ACTIVITY PATTERNS OF THE DEL NORTE SALAMANDER (*PLETHODON ELONGATUS)*: MONITORING PLETHODONTID BEHAVIOR USING PIT TAG SURVEYS

By

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ABSTRACT

ACTIVITY PATTERNS OF THE DEL NORTE SALAMANDER (*PLETHODON ELONGATUS*): MONITORING PLETHODONTID BEHAVIOR USING PIT TAG SURVEYS

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Semi-fossorial plethodontid salamanders exhibit behavioral plasticity to avoid desiccation, retreating underground to shelter from adverse conditions such as low precipitation and high temperatures. In this study, I used passive integrated transponder (PIT) tag surveys to monitor this behavior in the Del Norte salamander (*Plethodon elongatus*), a small plethodontid native to northwestern California and southwestern Oregon. Within its range, a climatic gradient exists in which coastal areas experience milder temperatures and high precipitation, while inland areas tend to have colder winters, hotter summers, and lower precipitation. By monitoring the activity patterns of this species in inland and coastal areas, I aimed to observe which environmental variables had the greatest impact on the detection of individuals within the detectable range of the PIT tag antenna (~10 cm underground). Using this method, I obtained a 61.4% overall re-detection rate, compared a 17% recapture rate of above ground salamanders.

The likelihood of detecting *P. elongatus* was significantly related to temperature, with the odds of making a detection increasing by 7.2% for every one-degree Celsius increase in ambient temperature. Relative humidity was also significantly associated with detection, with the odds of making a detection increasing by 12.3% for every one percent increase in humidity. Canopy cover and cloud cover were not significantly related to detection odds. Detection likelihood did not vary based on the body mass index or sex of each individual.

Portable PIT tag antenna surveys are significantly less labor intensive than traditional amphibian monitoring techniques and are minimally invasive after the initial tag insertion. Using this method allows for direct monitoring of individual salamanders over time, including near-surface level activity that would be impossible to observe with traditional methodologies. Given that climate projections predict rising temperatures within the range of *P. elongatus*, monitoring the species' activity patterns under current climate conditions can help predict how the species may respond to future climate conditions.

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INTRODUCTION

Amphibians have been widely used as “indicator species” because of their high sensitivity to environmental changes (Davic & Welsh, 2004; Estes-Zumpf et al., 2022; Gade & Peterman, 2019; Hager, 1998). Their thin, highly permeable skin makes them especially vulnerable to threats like environmental contamination, climate shifts, and habitat degradation (Lillywhite, 1975). Despite their sensitivity to environmental conditions, amphibians have evolved various adaptations to survive in harsher environments, as well as behavioral responses to help them avoid environmental stressors.

As amphibian populations worldwide are facing declines (Blaustein & Wake, 1990; Collins & Storfer, 2003; Kiesecker et al., 2001), monitoring population size to assess population and ecosystem health has become a common part of ecosystem management efforts (Harpole & Haas, 1999; Jung et al., 2000; Romano et al., 2017). Behavior is another useful indicator of population health, and deviations from expected behavioral patterns can alert us to changes in the environment or other potential stressors (Bailey et al., 2004; Hamed et al., 2008; Rissler et al., 2000). The activity patterns of lungless salamanders (Family Plethodontidae) are highly dependent on environmental conditions, making them ideal candidates for behavioral monitoring, but technological limitations have long made direct monitoring of small, fossorial amphibians challenging. Most plethodontids are terrestrial as adults and exhibit direct development of their young, meaning hatchlings emerge in a fully metamorphosed, terrestrial form rather than as aquatic larvae. This terrestrial lifestyle reduces their reliance on bodies of water, allowing them to inhabit a wider range of habitats than amphibians with an aquatic life stage. However, they are still highly dependent on moisture in their environment and spend significant amounts of time underground to avoid low moisture conditions (Feder, 1983; Grover, 1998; Keen, 1984). With recent technological advances, we can begin to observe the subterranean behavior patterns of these small salamanders and learn more about the drivers and effects of their activity patterns.

Osmoregulation is among the greatest challenges faced by terrestrial amphibians, and their reliance on moisture has significant impacts on their ecology, physiology, and behavior. Amphibians rely on cutaneous respiration, exchanging respiratory gases through their skin, either to supplement or replace gas exchange through the lungs and buccopharyngeal cavity. Cutaneous gas exchange requires that amphibian skin be highly permeable, which means resistance to evaporative water loss in terrestrial amphibians is negligible, ranging from ten to 3,000 times lower than that of other tetrapods (Lillywhite, 2006). In addition, they have a greater need to avoid water loss than most other animals, because they cannot conduct cutaneous gas exchange if their skin dries out (Feder & Burggren, 1985). The threat of desiccation is even more acute for plethodontid salamanders because they rely primarily on cutaneous respiration to conduct gas exchange, due to their lack of lungs. Terrestrial plethodontids live mostly in humid regions because they desiccate more readily than most animals and suffer increased metabolic and respiratory repercussions if they do dry out (Duellman, 1999). Even in those humid areas, exposure to open air will cause them to lose moisture through their skin over time (Ray, 1958).

Driven by these osmoregulatory challenges, salamanders have developed behavioral responses to avoid desiccation (Grover, 1998). When conditions are moist enough, salamanders can be active on the surface, but when it is too dry, they retreat underground or beneath cover objects to avoid desiccation. Due to their low metabolic rate, many plethodontids can stay in these refuges for months at a time without risking starvation, and they are known to increase their refuge use as the moisture levels in their habitat decrease (Feder, 1983; Keen, 1984). This behavioral plasticity may help plethodontids cope with environmental changes, increasing their refuge use to avoid desiccation when conditions are unfavorable (Gunderson & Stillman, 2015; Muñoz et al., 2016; Riddell et al., 2018; Urban et al., 2014). However, increased refuge use has repercussions, decreasing the amount of time available for foraging and finding mates. For plethodontids, prolonged use of refuges is often associated with decreased body size and general well-being, as well as a lower reproductive rate (Bickford et al., 2010; Reading, 2007; Sheridan & Bickford, 2011). To fully understand the limitations of this sheltering strategy and which factors have the greatest influence on plethodontid activity, we can use newly available methods to monitor the activity of individual salamanders over time.

In situ tracking of small salamanders has only recently become possible with the development of small enough microchip tags. Therefore, relatively little is known about the year-round activity patterns of these animals, particularly those with a partially fossorial lifestyle. Traditional trapping and survey methods for terrestrial salamanders are limited to detecting salamanders that are active on the surface level, and mark-recapture methods can be heavily biased against individuals that are “trap shy” (Marsh & Goicochea, 2003). New monitoring techniques using passive integrated transponder (PIT) tags coupled with remote detection antennas have the potential to help us understand salamander activity patterns in greater detail by allowing us to locate tagged individuals even when they are underground (Connette & Semlitsch, 2012, 2015). With relatively little additional work, existing sampling techniques can be expanded to include PIT tagging of individuals, and subsequent surveys conducted with remote sensing antennas are significantly less invasive than traditional survey methods.

While other studies have shown that using PIT tags for the remote detection of underground individuals is possible, little work has been done applying this method to an observational field study (Connette & Semlitsch, 2012, 2015; Ryan et al., 2014). Only one other study has utilized this methodology to study plethodontids in western North America (Brown, 2017). In the present study, I used a portable PIT tag antenna to track the position of individual salamanders over time, allowing detection of even subterranean individuals within a depth range of approximately 10 cm below ground (Ousterhout & Semlitsch, 2014). Previous work has also shown that the use of PIT tag surveys using a portable PIT tag antenna increases overall recapture rates when compared with more traditional cover object searches (Brown, 2017; Connette & Semlitsch, 2012; Ousterhout & Semlitsch, 2014). I used this novel technology to investigate how detections of Del Norte Salamanders might be influenced by a variety of environmental conditions.

Plethodon elongatus (Del Norte Salamander) is a plethodontid salamander found in northwestern California and southwestern Oregon, where it occurs mostly in old-growth forests (Stebbins, 2003; Welsh & Lind, 1995). Only in the moist, coastal parts of its range can it sometimes be found in second-growth forests, indicating that water availability, in addition to forest age, likely plays a key role in the species' ability to thrive (Welsh & Lind, 1995). The species is currently listed as “Near Threatened” by the IUCN, and as a “watch list” species by the California Department of Fish and Wildlife (Hammerson & Welsh, 2004; Thomson et al., 2016). A major threat to *P. elongatus* is a lack of suitable habitat, largely due to deforestation (Bolsinger & Waddell, 1993; Karraker & Welsh, 2006; Raphael, 1988). Throughout its relatively small range, climate change is predicted to cause higher temperatures and prolonged droughts (Diffenbaugh et al., 2015) that would result in increased evaporative water loss and a higher risk of desiccation for these salamanders.

The goal of this study was to monitor the small-scale movements and seasonal activity trends of individual *P. elongatus*, as well as to determine what factors may have an impact on these behaviors. By conducting surveys of *P. elongatus* at several sites for over a year using a portable PIT tag antenna, I was able to locate individuals even if they were under cover objects or underground but still within the antenna’s detection range (~10 cm). Because fossorial salamanders typically retreat deeper underground as conditions become less favorable, I hypothesized that:

1. Salamanders would be detected less frequently in conditions that pose a greater risk of desiccation (i.e., high temperatures, low precipitation).

2. Salamanders from inland sites would be detected less frequently than those from coastal sites because they would be subjected to unfavorable conditions more often than coastal individuals.
3. Individuals located in areas without significant canopy cover would be detected less frequently than those in heavily canopied areas, which tend to retain soil moisture longer and offer protection from direct sunlight (Harpole & Haas, 1999).
4. Inland salamanders would have lower body mass index values than coastal salamanders, due to the harsher environmental conditions associated with inland sites.

By observing how detection patterns are correlated with environmental factors, I aimed to learn more about the driving forces of *P. elongatus* behavior patterns and seasonal activity patterns, and to test the utility of PIT tag surveys in documenting subterranean behaviors.

METHODS

Study Sites

I located potential sites using reported observations of *P. elongatus* from the California Department of Fish and Wildlife's Natural Diversity Database (California Department of Fish and Wildlife, 2019) and locality data from museum specimens, and then conducted cover object searches at each site to confirm the species was still present. Within the range of *P. elongatus*, the climate in coastal areas is characterized by heavy winter rains and foggy summers, whereas inland areas tend to experience warmer, drier summers and colder winters (Table 1). In order to examine how these regional-level climate differences might impact the behavior of *P. elongatus*, I chose an equal number of sites within the inland and coastal regions. Coastal sites were located in Redwood National Park and inland sites were located in the Six Rivers National Forest.

Table 1. Summary of average climate conditions in the areas containing the study sites. Monthly averages for high and low temperatures and high and low precipitation were based on measurements taken 1981-2010 (U.S. Climate Data, 2021).

Area	Highest Temperatures (°C)	Lowest Temperatures (°C)	Highest Precipitation (cm)	Lowest Precipitation (cm)
Redwood NP South (Orick, CA)	20.6 (August/September)	2.2 (December)	34.0 (December)	0.8 (July)
Redwood NP North (Klamath, CA)	19.4 (July – September)	2.8 (December)	34.0 (December)	0.9 (July)
Six Rivers NF (Willow Creek, CA)	35.0 (July)	1.7 (January/February)	29.9 (December)	0.6 (July)

Sites ranged in size but did not exceed roughly one km in diameter. I initially planned to choose four to five sites within each region, but ultimately was only able to locate three sites in each region that contained large enough populations of *P. elongatus*, for a total of six sites (Figure 1, Table 2).

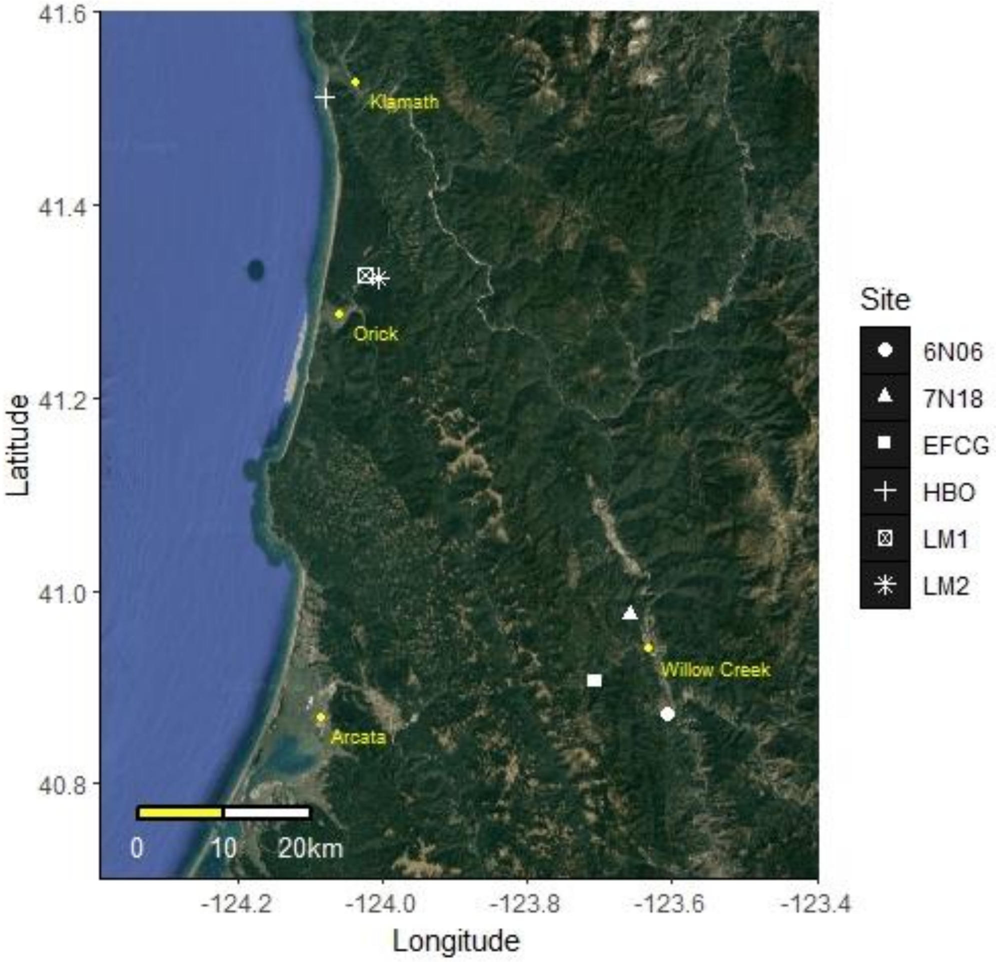


Figure 1. Map of site locations, located within Humboldt and Del Norte counties in Northern California. Sites 6N06, 7N18, and EFCG were classified as "inland," while sites HBO, LM1, and LM2 were considered "coastal." For detailed site maps showing the location of tagged salamanders at each site, see Appendix A.

Table 2. Study site details. Coordinates for each site are given as decimal degrees, using a point at the approximate center of the site area. A representative area of each site is pictured, along with an overview of key site characteristics.

Site	Description	Photo
High Bluff Overlook (HBO) 41.51164 °N, 124.08033 °W	A large pit filled with rocky debris, located within the overlook area in Redwood National Park. Area is completely unshaded, with only some sparse shrubbery.	
Lost Man Creek #1 (LM1) 41.32803 °N, 124.02446 °W	Located along the access road to Lost Man Creek trailhead in Redwood National Park. Unforested area, with a field covered in blackberry bushes backing up to a large talus slope.	
Lost Man Creek #2 (LM2) 41.32499 °N, 124.00592 °W	Along Lost Man Creek Trail in Redwood National Park, starting about 830 m from the trailhead and continuing roughly 500 m further along the trail. Old growth redwood forest with creek running alongside in the valley below.	
Forest Road 6N06 40.87061 °N, 123.60611 °W	Road within Six Rivers National Forest. Salamanders were tagged at several points along the road, primarily in areas with small talus slopes. Tree cover is highly variable, with some areas partially sheltered by mixed conifer forest, while other areas had no tree cover.	
Forest Road 7N18 40.97432 °N, 123.65877 °W	Road within Six Rivers National Forest. Salamanders were tagged at two points along the road, both with talus slopes. One area is significantly forested while the other is almost entirely devoid of trees.	
East Fork Campground (EFCG) 40.90545 °N, 123.70662 °W	Campground within Six Rivers National Forest. Campground is closed most of the year, only open in the summer dry season. Most of the area is heavily shaded and a creek runs through the center of the campground.	

Animal Capture & Tagging

I began tagging individuals on February 21, 2020, aiming to tag 10 to 15 salamanders at each site. Tagging concluded on July 11, 2020. I located salamanders by conducting daytime cover object searches, turning over any rocks or logs that would provide a suitable microhabitat for salamanders. If there was a salamander or other animal underneath the object, I removed the animal before replacing the cover object back in its original position (Olson et al., 1999).

When I located a *P. elongatus*, I marked its exact capture point with a flag in the ground to ensure that I could return it to the correct location. I also recorded GPS coordinates for each capture point. I used calipers to measure the snout-vent length (SVL) and total length of each salamander. Next, I placed the individual into a bag and weighed it with a spring scale. Body mass index (BMI) values were calculated by dividing each individual’s mass by its snout-vent length. If the salamander met the necessary size threshold for tagging (see next paragraph for details), I assigned it an identification number, with which I also labeled the corresponding marking flag. If the salamander was too small for tagging, I recorded its measurements but did not assign it a number. I attempted to determine the sex of the individual by observing the vent through a dissecting scope. I classified individuals with a smooth, uniformly light cloacal lining as males and individuals with deep furrows and dark stripes in the cloacal lining as females (Ollivier & Welsh, 2003). To determine reproductive status, I checked males for the presence of an enlarged mental gland, which secretes pheromones used in courtship and mating. I checked females for any developing ova visible through the ventral body wall, and if ova were observed, I measured the diameter of the largest ovum using calipers.

If the individual weighed over 1.5 g and had a SVL over 40 mm, I implanted it with a PIT tag (Ousterhout & Semlitsch, 2014). I submerged each salamander in a 0.02% Benzocaine solution to anesthetize it (Brown, 2017; Crook & Whiteman, 2006), then used a Biomark MK25 implanter (Boise, ID) to insert a pre-sterilized, 8 mm slim PIT tag into the abdominal cavity. Afterwards, I rinsed the salamander with distilled water, used a cotton swab to apply a small amount of Bactine (WellSpring Pharmaceutical Corporation; Sarasota, FL) to the insertion site, and placed it in a shallow dish with water to recover. Once the animal was able to right itself after being turned over, I considered it recovered from anesthetization and released it at its original capture point (Brown, 2017). Tagging took place from February 2, 2020 through November 7, 2020 (see Appendix B for a detailed summary of all tagged individuals). I tagged a total of 21 salamanders at my coastal sites: 5 at HBO, 4 at LM1, and 12 at LM2. At my inland sites, I tagged 25 salamanders: 11 at 6N06, 8 at 7N18, and 6 at EFCG.

Tracking

I conducted PIT tag surveys from May 18, 2020 through July 2, 2021. I used a Biomark HPR Plus PIT tag reader and a Biomark portable antenna (Boise, ID) to scan the surface of each site (Brown, 2017; Cucherousset et al., 2008). I used the last known detection site of each individual salamander as a starting point for these PIT tag surveys and scanned as much of the area within a 2 m radius of that point as possible. Vegetation, cliffs, and other obstacles sometimes made it impossible to scan parts of the search area, but all accessible areas were scanned. This species is “highly sedentary” (Welsh & Lind, 1992) and individuals rarely move large distances, so the 2 m search radius was selected to encompass the likely distance that an individual might travel in the relatively short amount of time between surveys (from one day to seven weeks). Whenever I detected a PIT tag, I measured the straight-line distance between the flag marking the individual’s last known location to the new detection point and moved the flag to the new position (Brown, 2017; Hamed et al., 2008). If there was a cover object near the detection point, I lifted it to check if the salamander was underneath. When I was able to find the individual, I classified it as “above ground,” but if the salamander was not visible, I classified it as “below ground.” If the salamander was above ground, I recaptured it and measured its weight, SVL, and total length for comparison to its previous measurements. I also examined the individual for any indicators of its current reproductive status (i.e., mental gland or visible ova), before returning it to its most recent capture location.

During phase one, from May 18 through October 23, 2020, I surveyed each site roughly once a week, visiting all my inland sites on one day and all my coastal sites another day. Site visits were alternated in this manner until late fall, when salamander activity finally ceased at all sites. While this provided an effective overview of salamander activity, it was not suitable for measuring individual movements due to the long period of time between re-visits to the same site. During phase two, from November 18, 2020 to July 2, 2021, I changed my survey schedule to better capture small scale movements over short periods of time and began surveying each site every other week.

Each week, I would visit either the coastal or inland sites on the first day of surveys, alternating between the coastal and inland sites on subsequent weeks. I re-surveyed the same sites the next day to determine if the salamanders had moved from their position the prior day. The rest of the survey techniques were the same as described for phase 1. Of the original 46 tagged salamanders, two (#39 and #40) were excluded from surveys after June 17, 2020, because repeatedly climbing up to their location on the hillside was causing too much slope erosion.

Abiotic Measurements

To quantify the habitat differences between coastal and inland sites and to account for variation among sites within each region, I took abiotic measurements at each site. To estimate relative canopy cover, I took wide angle photographs of the canopy above each individual, placing the camera at ground level. Canopy cover photos were taken at the end of the survey period, at each individual’s last known location, but a road closure prevented access to both sites at Lost Man Creek, so no canopy cover estimates were calculated for individuals at those sites. To capture seasonal conditions at each site, I recorded temperature and cloud cover conditions (either clear, light, moderate, or complete) during each survey visit. Aiming to capture more detailed temperature and humidity readings in between site visits, I placed a LogTag HAXO-8 data logger (Lafayette, NJ) in a waterproof case at each site. I programmed the loggers to take hourly measurements of temperature and humidity, and the loggers were positioned close to the ground to capture the conditions at ground level. Due to budgetary limitations at the beginning of the study, logger-recorded data were collected only from February 15, 2021 through the end of the survey period on July 2, 2021. When I attempted to retrieve it, the data logger at the High Bluff Overlook site was missing, so no daily climate measurements were available for that site.

Data Preparation and Analysis

To generate the canopy cover value for each individual's location, I used the "countcolors" package for R to analyze the photos taken of the canopy over each individual (Weller, 2019). Images were recolored to separate open sky from canopy, and then the percentage of pixels in each image corresponding to canopy cover was calculated.

Prior to modeling, all continuous variables (observed temperature, maximum temperature, minimum humidity, canopy cover, and BMI) were centered and scaled to produce a mean of zero and a standard deviation of one, to address the large difference in numerical scales among variables (e.g., temperature values ranging from -2 to 55℃ and BMI values from 0.029 to 0.07 g/mm). Temperatures measured on site during PIT tag surveys were referred to as "observed temperature." Temperature and humidity readings collected by data loggers were summarized by mean, minimum, and maximum values for each day. These measures were highly collinear, so only maximum daily temperature and minimum daily humidity readings were included in the model selection process. These measurements were chosen because high temperature and low humidity conditions come with the highest risk of desiccation for salamanders (Lillywhite, 1975).

I used multilevel logistic models to examine the effect of climate and habitat measures on the likelihood of detecting *P. elongatus*. All models were fit using maximum likelihood estimation, via Laplace approximation, with the “lme4” package for R (Bates et al., 2015). Multiple detection surveys were conducted for each individual and multiple individuals were located within each site, so the use of multilevel models was necessary to account for the lack of independence in the dataset. All subsequent models included a random intercept effect for individuals nested within sites.

I used the “dredge” function, from the “MuMIn” package for R, to fit models for every possible combination of predictor variables (Bartoń, 2022). Because observed temperature and cloud cover data were collected during the entirety of this study, detection data from phase two were also included in the phase one models. Logger-recorded temperature and humidity data were only collected during phase two, so the phase two models include data from phase two only. For the phase one model selection process, models contained up to three fixed effects, while for the phase two model selection, only models with one or two fixed effects were generated because of the smaller dataset for these models. The resulting models were then ranked by their small-sample corrected Akaike Information Criterion (AICc) values, and the model with the lowest AICc was selected as the final model for each phase. For each model parameter that was significant at the 95% confidence level, I calculated the parametric bootstrap confidence intervals (CI) and odds ratio.

To test whether there were any regional level differences in individual BMI, I conducted a Welch two-sample t-test to compare BMI values between the inland and coastal salamanders. The variation in BMI values was greater on the coast, so this test was selected because it is specifically designed to compare groups with unequal variances. Only seven individuals were ever re-captured and had multiple measurements taken, so only the BMI values from the initial capture and tagging of each salamander were used in this analysis.

Finally, because the study populations included noticeably more females than males, I tested whether the sex ratio of the sample population differed between the inland and coastal regions, and whether either ratio differed significantly from the expected 50:50 ratio of males to females. I fit a logistic regression model for the number of males and females at each site, with the "region" (inland or coastal) of each site as a predictor. To use sex as the binary response variable for this model, males were coded as "0" and females were coded as "1."

RESULTS

Detections of *Plethodon elongatus*

I conducted 40 PIT tag surveys at each inland site and 38 surveys at each coastal site. A total of 90 detections of the 46 PIT-tagged animals occurred over the entirety of the survey period. Only nine of those detections were of above-ground individuals, while the remaining detections were of underground individuals. Twenty-seven salamanders (58.7% of the 46 tagged individuals) were re-detected at least once after their original tagging, 12 in the coastal region and 15 in the inland region (Table 3, Appendix B). Only 17% of the original tagged population were ever detected above-ground.

Table 3. Summary of survey results at each study site, including the number of salamanders tagged at that site and the number that were re-detected at any point during the survey process, along with the percentage of tagged individuals that were redetected overall and the percentage that were recaptured above ground.

Site	# Individuals Tagged	# Individuals Redetected	% Redetected	% Recaptured
6N06 (Inland)	11	7	63.7	27.3
7N18 (Inland)	8	5	62.5	12.5
EFCG (Inland)	6	3	50.0	16.7
HBO (Coast)	5	3	60.0	20.0
LM1 (Coast)	4	1	25.0	25.0
LM2 (Coast)	12	8	66.7	8.3

Two individuals (#10 and #42) ceased movements entirely and remained in one location for over a year. These tags were dug up and located after the conclusion of surveys, with no sign of the salamanders present, indicating these individuals most likely died over the course of the survey period. These individuals were excluded from the dataset after the date of their last detected movements. Days between subsequent detections ranged from 1 to 395. The largest distance any individual moved between detections was 163 cm, while the largest movement over a 24-hour period was 84 cm.

For each survey day, the percentage of individuals detected at each of the three sites were averaged to generate the average detection rate for each day. Detection rates peaked from late fall to early spring but ceased almost entirely during late summer to early spring. Detection rate was negatively correlated (r = -0.261) with temperature (Figure 2).

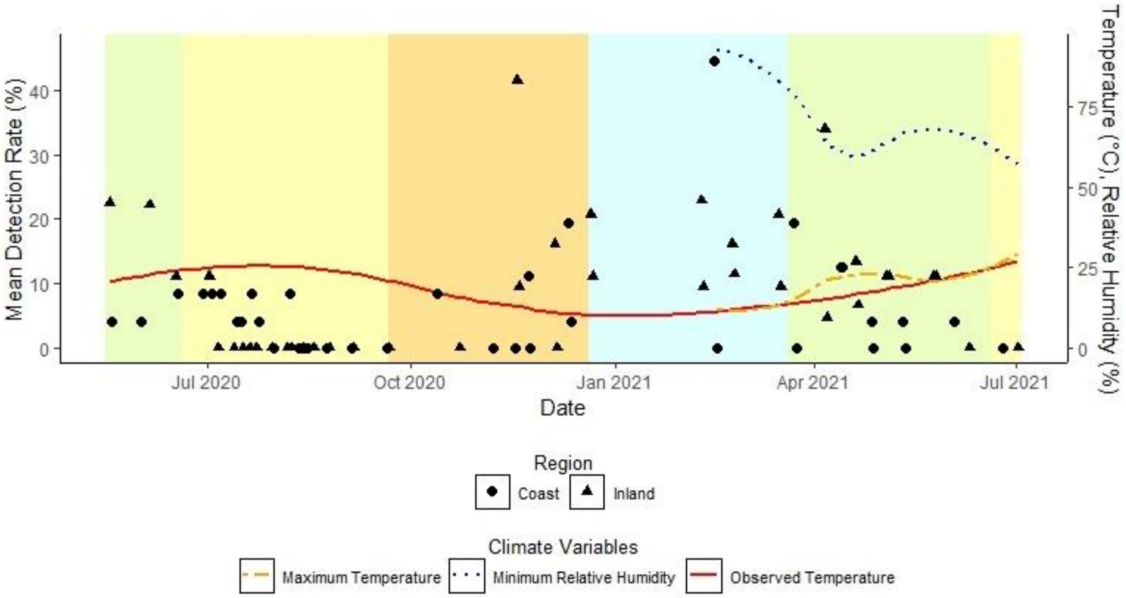


Figure 2. Average daily detection rate of *P. elongatus* as a function of the survey date, showing how the detection rate varied over time. Three local polynomial regression lines represent the observed temperature, maximum temperature, and minimum humidity. The plot background color corresponds to the season in which the survey took place: green – spring, yellow – summer, orange – fall, blue – winter. Maximum temperature and minimum humidity values were collected with data loggers that were not deployed until February 15, 2021.

I first fit a full model with every potential predictor variable (observed temperature, canopy cover, BMI, sex, and region) and random intercept effects for individuals within sites. The full model included too many predictor variables, which, in addition to the complexity of the random effects, resulted in a failure for the algorithm to converge on a single best fit for the model. The random effects were necessary to capture the hierarchical structure of the data, so the best solution was to reduce the number of fixed effect predictors.

Phase One Model

Phase one models included data from the entire study period (collected during phase one and two). The top four models included observed temperature as a predictor, and in all four models observed temperature was the only significant predictor. Models one and two had essentially identical AICc values, but because sex was not a significant predictor in model two, model one was selected as the final model because it was more parsimonious (Table 4).

Table 4. Summary of multi-level logistic regression models for the detection of *P. elongatus*. Of the 20 total models generated, the four summarized here have the lowest AIC values, which indicates these were the best fitting models. Each model also included a random effect for site and a random effect for individual within site. AICc, ΔAICc, and Akaike weights are listed for each model.

Model	Observed Temperature	BMI	Sex	Region	AICc	ΔAICc	Weight
1 (Final)	X				534.1	0.00	0.22
2	X		X		531.1	0.00	0.22
3	X	X			536.0	1.97	0.08
4	X			X	536.0	1.98	0.08

Table 5. Summary of the final multi-level logistic regression model for the detection of *P. elongatus*. The intercept estimate and a slope estimate for each predictor variable are listed, along with the variances of both random effects included in the model. AIC, log likelihood, and residual degrees of freedom values are also listed. Model parameters that were significant at the 95% confidence level (corresponding to a p-value less than 0.05) are boldfaced. The only significant parameters were the intercept estimate and the slope estimate for observed temperature.

Model Parameter	Estimate	p-value
Intercept	**-1.060**	**0.0015**
Observed Temperature	**-0.0744**	**$1.12*10^{-05}$**
ID:Site Random Effect Variance	0.339	–
Site Random Effect Variance	0.014	–
Df Residual	526	–
AICc	534.1	–
Weight	0.22	–
Log Likelihood	-263.0	–

The final model included observed temperature as the sole predictor variable, in addition to the random effects for individuals within sites (Table 5). Observed temperature showed a strong negative correlation with *P. elongatus* detections, with the proportion of detected individuals typically decreasing as temperature increased, though detections did decrease at temperatures below roughly 8℃ (Figure 3).

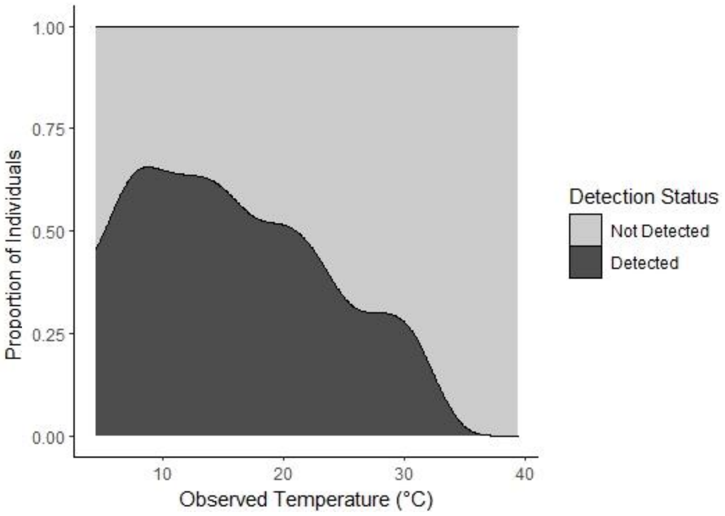


Figure 3. Conditional density plot showing how the actual ratio of detected to undetected individuals changed as a function of the temperature observed during surveys. Note the overall downward trend of *P. elongatus* detections as the observed temperature increases.

The final model indicated that the odds of *P. elongatus* being detected decreased 7.2% (odds ratio: 0.93, 95% CI: 0.90 – 0.96) for every one-degree Celsius increase in observed temperature (Figure 4).

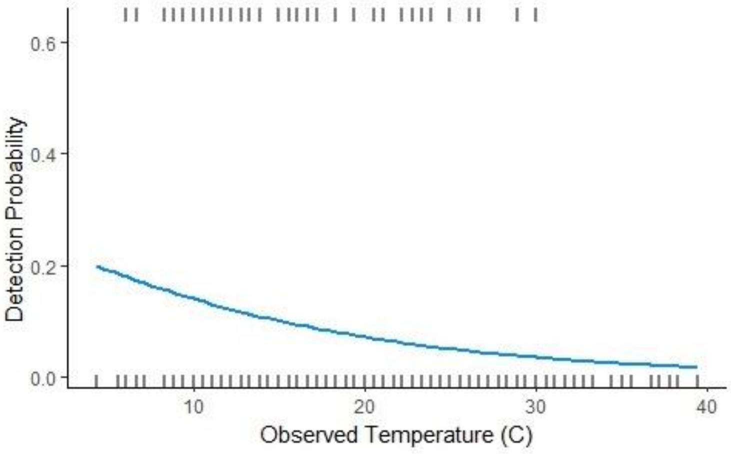


Figure 4. Response plot of the final phase one model for *P. elongatus* detection. Rug marks at the top of the plot indicate positive residuals, while rug marks along the bottom represent negative residuals. Note how the probability of detection decreases as temperature increases.

Phase Two Model

During phase two, the survey schedule was altered so that sites were surveyed two consecutive times, 24-hours apart, and data loggers were deployed to record temperature and relative humidity at each site. Phase two models only included data collected during phase two. The top three models all included daily maximum temperature as a predictor variable, and it was the only significant parameter in models two and three (Table 6). Model four had no statistically significant parameters.

Table 6. Summary of multi-level logistic regression models for the detection of *P. elongatus*. Of the 18 total models generated, the four summarized here had the lowest AIC values, which indicates these were the best fitting models. Each model also includes a random effect for site and a random effect for individual within site. AICc, ΔAICc, and Akaike weights are listed for each model.

Model	Maximum Temperature	Minimum Humidity	Cloud Cover	Region	AICc	ΔAICc	Weight
1 (Final)	X	X			162.3	0.00	0.66
2	X				167.3	5.07	0.05
3	X			X	168.7	6.47	0.04
4			X		168.7	6.47	0.03

The final model for *P. elongatus* detections during phase two included maximum daily temperature and minimum daily humidity as fixed effects, along with the random effect for individuals within sites (Table 7). Both temperature and relative humidity were significantly associated with the probability of detecting *P. elongatus* (temperature: p = 0.005, humidity: p = 0.012). With humidity held constant, for every one-degree Celsius increase in maximum temperature, the final model predicted a 12.3% (odds ratio = 0.877, 95% CI: 0.802 – 1.013) decrease in the odds of *P. elongatus* being detected within the survey area (Figure 5). With temperature held constant, for every one percent increase in minimum humidity, the final model predicted a 5.6% (odds ratio = 1.056, 95% CI: 1.017 – 1.094) increase in the odds of *P. elongatus* being detected (Figure 6).

Table 7. Summary of the final multi-level logistic regression model for the detection of *P. elongatus*, using data collected only during phase two of the study. The intercept estimate and a slope estimate for each predictor variable are listed, along with the variances of both random effects included in the model. AIC, log likelihood, and residual degrees of freedom values are also listed. Model parameters that were significant at the 95% confidence level (corresponding to a p-value less than 0.05) are boldfaced. The only significant parameters were the slope estimates for daily maximum temperature and minimum humidity.

Model	Estimate	p-value
Intercept	3.738	0.105
Maximum Temperature	**-0.131**	**0.005**
Minimum Humidity	**0.055**	**0.012**
ID:Site Random Effect Variance	2.817	–
Site Random Effect Variance	$1.855*10^{-10}$	–
Df Residual	223	–
Log Likelihood	-76.0	–
AIC	162.3	–
Weight	0.66	–

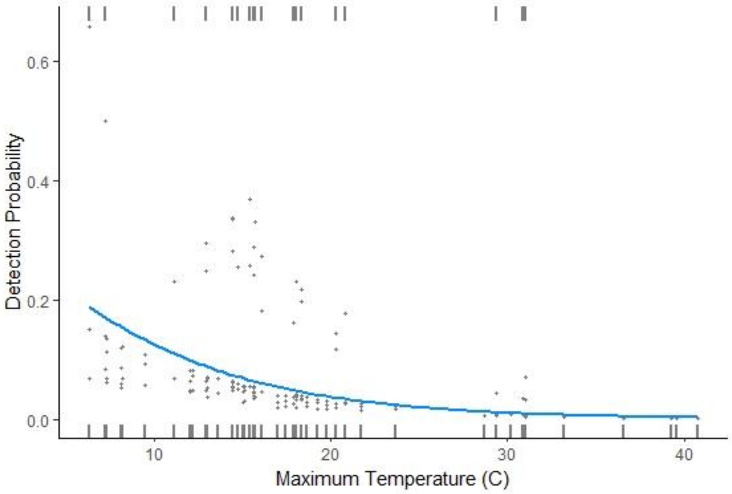


Figure 5. Response plot of the final phase two model for *P. elongatus* detection, showing how detection probability changed with the daily maximum temperature (with humidity held constant). Rug marks at the top of the plot indicate positive residuals, while rug marks along the bottom represent negative residuals. Note how the probability of detection decreases as temperature increases.

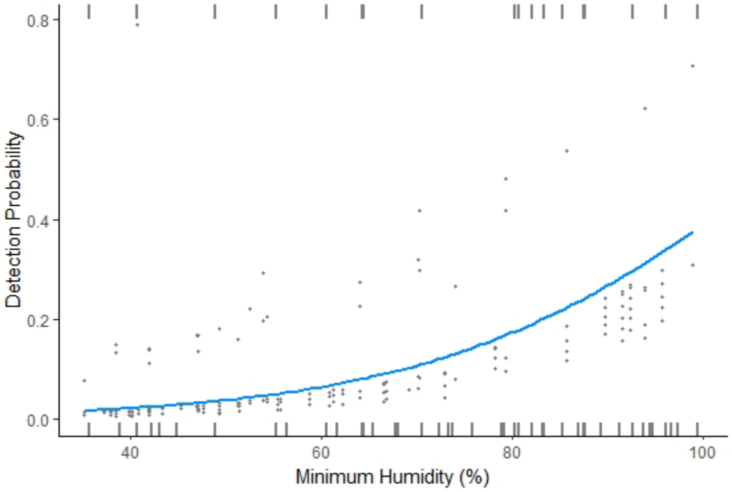


Figure 6. Response plot of the final phase two model for *P. elongatus* detection, showing how detection probability changed with the daily minimum relative humidity (with temperature held constant). Rug marks at the top of the plot indicate positive residuals, while rug marks along the bottom represent negative residuals. Note how the probability of detection increases as humidity increases.

Body Mass Index

The average BMI was nearly identical between the inland and coastal regions (inland: 0.0473 g/mm, coast: 0.0468 g/mm), but there was more variation in BMI at coastal sites (Figure 7). Because the variances of the inland and coastal sites were unequal, I conducted a Welch's two-sample t-test to determine if there was a significant difference in BMI between the inland and coastal populations of *P. elongatus.* Based on the results of this test, I was unable to reject the null-hypothesis that the BMI values did not differ significantly between the two regions (t = -0.189, df = 33.054, p = 0.8512). This indicates that BMI was not significantly different for salamanders from the inland and coastal regions.

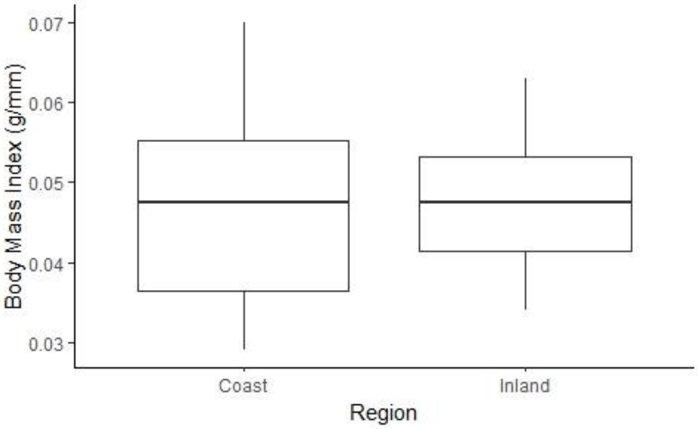


Figure 7. Boxplots displaying the BMI values from the coastal and inland regions. Note that while the spread of the BMI values is slightly narrower for the inland population than the coast, the means and interquartile ranges for both regions are very similar.

Population Sex Ratio

Given that there was a noticeable bias towards female salamanders in the study population, I examined whether there was a significant difference in the observed male to female ratios between the inland and coastal populations, and if these ratios differed from the expected 50/50 distribution. Inland sites appeared to have a more even distribution between male and female individuals, while the populations at coastal sites tended to have a lower ratio of males to females (i.e., more females than males) (Figure 8). I fit a logistic regression model with sex as the response variable (either male or female, with unidentifiable individuals excluded), and region as a predictor variable.

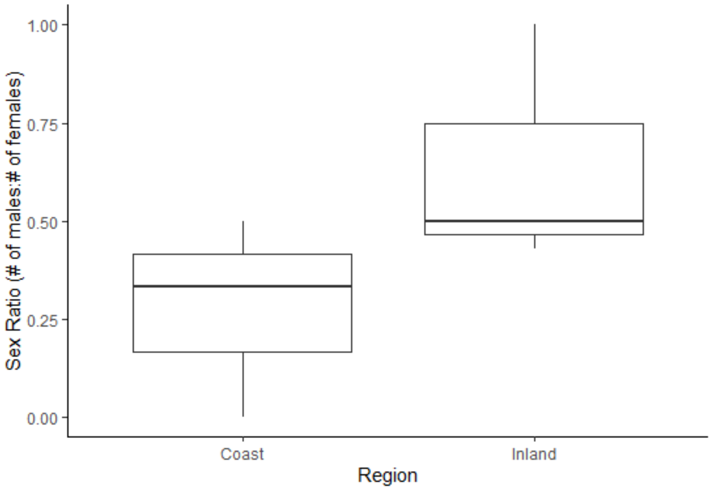


Figure 8. Boxplots displaying the variation in proportion of males between the inland and coastal regions. Higher values for sex ratio indicate a more even distribution of males and females. Both inland and coastal sites had higher numbers of females than males, but sites in the coastal region tended to have a lower ratio of males to females than inland sites.

The resulting model was not statistically significant (F=0.038; df=1,42; p=0.8462) at the 95% confidence level, indicating we cannot reject the null hypothesis that the sex ratio is the same between the two regions. Furthermore, the 95% confidence interval for the inland sex ratio (0.208-0.578) contains 0.5, which is equivalent to a 50:50 sex distribution, indicating there is no evidence that the inland population's sex ratio differs from that of the expected norm. The 95% confidence interval for the coastal sex ratio (0.103-0.460) does not contain 0.5, indicating the sex ratio of the coastal population could differ from the expected 50/50 split, however the lack of significance of the overall model or of the difference in slopes between the two regions (t= 0.195, p=0.846) makes this result inconclusive.

Focal Individuals

While most salamanders were redetected between one and five times, individuals 10, 23, 29, 37, and 46 were each detected seven times or more. Given these individuals had the most frequent detections, I examined their movement patterns over time.

Salamander 10, a male from site LM2, was detected a total of 7 times (Figure 9). The first detection occurred on June 18, 2020, approximately 4 months after the tag insertion date. Its last detected movement occurred on August 7, 2020, after which the tag remained detectable in the same position for the rest of the study, likely due to the death of the individual. At the end of the survey period, I retrieved this tag from its underground position and found no trace of the individual. Its maximum recorded movement was 96 cm, while the minimum was 0 cm.

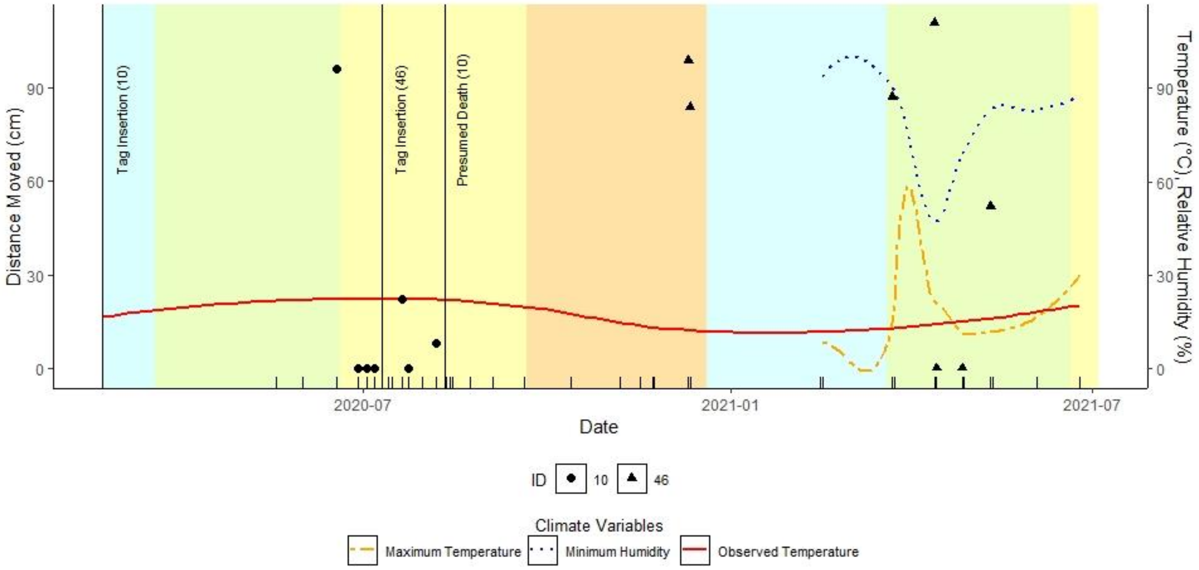


Figure 9. Focal plot highlighting the movements detected for coastal individuals 10 and 46, showing the distance moved between detections. Three local polynomial regression lines represent the observed temperature during each survey (solid red) along with logger recorded data for the maximum daily temperature (dashed orange) and the minimum daily humidity (dotted blue). Black tick marks along the x-axis indicate dates where a survey took place. The plot background color corresponds to the season in which the survey took place: green – spring, yellow – summer, orange – fall, blue – winter.

Salamander 46, a female from site LM2, was detected a total of 7 times (Figure 9). The first detection occurred December 11, 2020, exactly 5 months after tag insertion. Its period of detectable activity ended on May 11, 2021. Its maximum recorded movement was 111 cm (over 21 days), while the minimum was 0 cm.

Salamander 29, a male from site 6N06, was detected a total of 8 times (Figure 10). The first detection occurred on November 18, 2020, approximately 8 months after the tag insertion date. Its last detection occurred on March 17, 2021. Its maximum recorded movement was 79.0 cm, while the minimum was 0.3 cm. Individual 29 was never detected in the same place in two consecutive surveys.

Salamander 37, a male from site 7N18, was detected a total of 7 times (Figure 10). The first detection occurred on December 5, 2020, roughly 9 months after the tag insertion date. Its period of detectable activity continued until April 21, 2021. Its maximum recorded movement was 39 cm while the minimum was 0 cm.

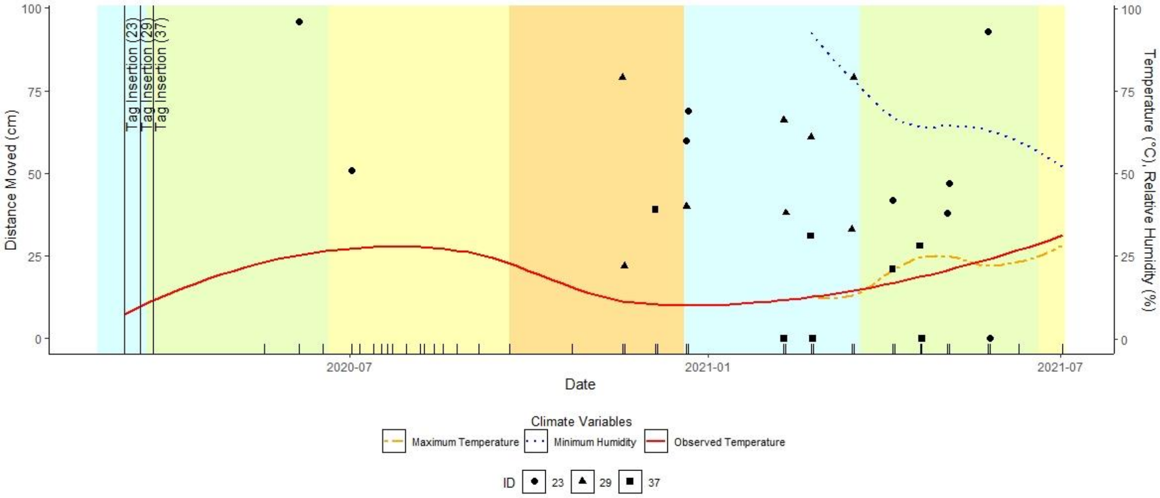


Figure 10. Focal plot highlighting the movements detected for inland individuals 23, 29, and 37, showing the distance moved between detections. Three local polynomial regression lines represent the observed temperature during each survey (solid red) along with logger recorded data for the maximum daily temperature (dashed orange) and the minimum daily humidity (dotted blue). Black tick marks along the x-axis indicate dates where a survey took place. The plot background color corresponds to the season in which the survey took place: green – spring, yellow – summer, orange – fall, blue – winter.

Individual 23 from site EFCG was detected a total of 9 times (Figure 10). The first detection occurred June 5, 2021, approximately 3 months after tag insertion. Its period of detectable activity continued through May 26, 2021. Its maximum recorded movement was 96 cm while the minimum was 0 cm.

DISCUSSION

In both phases of the study, temperature was strongly associated with *P. elongatus* detections, with detections decreasing as temperature increased, except at very low temperatures. This is to be expected, as salamanders experience significantly higher rates of evaporative water loss at higher temperatures (Thorson, 1955). If conditions are favorable, salamanders are able to remain at or near the surface level, but at high temperatures salamanders appear to retreat further underground, beyond the detection range of the PIT tag antenna (~10 cm). *Plethodon elongatus* detections appeared to be limited primarily by high temperatures, though there was evidence of a slight downward trend in detection rate at observed temperatures below about 8℃ (Figure 3). Throughout the study, I never detected salamanders on days when the observed temperature exceeded 30℃, and during phase two, I made no detections on days when the daily maximum temperature exceeded 31℃. The lowest observed temperature at which salamanders were detected was 1.7℃, but I conducted few surveys at temperatures lower than this and daytime temperatures rarely drop lower below 1.7℃ within the study area (Table 1, Appendix C). Climate change models predict increasing temperatures throughout the entire range of the species, which could lead to a decrease in surface activity (Diffenbaugh et al., 2015). Spending more time deep underground to shelter from adverse climate conditions can negatively impact salamander body condition and reduce the amount of time available for reproduction (Bickford et al., 2010; Reading, 2007; Sheridan & Bickford, 2011). Continued, long-term monitoring of individual detections, body condition, and reproductive indicators could provide valuable insight into how this species may respond to climate change.

Based on the phase two model, relative humidity was also significantly correlated with the probability of detecting *P. elongatus* individuals. The relationship between moisture levels and salamander behavior is well-documented, given that desiccation avoidance is one of the major reasons salamanders spend time underground (Feder, 1983; Keen, 1984; Spotila, 1972). I never detected individuals on days when the minimum relative humidity was below 61.2%, indicating that surface or near-surface-level activity is minimal when relative humidity is low. Throughout the past few decades, much of the area within the species' range has experienced recurring droughts, and climate models predict conditions will continue to become drier in this area (Diffenbaugh et al., 2015). Lower humidity and precipitation levels would increase the risk of desiccation for *P. elongatus*, which could cause individuals to spend more time deep underground and less time at or near the surface. This further demonstrates the need for continued monitoring of the species under various climate conditions.

The lack of significant difference in detection patterns between the inland and coastal regions was likely due to the high variability of conditions at sites within the same region. While I initially hypothesized that coastal salamanders would be detected more frequently due to the more temperate climate, two of the three coastal sites, HBO and LM1, had the lowest overall detection rates of all six sites (1.7% and 0.4%, respectively). This may be due to the lower sample size at these sites, but it is also noteworthy that these two sites were the only completely unforested areas included in the study. The lack of tree canopy means these areas have little to no protection from direct sunlight, which allows soil to dry out more quickly and ground level temperatures to exceed ambient air temperatures, which may be why there were so few detections at these sites (Hasselquist et al., 2018). Other areas that were more forested were surveyed prior to site selection, but no additional coastal sites were found that had large enough populations of *P. elongatus*. Canopy cover was not significantly related to detection probability in this study, but this may be due to a lack of data, because canopy cover estimates could not be calculated for sites LM1 and LM2, and detection data from the sites with no canopy cover (LM1 and HBO) were extremely limited. Unexpectedly, the highest detection rate was observed at one of my inland sites, EFCG, where 11.8% of surveys of the area surrounding an individual resulted in a detection (Appendix D). The second highest overall detection rate was at coastal site LM2, where 10.9% of individual surveys resulted in detections. EFCG and LM2 were the most densely forested sites, and both contained riparian areas, which may have contributed to the higher rates of salamander activity at these sites. LM2 was also the only site that included old growth redwood forest, which is the habitat typically associated with this species (Stebbins, 2003). The other sites were located in second growth mixed conifer or cedar forests or were entirely unforested. While these sites were able to sustain populations of *P. elongatus* despite not providing old growth conditions, the lower detection rates at these sites indicates that individuals may exhibit lower activity levels in unforested or second growth habitats. Given the lack of any regional patterns in *P. elongatus* detections, it appears that specific habitat and micro-habitat conditions are more related to salamander activity levels than regional level climate conditions.

At most sites, high summer temperatures correlated with a complete lack of detections for anywhere from four to six months. However, at coastal site LM2, the most heavily forested of all six sites, detections of subterranean individuals occurred nearly year-round, even when there was no evidence of surface level activity. Of the 14 detections that occurred during the summer months, seven of these detections indicated that the individual had moved from its last known location, with movements ranging from eight to 64 cm. While retreating underground in response to adverse conditions is well-documented in plethodontid salamanders, historically these periods of subterranean dwelling have been viewed primarily as a time of low activity, in which salamanders are not actively foraging or making significant horizontal movements (Taub, 1961; Woolbright & Martin, 2014). While it is possible these individuals emerged and moved above ground, given the high risk of desiccation associated with dry ground and higher temperatures during the summer, it seems likely these individuals moved while remaining underground. Alternatively, they may have emerged and made these movements at night, when conditions are least conducive to desiccation. Regardless of whether these movements were made under or above ground, they indicate that *P. elongatus* can remain more active during the summertime than previously reported (Jaeger, 1980). We know very little about the behavior of these salamanders during their “dormant” periods because they retreat underground and are too small for most tracking devices. Given that movements were still occurring when there was no evidence of above-ground movement, future research into plethodontid activity patterns should consider using methods like remote PIT tag surveys in order to avoid overlooking subterranean movements.

Using PIT tags for the remote detection of salamanders provides a number of benefits over more traditional marking and survey techniques. By utilizing PIT tag surveys with a portable antenna, I was able to detect underground salamanders that would have been overlooked with traditional amphibian survey techniques, resulting in re-detections of over half the initial tagged population (61.4% of the initial tagged population were detected at least once, while 18.2% were recaptured at least once), whereas only 17% of individuals were ever detected at surface level. Over the course of this study, I detected an average of 8.2% of the survey population on each survey day (excluding individuals who were tagged but never re-detected). This survey method is minimally invasive after initial marking, allows for the detection of salamanders even when underground, and produces higher recapture rates than traditional methods. A previous mark recapture study of *P. elongatus* had a sample size of over 900 salamanders but an overall recapture rate of only 6% (Welsh and Lind, 1992). For long term monitoring of specific individuals, PIT tag marking is an ideal method given the relatively low cost per tag, longevity, and unambiguity (each tag has a unique identifying number). A major difficulty encountered during surveys was the inability to consistently scan the entire 2 m radius around last known position of each individual. Certain individuals were in areas where large rocks, dense vegetation, steep drop offs, or other physical barriers prevented certain parts of the survey area from being scanned with the antenna. Because of this, salamanders that may have been present at or near the surface could have been missed during surveys if they were in an unscannable area; in other words, we cannot say with certainty that salamanders in these areas were undetected because they were too far underground to be picked up by the antenna. This method may be better suited for monitoring species that dwell in flat, even terrain, which would allow for more complete scanning of the area around an individual.

A major limitation of this study was that temperature (both observed and recorded by data loggers) and humidity data were collected for entire sites, rather than in the micro-habitat surrounding each individual. Micro-habitat fluctuations in temperature and moisture conditions would not have been reflected by these data but could play an important role in driving *P. elongatus* activity. Due to financial limitations, I only installed a single data logger at each site, which provided more detailed information than recording temperatures during site surveys. Ground level temperatures and the observed ambient temperatures during surveys were relatively collinear and followed the same overall patterns, but ground level temperature occasionally differed quite significantly from observed temperature. The highest daily maximum temperature recorded via data logger was 40.8℃, at site 6N06, but the observed temperature at this site on the same day was only 25.6℃ (it should be noted that temperatures may have exceeded 25.6 before or after the site visit, though likely not by 15℃). This indicates that ambient temperature and surface level temperatures (collected by the data loggers) may not be as correlated as expected. Even when ambient temperatures are not extremely high, the level of sun exposure, substrate type, presence or absence of vegetation, and other micro-habitat factors may influence surface temperatures (Lhomme et al., 2000; Roberts et al., 2015).

These factors can cause surface level temperatures to differ significantly from ambient air temperatures. Conditions at ground level may be highly variable in heterogeneous habitats like those surveyed in this study, and even salamanders within the same site are likely impacted by these micro-habitat level differences.

Repeated detections of the same individual were relatively rare during both phases of the study. Only five individuals were detected seven times or more over the entire survey period, and only 17 instances occurred where an individual was detected during an initial phase two survey and the re-survey 24 hours later. While the data were too sparse for statistical analysis, they do demonstrate that there is potential for PIT tag tracking to be used for monitoring small-scale movements made by plethodontid salamanders. With a larger sample size and more frequent surveys, this methodology could be used not just to observe the presence and absence of detectable salamanders, but also to examine movement distances and what factors may influence them. Such future research should prioritize recording micro-habitat level environmental variables, to accurately capture the conditions within each salamander's immediate area that might be driving their movement patterns. Additionally, using a larger sample size and including more sites, as originally planned for this study, would increase the statistical power of similar studies in the future.

Plethodontid salamanders display behavioral plasticity to avoid exposure to potentially dangerous conditions on the surface. This semi-fossorial lifestyle has historically made monitoring the behavior of plethodontids a challenging endeavor, but with the development of appropriately-sized PIT tags and portable antennas, we can begin to learn more about their subterranean behavior patterns. Monitoring the relationship between plethodontid activity levels and environmental conditions may offer insight into how climate change and other threats might alter these behavior patterns, as well as what effects these behavioral changes may have on other aspects of their behavior or physical condition. Climate change projections predict increasing temperatures throughout the range of this and many other plethodontid species, which could lead to lower levels of surface activity (Diffenbaugh et al., 2015; Gunderson & Stillman, 2015; Muñoz et al., 2016; Riddell, et al., 2018; Urban, et al., 2014). By utilizing strategies like remote PIT tag surveys, we can continue to monitor plethodontid behavior patterns as climate conditions shift and learn more about how decreased levels of surface activity might impact them over time.

REFERENCES

Bailey, L. L., Simons, T. R., & Pollock, K. H. (2004). Estimating Detection Probability Parameters for *Plethodon* salamanders using the robust capture-recapture design. *The Journal of Wildlife Management*, *68*(1), 1–13.

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 1–48.

Bartoń, K. (2022). *MuMIn: Multi-model inference.* (Version 1.46.0). R.

Bickford, D., Howard, S. D., Ng, D. J. J., & Sheridan, J. A. (2010). Impacts of climate change on the amphibians and reptiles of Southeast Asia. *Biodiversity and Conservation*, *19*(4), 1043–1062.

Blaustein, A. R., & Wake, D. B. (1990). Declining amphibian populations: A global phenomenon? *Trends in Ecology & Evolution*, *5*(7), 203–204.

Bolsinger, C. L., & Waddell, K. L. (1993). Area of old-growth forests in California, Oregon, and Washington. *Resource Bulletin PNW-RB-197*.

Brown, C. (2017). *Habitat use and movement patterns of two redwood forest salamanders,* Aneides vagrans *and* Ensatina eschscholtzii*, with an examination of the efficacy of PIT tags for marking small plethodontids* [Unpublished master's thesis]. Humboldt State University.

California Department of Fish and Wildlife. (2019, April). *California natural diversity database*. Government Version, accessed May 2019.

Collins, J. P., & Storfer, A. (2003). Global amphibian declines: Sorting the hypotheses. *Diversity and Distributions*, *9*(2), 89–98.

Connette, G. M., & Semlitsch, R. D. (2012). Successful use of a passive integrated transponder (PIT) system for below-ground detection of plethodontid salamanders. *Wildlife Research*, *39*(1), 1–6.

Connette, G. M., & Semlitsch, R. D. (2015). A multistate mark-recapture approach to estimating survival of PIT-tagged salamanders following timber harvest. *Journal of Applied Ecology*, *52*(5), 1316–1324.

Crook, A. C., & Whiteman, H. H. (2006). An evaluation of MS-222 and benzocaine as anesthetics for metamorphic and paedomorphic tiger salamanders (*Ambystoma tigrinum nebulosum*). *The American Midland Naturalist*, *155*(2), 417–422.

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*). *Wildlife Research*, *35*(8), 780–787.

Davic, R. D., & Welsh, H. H. (2004). On the ecological roles of salamanders. *Annual Review of Ecology, Evolution, and Systematics*, *35*, 405–434.

Diffenbaugh, N. S., Swain, D. L., & Touma, D. (2015). Anthropogenic warming has increased drought risk in California. *PNAS*, *112*(13), 3931–3936.

Duellman, W. E. (1999). *Patterns of distribution of amphibians: A global perspective* (W. E. Duellman, Ed.). The Johns Hopkins University Press.

Estes-Zumpf, W., Addis, B., Marsicek, B., Lee, M., Nelson, Z., & Murphy, M. (2022). Improving sustainability of long-term amphibian monitoring: The value of collaboration and community science for indicator species management. *Ecological Indicators*, *134*, 108451.

Feder, M. E. (1983). Integrating the ecology and physiology of plethodontid salamanders. *Herpetologica*, *39*(3), 291–310.

Feder, M. E., & Burggren, W. E. (1985). Cutaneous gas exchange in vertebrates: Design, patterns, control, and implications. *Biological Reviews*, *60*(1), 1–45.

Gade, M. R., & Peterman, W. E. (2019). Multiple environmental gradients influence the distribution and abundance of a key forest-health indicator species in the southern Appalachian Mountains, USA. *Landscape Ecology*, *34*(3), 569–582.

Grover, M. C. (1998). Influence of cover and moisture on abundances of the terrestrial salamanders *Plethodon cinereus* and *Plethodon glutinosus*. *Journal of Herpetology*, *32*(4), 489.

Gunderson, A. R., & Stillman, J. H. (2015). Plasticity in thermal tolerance has limited potential to buffer ectotherms from global warming. *Proceedings of the Royal Society Biological Sciences*, *282*(1808), 20150401.

Hager, H. A. (1998). Area-sensitivity of reptiles and amphibians: Are there indicator species for habitat fragmentation? *Écoscience*, *5*(2), 139–147.

Hamed, M. K., Ledford, D. P., & Laughlin, T. F. (2008). Monitoring non-breeding habitat activity by subterranean detection of Ambystomatid salamanders with implanted passive integrated transponder (PIT) tags and a radio frequency identification (RFID) antenna system. *Herpetological Review*, *39*(3), 303–306.

Hammerson, G., & Welsh, H. (2004). *Plethodon elongatus*. The IUCN Red List of Threatened Species 2004: e.T59339A11920133. Accessed March 2022.

Harpole, D. N., & Haas, C. A. (1999). Effects of seven silvicultural treatments on terrestrial salamanders. *Forest Ecology and Management*, *114*(2–3), 349–356.

Hasselquist, N. J., Benegas, L., Roupsard, O., Malmer, A., & Ilstedt, U. (2018). Canopy cover effects on local soil water dynamics in a tropical agroforestry system: evaporation drives soil water isotopic enrichment. *Hydrological Processes*, *32*(8), 994-1004.

Jaeger, R. G. (1980). Microhabitats of a terrestrial forest salamander. *Copeia*, *1980*(2), 265.

Jung, R. E., Droege, S., Sauer, J. R., & Landy, R. B. (2000). Evaluation of terrestrial and streamside salamander monitoring techniques at Shenandoah National Park. *Environmental Monitoring and Assessment 2000 63:1*, *63*(1), 65–79.

Karraker, N. E., & Welsh, H. H. (2006). Long-term impacts of even-aged timber management on abundance and body condition of terrestrial amphibians in northwestern California. *Biological Conservation*, *131*(1), 132–140.

Keen, W. H. (1984). Influence of moisture on the activity of a plethodontid salamander. *Copeia*, *1984*(3), 684–688.

Kiesecker, J. M., Blaustein, A. R., & Belden, L. K. (2001). Complex causes of amphibian population declines. *Nature*, *410*, 681–684.

Lhomme, J. P., Chehbouni, A., & Monteny, B. (2000). Sensible heat flux-radiometric surface temperature relationship over sparse vegetation: Parameterizing B−1. *Boundary-Layer Meteorology*, *97*, 431–457.

Lillywhite, H. B. (1975). Physiological correlates of basking in amphibians. *Comparative Biochemistry and Physiology Part A: Physiology*, *52*(2), 323–330.

Lillywhite, H. B. (2006). Review: Water relations of tetrapod integument. *The Journal of Experimental Biology*, *209*, 202–226.

Marsh, D., & Goicochea, M. (2003). Monitoring terrestrial salamanders: Biases caused by intense sampling and choice of cover objects. *Journal of Herpetology*, *37*(3), 460–466.

Muñoz, D. J., Miller Hesed, K., Campbell Grant, E. H., & Miller, D. A. W. (2016). Evaluating within-population variability in behavior and demography for the adaptive potential of a dispersal-limited species to climate change. *Ecology and Evolution*, *6*(24), 8740–8755.

Ollivier, L., & Welsh, H. H. (2003). Determining sex and life stage of Del Norte salamanders from external cues. *Northwestern Naturalist*, *84*, 129–134.

Olson, D. H., Clayton, D. R., Crisafulli, C. M., Jones, L. L. C., Lewendal, P. C., Nauman, R. S., Ollivier, L. M., Welsh, H. H., & Applegarth, J. S. (1999). *Survey protocols for amphibians under the survey and manage provision of the northwest forest plan (Version 3.0)*. Bureau of Land Management.

Ousterhout, B. H., & Semlitsch, R. D. (2014). Measuring terrestrial movement behavior using passive integrated transponder (PIT) tags: Effects of tag size on detection, movement, survival, and growth. *Behavioral Ecology and Sociobiology*, *68*(2), 343–350.

Raphael, M. G. (1988). Long-term trends in abundance of amphibians, reptiles, and mammals in Douglas-fir forests of northwestern California. In R.C. Szaro, K.E. Severson, & D.R. Patton (Eds.), *Management of Amphibians, Reptiles, and Small Mammals in North America, Proceedings of the Symposium*, 23–31. Rocky Mountain Forest and Range Experiment Station, US Department of Agriculture, Forest Service.

Ray, C. (1958). Vital limits and rates of desiccation in salamanders. *Ecology*, *39*(1), 75–83.

Reading, C. J. (2007). Linking global warming to amphibian declines through its effects on female body condition and survivorship. *Oecologia*, *151*(1), 125–131.

Riddell, E. A., Odom, J. P., Damm, J. D., & Sears, M. W. (2018). Plasticity reveals hidden resistance to extinction under climate change in the global hotspot of salamander diversity. *Science Advances*, *4*(7), eaar5471.

Rissler, L. J., Barber, A. M., & Wilbur, H. M. (2000). Spatial and behavioral interactions between a native and introduced salamander species. *Behavioral Ecology and Sociobiology*, *48*(1), 61–68.

Roberts, D. A., Dennison, P. E., Roth, K. L., Dudley, K., & Hulley, G. (2015). Relationships between dominant plant species, fractional cover and land surface temperature in a Mediterranean ecosystem. *Remote Sensing of Environment, 167*, 152–167.

Romano, A., Costa, A., Basile, M., Raimondi, R., Posillico, M., Scinti Roger, D., Crisci, A., Piraccini, R., Raia, P., Matteucci, G., & de Cinti, B. (2017). Conservation of salamanders in managed forests: Methods and costs of monitoring abundance and habitat selection. *Forest Ecology and Management*, *400*, 12–18.

Ryan, K. J., Zydlewski, J. D., & Calhoun, A. J. K. (2014). Using passive integrated transponder (PIT) systems for terrestrial detection of blue-spotted salamanders (*Ambystoma laterale*) in situ. *Herpetological Conservation and Biology*, *9*(1), 97–105.

Sheridan, J. A., & Bickford, D. (2011). Shrinking body size as an ecological response to climate change. *Nature Climate Change*, *1*(8), 401–406.

Spotila, J. R. (1972). Role of temperature and water in the ecology of lungless salamanders. *Ecological Monographs*, *42*(1), 95–125.

Stebbins, R. C. (2003). *A Field Guide to Western Reptiles and Amphibians* (3rd edition). Peterson Field Guides. Houghton Mifflin.

Taub, F. (1961). The distribution of the red-backed salamander, *Plethodon c. cinereus*, within the soil. *Ecology*, *42*(4), 681–698.

Thomson, R., Wright, A., & Shaffer, H. (2016). List of California amphibian and reptile species of special concern. In *California Amphibian and Reptile Species of Special Concern*. California Department of Fish and Wildlife.

Thorson, T. B. (1955). The relationship of water economy to terrestrialism in amphibians. *Ecology*, *36*(1), 110–116.

Urban, M. C., Richardson, J. L., & Freidenfelds, N. A. (2014). Plasticity and genetic adaptation mediate amphibian and reptile responses to climate change. *Evolutionary Applications*, *7*(1), 88–103.

US Climate Data. (2022). *Climate - California*. Version 3.0, accessed March 2022.

Weller, H. (2019). *Countcolors: Locates and counts pixels within color range(s) in images* (Version 0.9.1). R.

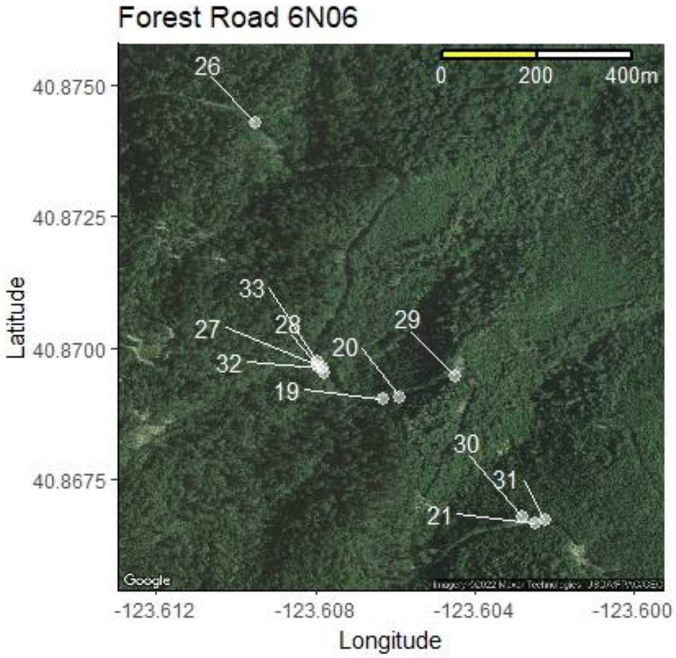
Welsh, H. H., & Lind, A. J. (1992). Population ecology of two relictual salamanders from the Klamath mountains of northwestern California. *Wildlife 2001: Populations*, 419–437. Springer, Dordrecht.

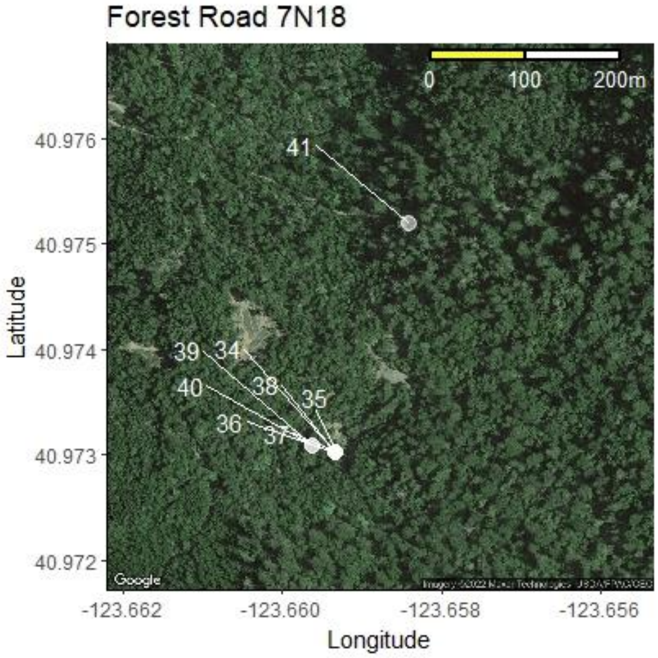
Welsh, H. H., & Lind, A. J. (1995). Habitat correlates of the Del Norte salamander, *Plethodon elongatus* (Caudata: Plethodontidae), in northwestern California. *Journal of Herpetology*, *29*(2), 198–210.

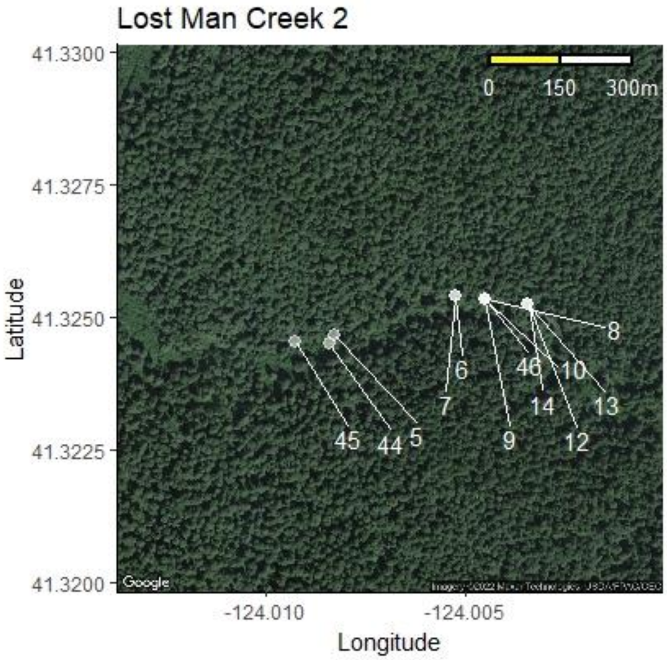
Woolbright, L. L., & Martin, C. P. (2014). Seasonal migration by red-backed salamanders, *Plethodon cinereus*. *Journal of Herpetology*, *48*(4), 546–551.

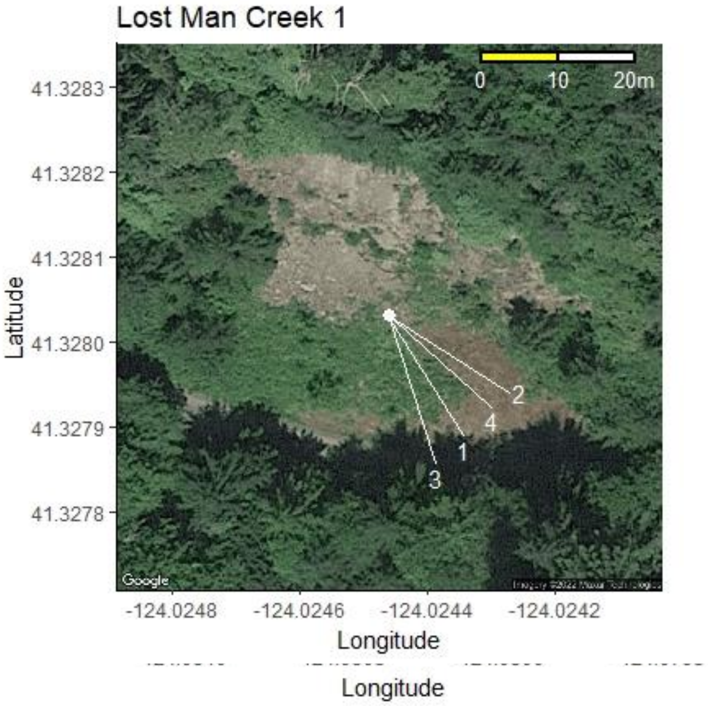
APPENDICES

Appendix A – Site Maps. Satellite maps of each study site, with points marking the location of each individual within the site.






Lost Man Creek 2
0
150
300m
41.3300
41.3275
41.3250
41.3225
41.3200
Latitude
-124.010
-124.005
Longitude
45
44
5
6
7
46
10
8
14
13
9
12
Google


Lost Man Creek 1
0
10
20m
41.3283
41.3282
41.3281
41.3280
41.3279
41.3278
Latitude
2
4
1
3
Google
-124.0248
-124.0246
-124.0244
-124.0242
Longitude
Longitude

Appendix B – Individual Data. A summary of all 46 individuals tagged during this study. Detection counts for each individual are given, and the number of those detections that resulted in physical recapture of the individual listed in parentheses. Body Mass Index (BMI) was calculated as the individual's weight divided by their snout-vent length, using measurements taken when each individual was initially implanted with its PIT tag. The listed coordinates represent the location where each individual was originally captured and tagged. SVL refers to snout-vent length, TL refers to total length. Canopy cover values are absent for sites LM1 and LM2 due to a road closure that made these sites inaccessible when canopy cover photos were taken.

Tag Insertion	Site	ID	Detections	SVL (mm)	TL (mm)	Weight (g)	BMI (g/mm)	Sex	Canopy Cover (%)	Latitude	Longitude
2/21/2020	LM1	1		61.7	100.5	3.3	0.053	F		41.32803	-124.024
2/21/2020	LM1	2		47.2	63.9	1.5	0.032	M		41.32803	-124.024
2/21/2020	LM1	3	1 (1)	64.9	113.5	3.9	0.06	F		41.32803	-124.024
2/21/2020	LM1	4		69.5	129.2	3.7	0.053	F		41.32803	-124.024
2/22/2020	LM2	5		56	94.3	2.3	0.041	M		41.32465	-124.008
2/22/2020	LM2	6		49.3	86.7	1.7	0.034	M		41.32541	-124.005
2/22/2020	LM2	7	3	53.3	94.7			F		41.32541	-124.005
2/22/2020	LM2	8		59.6	109.9	3.3	0.055	F		41.32534	-124.005
2/22/2020	LM2	9		62.5	120.9	4.4		F		41.32534	-124.005
2/22/2020	LM2	10	7	64.3	108.1	3.6		M		41.32534	-124.005
2/23/2020	HBO	11		48.3	75.8	1.7		F		41.51164	-124.08
2/22/2020	LM2	12	4	96.9	62.3	2.8		F		41.32525	-124.003
2/22/2020	LM2	13	1 (1)	63.4	111.3	2.7		F		41.32525	-124.003

Tag Insertion	Site	ID	Detections	SVL (mm)	TL (mm)	Weight (g)	BMI (g/mm)	Sex	Canopy Cover (%)	Latitude	Longitude
2/22/2020	LM2	14	2	68.2	131	4.1		F		41.32525	-124.0034
2/23/2020	HBO	15	1	51.2	81.3	1.8		F	25.6	41.51164	-124.0803
2/23/2020	HBO	16	1	59.4	109.2	3.1		F	6.7	41.51164	-124.0803
2/23/2020	HBO	18		51.5	98.4	2	0.039	F	28.7	41.51164	-124.0803
2/29/2020	6N06	19		61.4	113.6	2.8	0.046	F	46.3	40.86903	-123.6063
2/29/2020	6N06	20	1	59.7	112.8			F	68.1	40.86908	-123.6059
2/29/2020	6N06	21	5 (1)	65.4	124	3.5	0.054	F	67.8	40.86668	-123.6025
3/7/2020	EFCG	22		70.4	133.2	3.7	0.053	F		40.90654	-123.7066
3/7/2020	EFCG	23	9 (1)	60.1	102.1	2.7	0.045	F	63.1	40.90647	-123.7073
3/7/2020	EFCG	24	2	66.4	127.9	4.2	0.063	F	37.4	40.90449	-123.7065
3/7/2020	EFCG	25		66	120.9	3.8	0.058	M	54	40.9038	-123.7065
3/15/2020	6N06	26	2 (1)	64.7	109.2	3.6	0.056	F	63.3	40.87429	-123.6095
3/15/2020	6N06	27	2	64.8	120	3	0.046		77	40.86966	-123.608
3/15/2020	6N06	28		59.5	106.8	3	0.05	F	66.7	40.86954	-123.6078
3/15/2020	6N06	29	8	50.1	92.7	1.8	0.036	M	52.3	40.86946	-123.6045
3/16/2020	6N06	30	5	62	118.6	3.3	0.053	F	28	40.8668	-123.6028

Tag Insertion	Site	ID	Detections	SVL (mm)	TL (mm)	Weight (g)	BMI (g/mm)	Sex	Canopy Cover (%)	Latitude	Longitude
3/16/2020	6N06	31		54.9	100.5	2.3	0.042	M	59.3	40.86674	-123.6023
3/16/2020	6N06	32	2 (1)	54.9	102.8	2.2	0.04	M	29	40.86963	-123.6078
3/16/2020	6N06	33		62.5	119.8	3.6	0.058	F	20.6	40.86975	-123.6079
3/22/2020	7N18	34	1	61	114	3.1	0.051	F	67.1	40.97302	-123.6593
3/22/2020	7N18	35		55	105	2.4	0.043	F	67.1	40.97302	-123.6593
3/22/2020	7N18	36	1	61	114	3.3	0.054	F	78	40.97302	-123.6593
3/22/2020	7N18	37	7	56	95	2	0.036	M	74.5	40.97302	-123.6593
3/22/2020	7N18	38		59	103	2.9	0.049	M		40.97302	-123.6593
3/22/2020	7N18	39	1	49	90	1.7	0.034	M		40.97308	-123.6596
3/22/2020	7N18	40		53	99	2	0.038	M		40.97308	-123.6596
3/25/2020	7N18	41	2 (1)	58	105	2.7	0.046	F	40.4	40.9752	-123.6584
4/24/2020	EFCG	42	3	51	88	1.8	0.035	M	54	40.9038	-123.7065
4/24/2020	EFCG	43		62	79	3.1	0.05	F	69.2	40.9038	-123.7065
6/18/2020	LM2	44	5	61	113	3.6	0.059	M		41.32449	-124.0084
7/11/2020	LM2	45	4	63	113	3.4	0.053	F		41.32454	-124.0093
7/11/2020	LM2	46	7	54	96	2.1	0.039	F		41.32534	-124.0045

Appendix C – Continuous Variable Summary Statistics. Mean, standard deviation, and the range of values is given for each variable. Variables marked with * were only collected during the second phase of this study, when data loggers were deployed. Canopy cover statistics do not include sites LM1 and LM2 due to a road closure that prevented re-visiting these sites.

Continuous Variable	Mean	Standard Deviation	Range
Observed Temperature (℃)	19.9	7.526	4.4 – 39.4
*Maximum Temperature (℃)	19.6	9.711	7.2 – 40.8
*Mean Temperature (℃)	11.0	5.184	1.9 – 23.2
*Minimum Temperature (℃)	6.0	4.097	-1.0 – 16.8
*Maximum Humidity (%)	85.2	13.955	59.1 – 100.0
*Mean Humidity (%)	81.7	15.496	52.2 - 99.0
*Minimum Humidity (%)	75.0	18.948	35.6 – 99.5
Canopy Cover (%)	50.3	0.187	4.4 – 78.0
BMI (g/mm)	0.05	0.001	0.03 – 0.07
Weight (g)	2.8	0.800	1.5 – 4.4
SVL (mm)	59.7	8.257	47.2 – 63.6
TL (mm)	104.5	16.287	62.3 – 113.9
Distance Moved (cm)	43	36.637	0 – 163
Distance Moved Over 24-Hours (cm)	33	30.275	0 – 84

Appendix D – Categorical Variable Summary Statistics. For every factor level of each variable, the overall detection rate was calculated by dividing the number of salamander detections divided by the total number of surveys conducted for that factor level. For site, cloud cover, and region, the sample size *n* refers to the number of surveys conducted within each factor level, whereas for sex, the values given for *n* correspond to the number of individuals of each sex that were redetected at any point during the survey period.

Variable	*n*	Overall Detection Rate (%)
Site: 6N06	40	6.8
Site: 7N18	40	3.8
Site: EFCG	40	6.0
Site: HBO	38	3.6
Site: LM1	38	0.8
Site: LM2	38	8.3
Cloud Cover: Clear	87	8.3
Cloud Cover: Light	47	5.7
Cloud Cover: Moderate	88	12.3
Cloud Cover: Complete	12	11.6
Sex: F	19	8.5
Sex: M	7	13.7
Sex: unknown	1	5.3
Region: Inland	120	5.6
Region: Coast	114	5.7