prevented survey of the entire plot each visit). Occasionally, we encountered cover boards in transects and scanned them during these

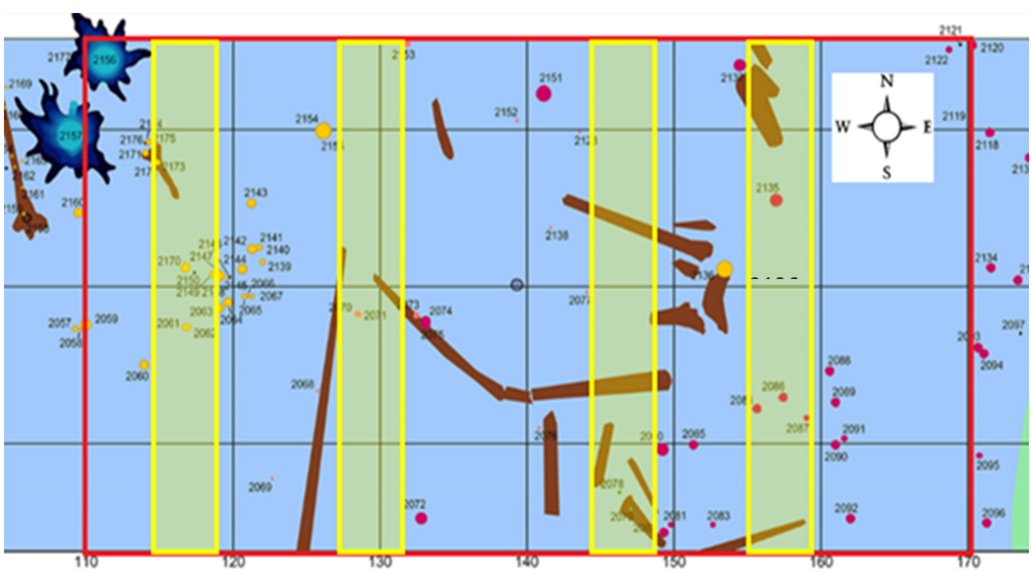


**Figure 2.** Diagram of representative 30 × 4 m belt transects surveyed to search for detected Ensatina (*Ensatina eschscholtzii*). Each vertical rectangle (yellow) represents one belt transect. Four belt transects were surveyed per plot visit due to limitation associated with battery life of PIT tag readers. Belt transects were run starting from random locations along the northern boundary of the plot; this is a representative set of transects, but the exact locations of the four belt-transects changed each survey. All belt transects were conducted within the boundaries of the plot, outlined with the larger, horizontal rectangle (red). Bigleaf Maples (*Acer macrophyllum*), Red Alders (*Alnus rubra*), and Sitka Spruces (*Picea sitchensis*) are represented by the circular polygons (yellow, pink, and blue, respectively) and the oblong polygons (brown) represent downed trees or logs. (Map generated in Excel).

remote detection surveys. We mapped all salamander locations and movements during this period. We used a *t*-test in RStudio (2020) Version 1.3, to compare average net displacement based on sex, because males have been observed moving further and more often than females (Rosenberg et al. 1998; Staub et al. 1995). We also used Logistic Regression for recapture rate on survey method, temperature, and precipitation. After conclusion of the field study (January 2017), we excavated tags that we detected in the same location for the duration of the study to check for animal survival or possible tag rejection. Tag excavation was accomplished by taking handfuls of soil from the area of detection, scanning each handful with a handheld reader, and setting handfuls without the tag aside until the tag was in-hand or a live animal was found; this process took < 5 min. After the initial surveys, we resurveyed this population once every December from 2017–2020.

**Aneides vagrans: *field study.***—Individuals from small populations of these arboreal salamanders may spend their entire lives in the complex crowns of old redwoods, using moist fern mats as refuges (Spickler et al. 2006); consequently, treating a physically linked group of trees as a single mark-recapture plot is reasonable. As such, we considered a pair of old-growth Coast Redwood (*Sequoia sempervirens*) trees with fused bases and interlaced crowns (Fig. 3; trees 2001 and 2002) along with the ground directly below their crowns, to be a mark-recapture plot (Fig. 3). These trees are roughly 120 m west of the previously described plot used for *E. eschscholtzii*, in the Redwood Experimental Forest in Klamath, California, USA. We captured salamanders using 42 (21 in each crown) 45.7 × 45.7 cm saddle-shaped cover objects constructed from 2.54 × 15.2 × 15.2 cm redwood fence boards, with redwood spacers used to create a 1-cm gap between the top and the bottom boards (Spickler et al. 2006). We established cover objects in the crowns of trees 2001 and 2002 in February 2013 for a previous mark-recapture study and they have consistently yielded *A. vagrans* since February 2014. From February 2014 to February 2015, we captured, anesthetized, measured for total length and SVL, weighed to nearest 0.0 g, and marked salamanders with VIEs, and subsequently released the newly tagged salamanders back under their cover objects. We injected VIEs subcutaneously at the antebrachium of one or more limbs, using hundreds of different color-limb combinations to create unique marks and positively identify individuals.

Beginning January 2016, we changed the marking technique from VIE to 8-mm PIT tags. We checked captured salamanders for VIE markers; if an individual was already marked, we anesthetized, measured, weighed, injected a PIT tag (as detailed above for *Ensatina*), and released it immediately at the point of capture. We anesthetized, measured, weighed, and PIT tagged newly captured individuals with no VIE markers applied. After recovery on a moist paper towel, we released each animal at the point of capture. We captured, PIT tagged, and released 20 *A. vagrans* in an old-growth redwood canopy.

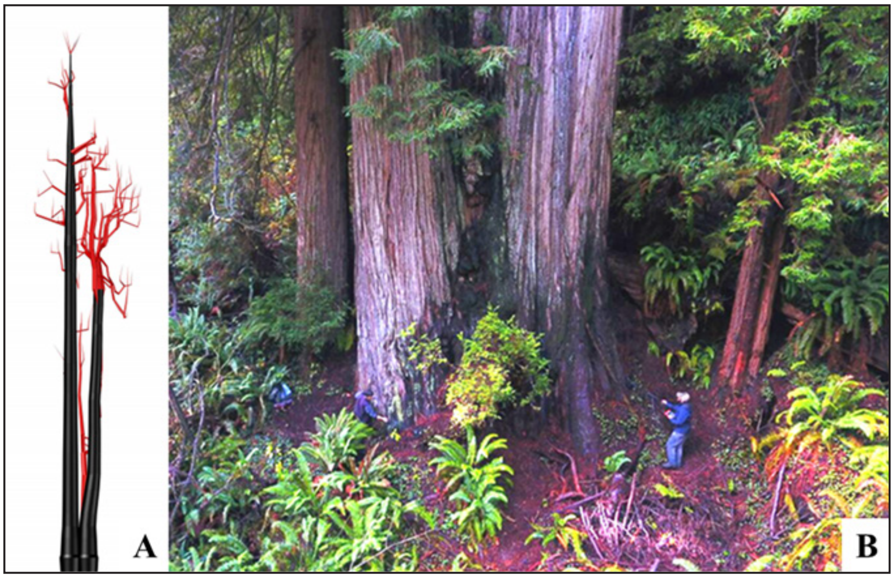


**Figure 3.** (A) Reconstruction of trees 2001 and 2002, a pair of old-growth Coastal Redwood (*Sequoia sempervirens*) trees with fused bases and interlaced crowns; black represents main truck whereas red represents branches and trunk reiterations. Trees 2001 and 2002 grew so closely together that we treated these trees, their crowns, and the forest floor directly below the crowns as a single mark-recapture plot for Wandering Salamanders (*Aneides vagrans*). (B) Researchers scan the base of trees 2001 and 2002 in the *A. vagrans* mark-recapture plot. (Photographed by Jim Campbell-Spickler).

From late January 2016 to December 2018, we conducted 10 redwood crown surveys within the plot searching for tagged *A. vagrans* using a Biomark HPR Plus PIT tag reader connected to a Biomark BP Plus portable antenna. Surveys at the base of these trees were intermittent but occurred at least twice annually. When we detected an individual remotely, we either flagged the capture site or recorded the location of the cover object. We began each survey of a plot by ascending the trees on rope, making sure to rescan detection points from the previous surveys. If an individual was not redetected, we scanned the fern mat or region of last detection; exact dimensions of these scans depend on the size, shape, and range of safely accessible fern mat, but we always attempted to scan the entire mat. We excavated two tags that were detected in the same location for more than a year (which only occurred at the base of the trees) to check for animal survival and possible tag rejection. During tag excavation, we assumed tag loss when we found only a PIT tag; whereas, we assumed animal death when we found both a PIT tag and a VIE within a few centimeters of one another. We used a single Logistic Regression model of recapture rate against survey method, temperature, and precipitation in RStudio (2020) Version 1.3.

**Ambystoma mavortium nebulosum: *field study.***—We studied a population of *A. m. nebulosum* in ponds near the Rocky Mountain Biological Laboratory in Gothic, Colorado, USA, that is currently the subject of a long-term mark recapture study (Wissinger and Whiteman 1992, 2005; Whiteman et al. 2012; Wissinger et al. 2010; Lackey et al. 2019). Because of environmental sensitivity and protective regulations, salamanders from this monitored population traditionally have been detected visually from shore and captured with nets attached to long-handled poles so as not to disrupt the benthic community. This capture method is effective for general sampling, but has several limitations associated with studying within-pond distribution, site fidelity, and movement of individual salamanders. Most notably, capturing one salamander with the traditional nets tends to alert other salamanders nearby. As salamanders escape towards the center of the pond, we are no longer able to measure the natural distribution of salamanders around the edges of the pond. PIT telemetry results in far less benthic disturbance and, if nearby salamanders are flushed from the pond edges, allows researchers to capture multiple PIT tag identification codes simultaneously as they swim by, thus capturing their location.

More than 4,000 Biomark PIT tags have been placed in salamanders in three permanent ponds since 2005 using a technique that is quick, safe, effective, and requires no anesthesia (Whiteman et al. 2016). Based on the size of tiger salamanders, we implanted PIT tags ranging from 8 mm to 12.5 mm, whereas salamanders of the other, smaller species all received 8 mm tags. Many individuals PIT tagged from 2005 to 2020 were still alive and new individuals continue to be tagged each year, so the initial marking effort was (and still is) already in place. In this study, we focused on larval, paedomorphic adult, and metamorphic adult (Whiteman 1994) salamanders that are occupying the ponds: ponds L01, L05, and L12.

In these populations, thermoregulating salamanders make their way to shallow, vegetated thermal zones at the edge of the pond each day (Heath 1975; Fig. 4). We used PIT tag telemetry to correlate thermal zone fidelity and life-history characteristics, such as size (SVL), sex (male, female, or immature), or morph (paedomorphic adult, metamorphic adult, or juvenile), and used GIS mapping to determine if the salamanders were partitioned within habitat based on these characteristics. Thermal zones are shallow areas around the edges of the pond, associated with high midday temperatures and ample aquatic vegetation, where the salamanders spend much of their time during the day.

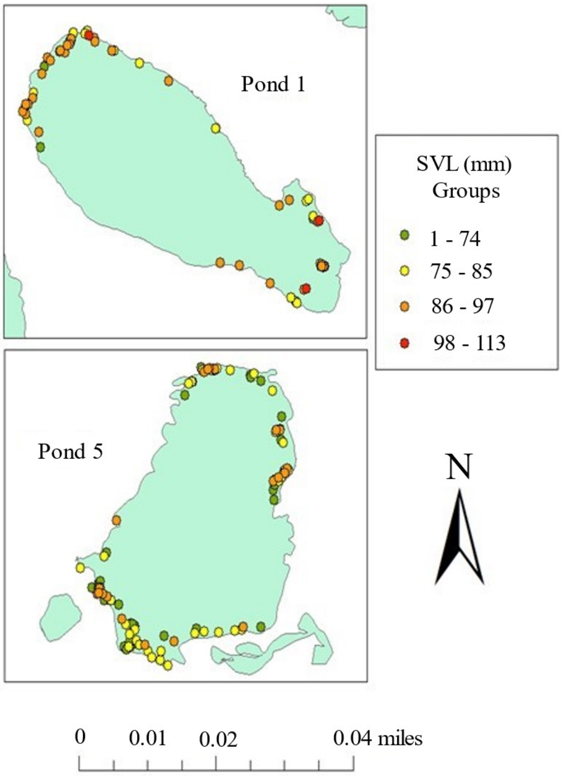


**Figure 4.** Map of salamander locations (points) in ponds L01 and L05 (polygons) of the Arizona Tiger Salamanders (*Ambystoma mavortium nebulosum*) plot near the Rocky Mountain Biological Laboratory, Colorado, USA. Points representing salamander detections are colored according to the snout-vent length (SVL) of the individual salamander detected; color codes for SVL are indicated in the key (upper right). (Map generated in ArcMap).

We walked pond perimeters with the HPR-Plus PIT reader and a BP-Plus portable antenna, scanning the edge of each pond and everything 1 m from the edge of the pond in both directions, covering both the terrestrial and aquatic habitats, submerging the antenna to scan the benthos of the pond (Fig. 1). Importantly, the tag reader is capable of recording a rapid series of different PIT tag numbers and stores the record with date and time. We walked the perimeters of the ponds only once per day and in a single direction to avoid detecting the same individual twice. We recorded pond perimeters, shallow thermal zones, and exact salamander locations with a GEO XT 6000 handheld GPS receiver (Trimble Inc., Sunnyvale, California, USA), which is accurate to 15 cm (Fig. 4). We surveyed each pond once weekly from June-July 2018 for a total of seven surveys per pond, and twice weekly in June 2020 until a total of seven surveys was reached for each pond. Pond surveys lasted approximately 2 h per pond and were always conducted from 1100–1300 or from 1300–1500, timeframes selected based on current and past observations of daily migrations (Heath 1975).

We calculated a rough estimate for within-pond thermal zone fidelity for each salamander and each shallow, thermal zone (4–6 per pond, depending on pond size and benthic topography). Thermal zones are defined by warmer temperatures relative to the rest of the pond and encourage daily salamander migrations from the deeper pond-center to these shallower edges (Heath 1975). We mapped the perimeters of the thermal zones according to obvious visual cues, such as distinct shallow areas abutting the edge of a pond with little to no depth changes, presence of aquatic vegetation protruding from the surface of a pond in these shallow areas, and a clear benthic shelf that drops off towards pond-center where the aquatic vegetation ends. Subtracting the number of surveys in which a salamander was not detected in a given thermal zone by the total number of surveys conducted, and then dividing by the total number of surveys conducted, resulted in a fidelity metric between 0–1.0. Salamanders found in the same thermal zone for all seven surveys earned a fidelity metric of 1.0, whereas salamanders found in a thermal zone only once earned a fidelity metric of 0.14 at that particular zone. For salamanders detected in multiple thermal zones, independent fidelity metrics were calculated for each zone. We used RStudio (2020) Version 1.3, to run regressions of size (SVL measured within the last two field seasons) against our thermal zone fidelity metrics, and used Analyses of Variance (ANOVA) to compare fidelity by sex and morph.

We also scanned the terrestrial habitat around and between all ponds for PIT tagged metamorphic adults. Guided by previous observations of terrestrial metamorphic adults at this sub-alpine site, we focused our scanning on small-mammal burrows (Heath 1975) and other routes between ponds inferred by occasional, spontaneous terrestrial captures. We used landscape topography to find natural low-lying points between ponds and scanned those first, eventually making our way to rocky, upland habitat. When scans around and between the permanent ponds yielded no detections, we scanned the areas around and between the semi-permanent ponds known to host feeding metamorphic adults later in the summer.

## Results

**Ensatina eschscholtzii.—**There was no significant difference between control and experimental groups in initial mass ($t$ = 0.687, df = 27.996, $P$ = 0.498) or SVL ($t$ = -1.19, df = 26.28, P = 0.245). For all salamanders, incision points had healed to the point of scarring after 2 d and we observed no signs of infection, lethargy, thrashing, impaired locomotion, or impaired feeding. At the end of 90 d, there was 100% survival and tag retention. There were slight increases in mass for both control and experimental groups, but implantation of a PIT tag had no significant effect on percentage change in mass ($t$ = 0.332, df = 25.535, $P$ = 0.742). The SVL of both groups was almost unchanged after 90 d, with averages for both groups increasing by < 1 mm.

**Ensatina eschscholtzii.—**We remotely detected 112 PIT tags from July 2016 to January 2017, 77 of which (69%) were away from cover objects. Recapture rate averaged 14% of marked salamanders per plot survey from February 2016 to June 2016 using cover object surveys alone and 22% from July 2016 to January 2017 using PIT telemetry and cover objects combined. The recapture rate of Ensatinas was determined by both survey method ($t$ = 3.695, df = 19, $P$ = 0.002; Fig. 5) and temperature ($t$ = -3.015, df = 19, $P$ = 0.008), but not precipitation ($t$ = 1.987, df = 19, $P$ = 0.064). At the conclusion of the intensive telemetry efforts in January 2017, we found 40 of the 51 tagged individuals (78%) via remote detection, and we found that 95% of those salamanders had moved at least once, thus confirming short-term survival and tag retention (< 1 y). We also found tagged *E. eschscholtzii* during all four of the annual December surveys (2017–2020), confirming survival and tag retention for at least 5 y. During these surveys, we remotely detected 3–5 PIT tagged individuals per survey, a 5–10% recapture rate relative to the number of animals originally tagged and released.

We mapped detection locations and subsequent net displacements to examine Ensatina movement patterns (Fig. 6). Free-ranging salamanders detected in sampling between July 2016 to January 2017 exhibited an average of 2.9 m net displacement per detected location change,

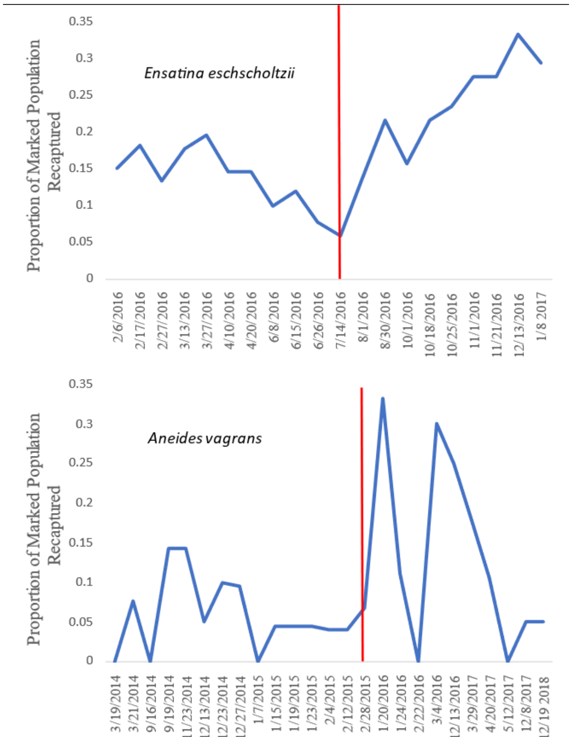


**Figure 5.** Recapture rates of (A) Ensatinas (*Ensatina eschscholtzii*) for 10 cover object surveys and 10 remote detection surveys conducted in the angiosperm understory and (B) Wandering Salamanders (*Aneides vagrans*) for 15 cover object surveys and 10 remote detection surveys conducted in the crowns of old growth Coastal Redwood (*Sequoia sempervirens*) trees 2001 and 2002 of the Redwood Experimental Forest in Klamath, California, USA. Survey dates (mm/dd/yyyy) are listed along the x-axis. The red, vertical lines indicate the transitions from cover object survey to remote detection survey methods.

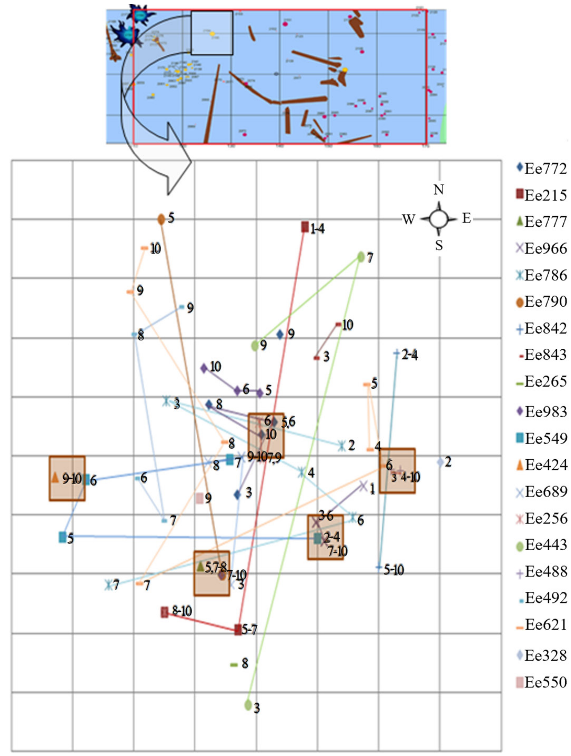


**Figure 6.** Map of locations of Ensatinas (*Ensatina eschscholtzii*) over 10 remote detection surveys. The plot map and arrow (top) show an 8 × 10 m area used by a subset of the marked population from July 2016 to January 2017. We mapped 20 actively recaptured *E. eschscholtzii* in this area to visualize habitat use and movement. Each unique symbol represents a different salamander, each occurrence of a symbol represents a salamander detection location, and the numbers beside each symbol represent the survey number (1–10). Brown, transparent squares represent wooden cover objects used by researchers to initially capture and PIT tag *E. eschscholtzii*. Gridlines are set at 1 m.

with the single longest net displacement recorded at 13.4 m. Average net displacement did not differ based on sex ($t$ = 1.639, df = 80, $P$ = 0.105), and size was too uniform for a meaningful regression. Two salamanders did not move for > 90 d. We found the PIT tags of these two individuals next to the VIEs injected into their tails, which we interpreted as an indication that the salamanders died and decayed at that location leaving the tagging materials behind. From 2017–2020, we excavated two additional PIT tags that remained motionless for 12 mo; however, we did not find any nearby VIE material. We could not determine if the tags were dropped, or the salamanders had died.

Surprisingly, we remotely detected two *E. eschscholtzii* in the lower crown (about 5 m off the forest floor) of a Bigleaf Maple, *Acer macrophyllum* (tree 2136; Fig. 2) in December of 2017. In subsequent surveys that month, we did not detect these salamanders; however, in December 2018, we detected them in the same location and one of them was captured *in situ*. The captured salamander showed no signs of external damage from PIT tag injection, had retained its tail VIE, and had grown in both mass (about 8%) and SVL (about 6%) since tagged 2 y prior. In December of 2019, we recaptured this individual at the base of the tree. In December of 2020, we did not locate either of these salamanders in the maple tree or elsewhere within plot boundaries.

**Aneides vagrans**.—On average, we detected 14% of the marked salamanders per plot survey from January 2016 to December 2018 using PIT telemetry and cover object surveys combined, which is greater than the 8% average detected from February 2014 to February 2015 using cover objects alone. We found that recapture rate of *A. vagrans* was determined by survey type ($t$ = 2.2, df = 24, $P$ = 0.039; Fig. 5) but not temperature ($t$ = -0.163, df = 24, $P$ = 0.872) or precipitation ($t$ = -0.284, df = 24, *P* = 0.779). At the conclusion of the intensive telemetry efforts in December 2018, we recaptured or remotely detected 45% of the 20 PIT tagged individuals. Detections at flagged locations were intermittent, confirming animal movement and short-term survival and tag retention (> 1 y). We continued to detect PIT-tagged *A. vagrans* in the crowns of the same redwood trees as late as December 2018 when the most recent survey was conducted, and we saw no evidence of tag loss in captures without PIT tags.

Of the 20 PIT-tagged *A. vagrans*, we remotely detected two inside the main trunk of a redwood tree. Both of these salamanders later moved, though it was not obvious whether these animals were under bark or deep within crevices. We detected three on the forest floor at the base of the redwood trees in October of 2017. No movement occurred for two of these three tags over a 14-mo period, so we excavated those two PIT tags (as described in Methods) and found their VIE within the same handful of soil, confirming death, in December of 2018. The third tag moved locations between 2017 and 2018 and thus we did not disturb the presumably living salamander.

**Ambystoma mavortium nebulosum**.—Despite our best efforts, we did not detect any PIT tags in the terrestrial habitat in either sampling year; consequently, the following data refer strictly to fully aquatic larval and paedomorphic salamanders occupying permanent ponds. Of hundreds of tagged animals (see discussion below), the average number of remote detections using PIT telemetry was 106 ± 19 (standard deviation) salamanders per pond survey from 2018–2020. In our tests of thermal zone fidelity, the average estimated fidelity was 0.20 for metamorphic adults (ranged from 0.14–0.57), 0.22 for paedomorphs and 0.24 for larvae (ranged from 0.14-0.67 for paedomorphs and juveniles together). We found no significant differences in thermal zone fidelity based on sex ($F_{2,275}$ = 2.09, *P* = 0.126) or morph ($F_{2,325}$ = 1.44, *P* = 0.238). Removing salamanders that were only detected once from the analyses did not change the overall conclusions, suggesting the results of the ANOVAs are robust to the effects of salamanders with few recaptures that could skew site fidelity comparisons. There was a significant but weak negative relationship between SVL and thermal zone fidelity, both when using all animals detected ($r^2$ = 0.02, $F_{1,289}$ = 6.25, *P* = 0.013; Fig. 7) and after removing single-detections ($r^2$ = 0.06, $F_{1,77}$ = 4.74, *P* = 0.033).

At the end of the study in July 2018, 20 individuals had tags that had not moved all summer. Over the course of the summer, it was obvious there were no longer live animals associated with these tags when the water was shallow, perfectly clear, or receded to the point of exposing the tag to desiccation. To confirm death (or possibly tag rejection), we excavated all 20 tags upon conclusion of the 2018 field season.

## Discussion

**Ensatina.—**Our data does not indicate any negative effects of PIT tag implantation on growth and survival in *E. eschscholtzi* and adds to a growing body of evidence indicating that salamanders recover quickly from, and do not suffer loss of body mass following, surgical implantation of PIT tags (Connette and Semlitsch 2012; Ousterhout and Semlitsch 2014). Furthermore, salamanders appear to tolerate tags well. For example, all of the salamanders survived and retained tags for the duration of our study, data which are comparable to those of other laboratory experiments that used PIT tags (Connette and Semlitsch 2012; Ousterhout and Semlitsch 2014), though our results are more robust temporally because they were measured over several years.

Although we found no evidence for tag rejection by *Ensatina eschscholtzii* in the field, we cannot unequivocally state tag loss did not occur because some individuals evaded redetection; however, results from our laboratory study coupled with existing field tests of salamander PIT tag retention (Messerman et al. 2020) suggest that *in situ* tag loss is a rare event (about 3.5 %). The high percentage of *E. eschscholtzii* remotely detected in a wild population from July 2016 to January 2017 and in December 2017–2020 confirm that the technique can be effective for not only short-term (Connette and Semlitsch 2012) but also long-term PIT telemetry studies of terrestrial plethodontid salamanders *in situ*. PIT telemetry can also boost recapture rates compared to traditional visual encounter surveys with VIE, though recapture rates for *Ensatinas* may depend just as much on temperature based on our findings.

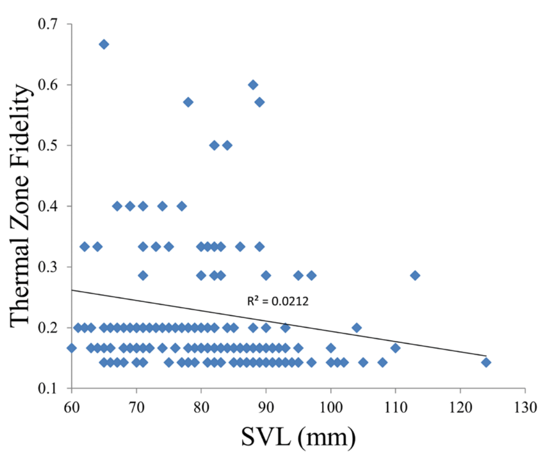


**Figure 7.** The relationship between site fidelity and snout-vent length (SVL) in Arizona Tiger Salamanders (*Ambystoma mavortium nebulosum*).

Our data indicate that *E. eschscholtzii* move only occasionally and in short bouts, which is consistent with findings from previous investigations using traditional visual encounter surveys (Rosenberg et al. 1998; Staub et al. 1995; Wells and Wells 1976). The ability to detect marked animals away from cover objects is an important practical application of PIT tag telemetry. Indeed, remote detection allowed us to locate and capture *E. eschscholtzii* repeatedly in the lower crown (roughly 5 m off the forest floor) of an *A. macrophyllum* tree completely covered in *Isothecium* moss and growing at roughly 45° relative to horizontal. Although *E. eschscholtzii* is known to climb vegetation (McEntire 2016), the seasonal and repeated occupation of lower crown habitat in a hardwood understory tree is surprising.

**Aneides vagrans**.—Although our initial efforts with VIEs were effective in identifying individual *Aneides vagrans*, we faced limitations because we needed to have the animals in-hand to confirm identity and we were unable to find them away from artificial cover objects. Furthermore, VIEs injected into the antebrachium of *A. vagrans* migrated, usually up the brachium and occasionally to the lateral torso of the salamander. PIT tags injected into the body cavity of *A. vagrans* avoid the issue of subcutaneous tag migration towards major appendages that could hinder locomotion. Previous investigations of *A. vagrans* in their canopy niche focused heavily on cover objects placed on fern mats (Spickler et al. 2006). PIT telemetry allowed us to remotely detect salamanders away from cover objects; the most noteworthy of these observations were of *A. vagrans* occupying habitat within the main stems of trees, away from the fern mats entirely.

We detected three (15%) of 20 salamanders PIT tagged in the canopy on the forest floor, supporting previous work that suggests that *A. vagrans* can persist for long periods, possibly entire lifetimes, in the canopy (Spickler et al. 2006). PIT telemetry allowed us to confirm the death of two salamanders detected on the forest floor. Old and complex redwood crowns can support about 30 adult *A. vagrans* (Spickler et al. 2006); consequently, confirmation of death of one individual contributes to our understanding of population dynamics of *A. vagrans* in this unique niche.

One advantage of PIT telemetry specific to salamanders in the redwood canopy relates to temporal limitations on crown monitoring. Year-round monitoring of *A. vagrans* in the redwood forest canopy of our study is prevented because of restrictions to access associated with the use of the canopy for nesting by Marbled Murrelets (*Brachyramphus marmoratus*), a federally listed Endangered species (Spickler et al. 2006). Some of these crowns are now equipped with solar power that can support a stand-alone PIT tag reader to records tags crossing a fixed point (Taylor et al. 2012; Van Harten et al. 2019). This alternative, remote method of data acquisition potentially allows for year-round data collection without disturbing the canopy during murrelet nesting season, and thus has important applications in redwood canopy monitoring.

Our results indicate that PIT telemetry is an effective technique for studying the movement of arboreal salamanders. In the redwood canopy, we found that the PIT tag scanner and antenna can detect tags through both arboreal humus and the main stem of the tree. Arboreal salamanders are not limited to the genus *Aneides* (McEntire 2016); we assume that PIT telemetry would be effective in any arboreal species of appropriate size. For example, several species of *Bolitoglossa* dwell beneath the bark of banana trees and within the bromeliads of tree crowns (Wake and Lynch 1976; Ruano-Fajardo et al. 2014), comparable to *A. vagrans* living under redwood bark and within epiphytic humus mats. Moreover, PIT telemetry should be effective for salamanders in tropical rainforest canopies as is the case in our temperate rainforest canopy.

**Ambystoma mavortium nebulosum.—**We were surprised to not find any PIT tags from *A. m. nebulosum* in the terrestrial habitat surrounding the ponds. Metamorphic adults spend a significant portion of time in a terrestrial environment, including overwintering in mammal burrows (Heath 1975). Although some PIT-tagged salamanders can be detected up to 30 cm away, the distance that salamanders can be detected depends on terrain and animal burrowing behavior. Ambystomatid salamanders in particular are rarely detected from more than 5 cm away in a terrestrial environment (Ousterhout and Burkhart 2017). PIT tags were not used in salamanders in this population until 2005, however, and metamorphic adults in this population are generally longer lived than paedomorphic adults (Lackey et al. 2019). Also, several metamorphic adults in this population marked in the late 1980s are at least 33 y old (unpubl. data). When a toe-clipped metamorphic adults marked before 2005 is captured, no PIT tag is injected; therefore, most of the more than 4,000 PIT tags deployed have been assigned to paedomorphic adults and larger juveniles. Possibly, a lower relative death rate and a skewed PIT tag ratio between metamorphic adults and fully aquatic morphs influences detections. Also, the freezing and thawing of this sub-alpine habitat has important implications for soil erosion and deposition. As over a 1 m of snow melts away each spring, the water rushing down the mountainside leave scours that dry and remain on the landscape through the drier summers. PIT tags from shallow mammal burrows could be swept away with the melting snow or could be buried too deeply for detection by soil scoured out from above. Lastly, the geology of this habitat may have interfered with PIT tag detection. Mammals such as marmots, ground squirrels, and chipmunks often burrows beneath massive boulders in this sub-alpine system; they can be seen consuming plant material or chirping from atop the boulders that surround the ponds. Metamorphic adults, alive or dead, potentially evade detection beneath boulder and rock that make up most of the landscape. Similarly, many of the larger boulders set on steep slopes feature a labyrinth of cracks and crevices and because of the steep terrain, a salamander moving a couple meters back into these cracks would functionally position itself several meters below the surveyable ground and beyond the range of the PIT tag antenna. A number of other nonaquatic salamanders specialize in high-elevation, rocky habitats (e.g., web-toed salamanders, Hydromantes) and rocky caves (e.g., splayfoot salamanders, *Chiropterotriton,* and *Hydromantes*); PIT telemetry may not be effective for such species occupying rocky niches.

PIT telemetry was highly successful in the remote detection and identification of fully aquatic *A. m. nebulosum* occupying permanent ponds. Although thousands of PIT tags have been deployed in ponds L01, L05, and L12 since 2005, we lack data needed to estimate the population size. Nevertheless, our average of 106 detections of salamanders per survey indicates that PIT telemetry is a viable technique to identify salamanders in a short period of time. The ease of recapture allows successful determination of thermal zone fidelity: fully aquatic (larval and paedomorphic) tiger salamanders occupy the same thermal zone 14–67% of the time. The weak relationship ($r^2$ = 0.02–0.06) suggests SVL is not a reliable predictor of thermal zone fidelity in this population; however, any existing negative relationship between SVL and thermal zone fidelity could be explained by the short growing season in the high Rockies and larval preference for warmer water (Heath 1975).

Our data suggest that salamanders cluster near pond edges during the day. Some areas of pond edge (e.g., the east and west sides of pond L05) have little to no detections; whereas, other regions of pond edge (e.g., the north and south sides of pond L05) registered hundreds of detections throughout this study. Data from additional field seasons are needed to determine if individual thermal zone fidelity persists across years and if individuals adjust to different thermal zones as size structure dynamics in the pond change over time (Wissinger et al. 2010; Whiteman et al. 2012).

Fine-scale information on how salamanders use their habitat will allow us to develop hypotheses on their potential response to a rapidly changing climate in the high Rockies. Fully aquatic salamanders are limited in their dispersal, a barrier not uncommon for amphibians. Smaller snowpacks and longer, warmer summers are predicted for alpine wilderness in North America due to climate change (Hall et al. 2008). Drying ponds, shorter hydroperiods, and variable water temperatures are linked frequently to amphibian declines in other systems (Pounds et al. 2006; Rohr and Raffel 2010). The apparent clustering of tiger salamanders in the aquatic habitat potentially affects disease dynamics and we aim to monitor the situation annually. The ability to confirm death at an individual level using PIT telemetry should assist in efforts to recognize and document disease outbreaks.

PIT telemetry allows fine-scale monitoring of *A. m. nebulosum* previously unavailable. This population has been studied since the 1960s, and mark-recapture efforts that began in the early 1990s (Wissinger and Whiteman 1992) continue to this day. This long-term mark-recapture dataset, however, only describes capture location at the scale of the pond (i.e., researchers record which pond each salamander is captured in, but not the specific location within that pond). With PIT telemetry, we are able to detect within-pond locations of fully aquatic individuals using shallow, thermoregulatory areas and record them with a GPS unit. Fine-scale location data enables studying within-pond distribution and thermal zone fidelity of salamanders, potential competition for space in the most optimal thermoregulatory or feeding areas, and behavioral adjustments to environmental changes. Potential drawbacks include a near-shore bias in location data because detection of individuals requires that they are within a few meters of the edge of a pond, and ponds can be deeper than the detection reach of antennae.

***Conclusions***.—We confirmed several practical advantages to incorporating PIT telemetry into ongoing mark-recapture research involving salamanders, but more importantly it provides insight into the efficacy of PIT telemetry in three distinct ecological niches and for salamanders with unique natural histories. The ability to remotely detect salamanders underground and underwater, to glean information about where salamanders spend their time while away from cover-objects and traps, and to confirm death of specific individuals opens the door to investigations of habitat use and movement patterns at finer scales. Given that PIT tags are encased in glass and do not require a power source, PIT telemetry could also expand the temporal range of mark-recapture studies using salamanders. PIT telemetry has the potential to enhance mark-recapture studies of small-bodied amphibians, to reduce the level of disturbance associated with drift fences, pitfall traps, stump ripping, log flipping, and other popular herpetological mark-recapture survey techniques, and to eliminate the need for bulky transmitters, belts, and collars. A considerable drawback to incorporating PIT tags compared to marking with VIE or toe-clipping was the initial cost associated with purchasing detection equipment; however, in our experience this is a one-time expense. Another notable drawback of PIT telemetry is that unmarked animals cannot be detected and thus the approach is not suitable for standard mark-recapture designs that estimate population size and density unless coupled with explicit searches for unmarked animals. Furthermore, even the smallest PIT tags currently available are too large for some species and life stages of salamander.

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