# How far does the salamander go? Estimating migration distances and quantifying range wide suitable habitat availability for an imperiled salamander

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## Abstract

Many organisms with complex life cycles rely on both terrestrial and aquatic habitats to survive, which increases their susceptibility to habitat fragmentation as they require access to sufficient amounts of both habitats and connectivity between them. Amphibians are particularly susceptible to fragmentation and are declining globally. We conducted the first range-wide geospatial analysis for the federally endangered Santa Cruz Long-toed Salamander (SCLTS; *Ambystoma macrodactylum croceum*) to address the impacts of land use change and habitat fragmentation as barriers to recovery. First, we used data from an extensive drift fence array to determine migration distances of SCLTS. We then used these calculated distances to determine the amount of suitable and accessible habitat around all current breeding ponds as well as those being considered as potential release sites. Land use changes have reduced the amount of suitable upland habitat within migration distance of SCLTS breeding ponds by 34% across the range. Habitat fragmentation due to roads has further reduced uplands by another 12% and sea level rise projected by 2060 reduces it another 14%, leaving only 40% of potential terrestrial habitat suitable, accessible, and unflooded. Based on a population viability analysis (PVA) developed for the congeneric California tiger salamander, this would render only 24% of SCLTS breeding populations viable in the long term based on terrestrial habitat quality. This range-wide assessment provides guidance on which breeding populations should be targeted for land use restoration and experimental road crossing structures, and which potential breeding sites should be prioritized for release of captive-bred animals.


## Introduction

Many organisms with complex life cycles need access to both terrestrial and aquatic habitats in order to thrive and carry out all parts of their life histories. These multimodal species include insects, birds, amphibians, reptiles, and even some mammals (Moran 1994; Baldwin et al. 2006; Bueno et al. 2013; Jackson et al. 2019). Animals with these multimodal life histories can be difficult to study and conserve because these unique requirements make them hard to track as they traverse multiple habitat types and pass through multiple body forms (Baldwin et al. 2006; Bueno et al. 2013; Jackson et al. 2019, Pittman et al. 2014). Such species are often susceptible to movement barriers such as roads, urbanization, and other habitat alterations that inhibit migration between or use of terrestrial and aquatic habitats (Spinks et al. 2003; Semlitsch and Bodie 2003; Wells 2007; Brand and Snodgrass 2010; Reid et al. 2016; Rothenberger et al. 2019). For example, habitat degradation, like loss of wetlands from urbanization (Hamer et al. 2012), or a high density of roads in the uplands (Bueno et al. 2013; Zhang et al. 2022) can lead to reduced populations through diminished recruitment or high adult mortality. This pattern can be observed with sampling, and assessing species at multiple scales (Marchland and Litvaitis 2004).

Biphasic pond-breeding amphibians breed and develop as larvae in ponds, but also have a terrestrial life stage. They are a group of semi-aquatic organisms that are declining globally; in fact, amphibians are the most imperiled vertebrate class (Luedtke et al. 2023). Major threats include habitat loss and fragmentation, invasive species, pollution and chemicals, climate change, and disease (Gallant et al. 2007; Nolan et al. 2023). As biphasic pond-breeding amphibians need aquatic and terrestrial habitats to complete their life cycles, assessment of habitat preferences and habitat availability in both habitat types are required for building ecological understanding and proposing sound conservation actions (Wells 2007; Semlitsch et al. 2017; Stokes et al. 2021). Historically, many studies on amphibians have focused on aquatic life stages, even though most species spend the majority of their lives on land (Pittman et al. 2014). As these terrestrial life stages are critical for population viability, if terrestrial (also known as upland) habitat is not considered for conservation actions, demographic rates may suffer due to loss of dispersing juveniles and migrating adults at roads, and loss of favorable habitat types near ponds that would support high survival and growth rates needed to reach maturity (Rothermel and Semlitsch 2002; Gibbs and Shriver 2005; Semlitsch et al. 2017; Messerman et al. 2023). For example, if terrestrial habitats become too hot and/or dry, dispersing small-bodied juveniles may encounter greater landscape resistance due to an increased risk of desiccation (Rothermel and Semlitsch 2002; Lee-Yaw et al. 2015). Many amphibians benefit from forested habitats, for example, juvenile spotted and smallmouth salamanders have four-fold greater movement and recapture rates in forest compared to open fields (Rothermel and Semlitsch 2002). While terrestrial migration distances, movement, and upland habitat preferences are important aspects of amphibian ecology, the distribution of individuals across the upland landscape is understudied because their subterranean lifestyle makes it difficult for researchers to track them (Pittman et al. 2014).

Furthermore, many amphibian species are understudied in all aspects of their ecology. Despite being listed among the inaugural class of US Endangered Species in 1967, the Santa Cruz Long-toed Salamander (SCLTS, *Ambystoma macrodactylum croceum*) falls in this category of understudied species as there is very little information on SCLTS in the scientific literature. Their habitat is inundated with human pressures, including a high-density road network and expanding suburbs at the northern edge of their range, and dense agriculture in the southern portion. Additionally, many of the breeding ponds in the southern portion of the range are at low elevation along the edge of estuaries, which makes them susceptible to sea level rise (Camera et al. 2019; Stemle unpublished data). Without information on their ecology, it is difficult to manage their dwindling populations using tools such as constructed breeding ponds, land acquisition of high-priority sites, restoration of suitable vegetation, and captive-breeding programs. Previous studies undertaken on SCLTS are few and focus on courtship behavior and diet (Anderson 1961, 1967, 1968, 1972) and do not provide the information on habitat requirements needed to effectively recover the species. There are recent efforts to develop a captive breeding program for the species. This program involves releasing captive bred larvae into mostly constructed ponds. To optimize which locations should be targeted for release of captive-bred larvae, we need more robust estimates of distances SCLTS travel across the terrestrial landscape and the distribution of suitable and accessible habitat within these migration distances.

To address this gap in knowledge, our study analyzes 15 months of historic drift fence data from a pond in Santa Cruz County to determine the magnitude of SCLTS migration distances. Using these data, we then conduct the first comprehensive range-wide GIS analysis of what suitable habitat is available to SCLTS around 47 current (2019–2023) and potential breeding sites. Understanding available habitat in the context of these distances will aid in providing: 1) targets for which upland habitat should be prioritized for restoration and management of vegetation types, 2) which breeding sites would benefit from mitigation of road barriers, 3) which ponds and terrestrial habitat may be inundated with saltwater due to sea level rise, and 4) which ponds should be selected for release of captive-bred individuals.

## Materials and Methods

# Species Distribution

SCLTS' range spans southern Santa Cruz and northern Monterey Counties, California, USA (Fig. 1), and there are only approximately 38 known breeding ponds recently used by SCLTS (Camara et al. 2019; USFWS 2019; Stemle and Searcy unpublished data). These ponds range from ephemeral vernal pools to seep-fed, perennial ponds. In Monterey County, breeding locations are often at low elevations and near the edge of estuaries. The number of available ponds fluctuates depending on private land management and the timing and amount of rainfall, which affects pond hydroperiod (USFWS 2009; Camara et al. 2019). California has a Mediterranean climate with dry summers (4 cm precipitation total across May-Oct) and wet winters (44 cm precipitation Nov-Apr), and across the coastal range of SCLTS temperatures are mild year-round (11°C – 16°C). There are six recognized metapopulations with 2–13 ponds per metapopulation (Savage 2009; USFWS 2019). In general, the range of SCLTS is heavily populated and characterized as rural-residential (Bury and Ruth 1972; USFWS 1999; note density of roads in Figs. 2 and 4). For example, the initial site of SCLTS discovery in 1954, Valencia Lagoon, is surrounded by a major highway on one side and a residential neighborhood on the other (Anderson 1966; Ruth 1974, 1998; Kasteen, et al. 2021). Natural upland areas around ponds range from oak-woodland to grassland/scrub habitat, whereas suburban areas include houses on large plots of land, and residential neighborhoods. Areas close to ponds are often bisected by gravel or paved roads or even highways.

# Drift Fence Data

A large drift fence array was monitored from February 2, 1986 - May 5, 1987 around a breeding pond in Seascape Uplands in Santa Cruz County, California. Seascape Uplands is an area of oak-woodland and scrub habitat adjacent to residential neighborhoods and roads (Fig. 2). It is thus representative of the fragmented habitat that SCLTS are currently confronted by across their range rather than pristine conditions in which migrations of any distance could be undertaken without impediment, although there are no anthropogenic barriers between the breeding pond and the drift fences themselves. Rainfall across the entire study period was 99% of average, but arrived unevenly, with above average precipitation in Feb-Mar 1986 at the beginning of the study period, followed by very dry conditions in Oct-Dec 1986, before average rainfall returned in Jan-Mar 1987 (see Appendix S1: Table S1). The high rainfall in early 1986 led to a large number of juveniles being present in late 1986, but their dispersal was delayed by the lack of rains in late 1986, as was the 1986-87 breeding season that ended up occurring in early 1987 and was male-biased. The drift fence study was conducted to support a Habitat Conservation Plan that conserved approximately 147 acres and permitted additional residential development beginning in 1998 (Thomas Reid Associates 1995). Dominant vegetation communities in the vicinity of the focal breeding pond include: oak woodland (coast live oaks (*Quercus agrifolia*) and poison oak (*Toxicodendron diversiloba*)), Eucalyptus forest, coastal scrub, coyote bush scrub (coyote bush (*Baccharis pilularis*)), and grassland, while vegetation at the pond includes bulrush (*Scirpus sp.*), knotweed (*Polgonum sp.*), spikerush (*Eleocharis sp.*), and cattails (*Thypha sp.*). We analyzed this drift fence data contained in a report by Stephen Ruth (1989). The dataset consisted of 8277 SCLTS captures at 353 trapping locations (pitfall traps deployed every 6–13 m (mean = 8.3 m) along drift fences). We digitized the locations of drift fences based on maps provided in the report (Fig. 2., Ruth 1989). Trapping locations ranged 3-838 m from the edge of the breeding pond.

# Migration Distances

We calculated the density of SCLTS in each 20-m interval from the pond shoreline up to 840 m into the terrestrial habitat. This provided density estimates from 38 distance intervals (no data from the intervals 700–780 m from the pond edge). The number of trapping locations per interval ranged from 1–35 (median = 6.5). Captures included both juveniles and breeding adults, so in order to combine the data from the two age classes in a manner that reflected their relative importance to the population, we weighted each age class by its relative reproductive value (Searcy and Shaffer 2008). Based on demographic rates from the congeneric and co-occurring *Ambystoma californiense* (Messerman et al. 2023), we estimated reproductive value of a juvenile to be 0.26 that of a breeding adult, representing that 26% percent of juveniles make it to adulthood. After calculating the density of reproductive value for each 20-m distance interval, we applied a square-root transformation to increase normality and fit a non-linear regression (exponential decay) to the data (Fig. 3). Using this function to represent SCLTS density in relation to distance from the breeding pond, we used integrals (Wolfram Research Inc. 2022) to estimate how far from the pond edge a preserve would need to extend in order to include 50%, 95%, or 99% of the SCLTS population. The integration procedure accounts for both the radius of the breeding pond itself and the fact that more terrestrial habitat occurs at increasing radii away from the pond edge (Searcy and Shaffer 2011).

# GIS Habitat Analyses

We examined upland habitat around all known breeding sites across the range of SCLTS (38 ponds), as well as 9 nonbreeding constructed ponds that are being considered as potential translocation sites. To create pond shoreline polygons, we used satellite imagery to determine the maximum fill line of each pond based on the transition from aquatic to terrestrial vegetation. We then created two upland habitat buffers for each pond using the distance that would encompass 50% or 95% of the SCLTS population. We calculated the area of different habitat use classifications that are within these buffers (National Land Cover Database (NLCD) 2019; 30-m resolution) using the “tabulate area” function in ArcGIS Pro (ESRI, v. 10.7.1). After discussing with SCLTS experts (Allaback, personal communication), we defined suitable habitat types to include: developed open space, mixed forest, deciduous forest, evergreen forest, scrub/shrub, emergent wetlands, and woody wetlands. We considered developed (low, medium, and high intensity), barren land, open water, grassland/herbaceous (possibly okay for dispersing but not over summering), cultivated crop, and hay/pastureland (pastureland possibly okay for dispersing but not over summering) as unsuitable habitats. While there is variation among the habitat types classified as unsuitable in terms of their permeability to SCLTS movement, they are all considered unsuitable as maturation habitat (i.e., habitat where SCLTS could spend multiple years while growing to the size needed for reproductive maturity). To account for habitat that is blocked from SCLTS use by roads, we split the buffers by any roads that had Average Daily Traffic (ADT) > 1,000, which we consider a significant barrier due to *Ambystoma californiense* and *Ambystoma maculatum* mortality on roads with this volume (Allaback and Laabs 2003; Cook unpublished data; Gibbs and Shriver 2005; Hobbs 2013). We used a road layer from the US Census Bureau, Department of Commerce (2017) TIGER/line road and highway data, and gathered ADT data from Monterey 2020 road counts (https://www.tamcmonterey.org/traffic-counts), California 2022 Highway counts (https://www.tamcmonterey.org/traffic-counts), or by gathering local expert opinion on roads where no governmental data were available (Allaback personal communication). With these altered buffers accounting for roads as barriers, we then calculated the percentage of total potential habitat around each pond that was both suitable and accessible.

All upland habitat within the terrestrial buffers is not of equal value to SCLTS populations. Instead, SCLTS density declines as a function of distance from the breeding pond (Fig. 3). We used this function to calculate the percentage of SCLTS associated with each breeding pond that would live within the suitable and accessible habitat buffer. To do this in ArcGIS Pro, we measured Euclidean distance from each pond polygon and then used the Raster Calculator to calculate the value of each pixel based on the function in Fig. 3. Lastly, using the Zonal Statistics tool, we summed the values of the pixels within the suitable and accessible habitat buffer and divided this by the summed values of all the pixels within the relevant migration distance (50% or 95%) of the pond shoreline. This ratio represents the fraction of SCLTS associated with each pond expected to live within the suitable and accessible habitat buffer.

Next, we intersected the suitable and accessible habitat buffers with a GIS layer of protected lands (USFWS, CDFWS, NOAA, Elkhorn Slough Foundation, Seascape Uplands, conservation easements; California Protected Area Database 2023). For each breeding pond, we calculated the percentage of the suitable and accessible habitat buffer that is currently protected.

## Sea Level Rise Analysis

We intersected the pond polygons and suitable and accessible habitat buffers with two sea level rise projection layers representing 2060 and 2100 (Environmental Science Associates & Phillip Williams Associates 2014). This layer was made as a part of the Monterey Bay Sea Level Rise Vulnerability Assessment using elevation, topography, and Intergovernmental Panel on Climate Change data to predict storm surge, frequent flooding, and tidal inundation that would case saltwater intrusion (Environmental Science Associates & Phillip Williams Associates 2014). Based on the overlap between the pond and sea level rise layers, we calculated the percentage of ponds that would be inundated with saltwater, or for those ponds not directly impacted the percentage of their accessible habitat buffers that would be.

# Results

## Migration Distances

An exponential decay function worked well and accounted for 75% of the variance in the relationship between SCLTS density and distance from the breeding pond ($R^2$ = 0.75; Fig. 3). By integrating this function, we determined that terrestrial buffer widths of 196 m (95% CI: 154–264 m) and 598 m (95% CI: 479–792 m) would encompass 50% and 95%, respectively, of the SCLTS reproductive value around a breeding pond. An exponential decay function fit solely to breeding adult captures and ignoring juvenile captures accounted for 73% of the variance in SCLTS adult densities, and the terrestrial buffer widths needed to encompass 50% and 95% of the breeding adult population varied less than 2% from those calculated above (193 m and 591 m). A buffer of 847 m (95% CI: 680–1119 m) from the pond edge would encompass 99% of the SCLTS reproductive effort, although this is clearly an extrapolation since it is just beyond the farthest fences employed in this study.

## GIS Habitat Analyses

Range wide, a mean of 64.5% of upland habitat within 598 m of the breeding ponds (encompassing 95% of the SCLTS populations) is of suitable land use types, with unsuitable habitat being mostly grassland/herbaceous (16.1%; possibly okay for dispersing but not over summering), developed low intensity (7.6%), or cultivated crops (5.3%). Suitable habitat within the 95% buffers ranged from 13.9–94.9% (Table 1; Fig. 5) and was mostly mixed forest (16.7%), scrub (13.8%), or developed open space (13.5%). The amount of suitable habitat increases when considering the mean migration distance (196 m buffers), with a mean of 75.1% (range 29.6–100%) of terrestrial habitat suitable for SCLTS.

## Road analyses

When road barriers were considered, uplands both suitable and accessible to SCLTS were reduced another 12% on average to a total of 52.7% of terrestrial habitat being both accessible and suitable within the 598 m buffers (ranging from 1.9–91.6%; Table 1; Fig. 4C and D). Only 8 out of the 38 breeding ponds have 598-m buffers that do not intersect roads with ADT > 1,000 cars/day. The situation was again more favorable when considering the mean migration distance, with 69.9% of terrestrial habitat being both suitable and accessible (range 9.8–100%). Eleven out of 38 196-m buffers intersected roads with ADT > 1,000 cars/day.

When using the dispersal kernel function to calculate the percentage of SCLTS expected to live within the suitable and accessible habitat buffers, we reach a range wide average of 67.6% (range 9.6–98.3%). When roads aren't considered as barriers, the average is 71.2%. Based on a population viability analysis for the congeneric and co-occurring *Ambystoma californiense*, populations can withstand 16.9% of additional human-induced mortality while still remaining viable in the long-term (< 5% extinction probability over the next 100 years; Messerman et al. 2023). Only 9 of the 38 SCLTS breeding ponds reach this threshold for long-term viability, with > 83.1% of their populations projected to live within their suitable and accessible habitat buffer (see Table 2).

## Sea Level Rise Analysis

Thirteen of the 38 (34%) SCLTS breeding ponds are expected to be inundated with saltwater by the year 2060. All 13 of these ponds are in Monterey County, where many of the breeding sites are on estuary margins or in their associated floodplains. One of the breeding ponds is already often unusable for SCLTS due to ground saltwater intrusion in drier years, and two other breeding ponds were breached with saltwater in 2015 and had no recorded breeding until 2019 (South Moro Cojo) or the recent 2023 El Niño (Lower Cattail; Searcy and Stemle unpublished data). It is possible that other historic breeding ponds in Monterey County have already been extirpated by saltwater issues (Camara et al. 2019; Chad Mitcham communication). Only one current breeding pond in Monterey County has a 598 m buffer that is not projected to have some saltwater intrusion by 2060 (Daniel's Pond). Overall, we predict an 86.7% decline in usable breeding pond habitat in Monterey County by 2060. In contrast, none of the breeding ponds (or their 598 m buffers) in Santa Cruz County are projected to become saline by 2060 or 2100. When compounding the effects of land use change, road barriers, and sea level rise, only 40.0% of SCLTS habitat is projected to be usable by 2060.

## Latitudinal Analyses

There is a positive correlation between latitude and suitable and accessible habitat within the 598 m buffers of breeding ponds ($R^2 = 0.29$, $p = 0.0005$; Fig. 5). There is an even stronger relationship between latitude and suitable habitat within 598 m of the breeding ponds when barriers are not considered ($R^2 = 0.55$, $p < 0.0001$). We observed the same trend with the 196 m buffers (barriers considered: $R^2 = 0.19$, $p = 0.006$; no barriers: $R^2 = 0.31$, $p = 0.0002$), but with less significance overall, as more ponds had suitable habitat closer to the ponds throughout both counties. The latitudinal gradient was driven by a greater amount of agricultural development in Monterey County compared to Santa Cruz County ($R^2 = 0.20$, $p = 0.005$) and a greater amount of forest habitat in Santa Cruz County ($R^2 = 0.47$, $p < 0.0001$; see Fig. 5).

Overall, 31 of the 38 (82%) breeding ponds are on protected land. Thirty-seven of the 38 (97%) ponds have suitable and accessible habitat buffers that intersect with protected land, but none of the 38 have fully protected buffers. On average, 39.5% of the habitat associated with each pond is protected (0.149–98.80%). In Monterey County, the Elkhorn Slough Foundation, and then California Department of Fish and Wildlife are the owners of SCLTS habitat. In Santa Cruz County, the California Department of Fish and Wildlife and the United States Fish and Wildlife Service owned the most abundant amount of SCLTS habitat.

# Constructed Ponds

The variation in habitat status of the constructed ponds can be used to guide where releases of captive-bred animals should take place. On average, 86.4% of the habitat associated with each constructed pond is protected (55.7% – 100%). Five out of the 9 constructed ponds have 598-m buffers that do not intersect roads with ADT > 1,000 cars/day and 8 out of the 9 196-m buffers do not intersect with high volume roads (Hix is the only exception). In the 598 m buffers, the average suitable and accessible habitat is 66.1% (45.4% – 80.5%). The mean percentage of the SCLTS populations expected to occur within this suitable and accessible habitat is 68.7% (43.7% – 84.4%). One of the nine newly constructed ponds will be inundated with saltwater by 2060 (Swimming Pool) and a second of the nine by 2100 (Hix). In fact, the first of these (Swimming Pool) is already too saline in drier years (> 5 ppt). Among the other constructed ponds, the amount of saltwater intrusion expected by 2060 in the 598 m buffers ranged from 0 to 11.3% (n = 8).

## Discussion

Our study is the first to estimate the migration distance of the endangered Santa Cruz Long-toed Salamander (mean distance: 196 m, 95% within 598 m, 99% within 847 m). These migration distances can be used by government agencies and land managers to inform mitigation, conservation, and pond construction efforts to better conserve SCLTS populations and metapopulations. Moreover, we used these migration distances to conduct a complete range-wide assessment of suitable and accessible upland habitat around all known SCLTS breeding sites. There are three key stressors affecting the amount of terrestrial habitat available for the federally endangered SCLTS, including (1) land use change, (2) habitat fragmentation caused primarily by roads, and (3) sea level rise. We found that, on average, only 66% of habitat within the 95% migration distance of SCLTS is suitable for their use. When roads are considered as barriers, this is reduced to 54%. For a species that spends the vast majority of its life in subterranean upland habitats, having such a low percentage of this habitat usable is likely detrimental to population trends (USFWS 2019; Messerman et al. 2023). There is also a clear latitudinal gradient in the amount of terrestrial habitat available to SCLTS, with more agricultural development at the southern end of the range. This is also the part of the range at greater risk from sea level rise. In Monterey County, 13 of 15 (87%) breeding ponds are faced with probable saltwater intrusion by 2060. The compounding effects of all these stressors (land use change, roads/habitat fragmentation, sea level rise) leaves only 40% of SCLTS habitat suitable, accessible, and unflooded by 2060, highlighting the plight of this species and its need for rapid implementation of recovery strategies.

While the migration distances of SCLTS are not as long as those of the congeneric and co-occurring *Ambystoma californiense* (504 m and 1703 m for the 50% and 95% buffers, respectively; Searcy and Shaffer 2011; USFWS 2016), their distribution across the uplands is comparable to many other species of amphibians. For instance, amphibians generally have core (mean migration) terrestrial habitat ranging from 159–290 m into the uplands (Semlitsch and Bodie 2003). SCLTS migration distances are analogous to congenerics in the eastern US, e.g., mean migration distance for experienced breeders of *Ambystoma opacum* is 197 m (maximum 439 m; Semlitsch 1998; Gamble et al. 2007). The 95% migration distance for *Ambystoma jeffersonianum* is almost as large as for SCLTS (483 m; Ontario Ministry of Natural Resources, 2008 unpublished study; Van Drunen et al. 2020). *Ambystoma maculatum* have only been found a maximum of 300 m from pond edges (Semlitsch 1998; Vasconcelos and Calhoun 2004), but are impacted by habitat quality up to 1 km around their breeding ponds (Homan et al. 2004, 2008; Porej et al. 2004).

The presence of roads in terrestrial buffers also affects habitat quality, with overall salamander diversity being negatively correlated with the total amount of paved road within 1 km of breeding ponds (Porej et al. 2004). Thus, our geospatial mapping took the added step of investigating which roads might be shrinking accessible habitat within migration distance of SCLTS breeding ponds, impeding movement between upland and aquatic habitat and between ponds within the six metapopulations. This analysis also indicates which roads could be considered for road signs, road crossing brigades, seasonal road closures, and road tunnels/bridges. Roads with > 250 cars/day have been documented as being essentially impenetrable to *Ambystoma maculatum* (Gibbs and Shriver 2005). With 65% of breeding ponds across the range of SCLTS having a road with > 1000 cars/day within migration distance, road mortality constitutes a major threat to species persistence. Road mortalities have been documented on many roads with the above traffic volume, including San Andreas Road next to Ellicott Pond (USFWS unpublished data), Larkin Valley Road next to Calabasas Pond (USFWS, unpublished data), Bonita Drive next to Valenica Lagoon and Seascape Pond 3 (Allaback and Laabs pers comm), and White Road next to Millsap Pond (Allaback and Laabs pers comm). Valenica Lagoon, which is bounded by both Bonita Drive and Highway 1 and thus only has access to 2% of its potential upland habitat, is a top target for possible road-focused solutions to reduce mortality such as road signs, periodic road closures, or an elevated road (Brehme et al. 2023). For many taxa, including many herpetofauna, roads have been shown to destabilize populations and impact sex ratios (Carr and Fahrig 2001; Aresco 2005; Steen et al. 2006); thus, we cannot ignore road impacts including direct mortality and the genetic barriers they create between populations.

Another challenge this species faces is sea level rise and saltwater inundation of both breeding pools and terrestrial habitat. Some amphibians are more salt tolerant than other groups (Hopkins and Brodie 2015; Albecker and McCoy 2017). In the family Ambystomatidae, observed environmental salinity tolerances range from 1–15 ppt (Hopkins and Hopkins 2015; Duerr and Ness 1970), while some Ranid frogs have been documented with salinity tolerance up to 39 ppt (McCoid 2005). Local adaptation to salinity has been reported in *Ambystoma maculatum*, but fitness of all genotypes is still reduced in the saline habitat compared to freshwater (Brady 2012). Thus, even if adaptation to salinity does occur in SCLTS, it may not be sufficient to rescue saline habitats from becoming population sinks. In this case, SCLTS populations in Monterey County, where there is already less suitable habitat due to agriculture, stand to lose a great deal of their currently utilized breeding and adjacent upland habitat by 2060. Saltwater intrusion has already begun, making three Monterey ponds (Howell, Lower Cattail, South Moro Cojo) unusable for the salamanders in drier years because the salinity level exceeds 3 ppt, which is known to cause larval die-offs in this species (Camara et al. 2019). For releasing captive-bred individuals, we suggest focusing most effort on ponds that will not be inundated with saltwater and will have little flooding of the terrestrial buffer by 2060. This includes a plethora of ponds in Santa Cruz County and many constructed ponds on Elkhorn Slough Foundation land in Monterey County with substantial patches of adjacent oak woodland.

All of these aforementioned factors compounded together reduce SCLTS terrestrial habitat to only 40% suitable, accessible, and unflooded, raising concerns about long-term viability (Tables 2 and 3). Accessible and usable terrestrial habitat is required for population persistence of biphasic pond-breeding amphibians because the survival rates of terrestrial juveniles and adults have high elasticity values in demographic models for these species (Biek et al. 2002; Trenham and Shaffer 2005; Searcy and Shaffer 2008; Stokes et al. 2021). For instance, Cayuela et al. (2015) found that the amount of urbanization and road networks within a 1500 m buffer around ponds had detrimental effects on the distribution of an imperiled toad. Similarly, Homan et al. (2004) found a critical habitat threshold for spotted salamander occupancy was 51% forest cover within 1000 m of a pond and Guderyahn et al. (2016) showed 25% built land cover within 200 m was a critical threshold negatively related to northwestern salamander occurrence.

Applying the cutoff for long-term viability from the *Ambystoma californiense* population viability analysis (PVA; Messerman et al. 2023; Akçakaya 2000) to our study's results revealed that only 24% of the current SCLTS breeding sites have sufficient terrestrial habitat. Even though SCLTS are currently persisting at the other 76% of sites, this does not mean those sites are viable in the long term. Extinction debt refers to delayed species loss after habitat destruction or degradation has occurred (Semlitsch et al. 2017). Basically, when mortality rates are increased due to an anthropogenic disturbance, it may still take many generations before a population is extirpated. This time lag between when a disturbance occurs and when the affected population reaches the new equilibrium created by that disturbance is a window of opportunity. It is a period during which restoration measures can be implemented to reverse the decrease in habitat quality/quantity that has occurred and return to a state in which the equilibrium favors population persistence (Semper-Pascual et al. 2018). We believe that many of the SCLTS populations are currently in that window in which taking action is of critical importance.

It is also important to acknowledge that while the maximum human-induced mortality rate that still allows for long-term viability (16.9%) identified by the CTS PVA is likely accurate, how this is converted into a necessary percentage of suitable and accessible upland habitat requires additional assumptions. In particular, some fraction of salamanders may successfully navigate road barriers and locate suitable habitats on the far side, or even settle in unsuitable habitat for a period of time depending on its type (e.g., over summering in grassland). Others may remain within the suitable habitat boundary and persist within the suitable habitat at higher-than-normal densities. The inability of SCLTS to persist at higher-than-normal densities within the suitable habitat depends on the existence of terrestrial density dependence, which is difficult to prove in amphibians like SCLTS that spend the majority of their post-metamorphic lives underground. However, when sufficient data has been collected (Pechmann 1995; Berven 2009), the indication is that resources within the terrestrial environment are indeed limiting. In summary, while breeding ponds with less than 83.1% of suitable and accessible upland habitat are a cause for concern (especially the fact that > 75% of the SCLTS ponds fall into this category), such ponds should be viewed as a call for additional management actions (e.g., habitat restoration, road mitigation) rather than written off as of no value to SCLTS persistence.

This study's calculations of which ponds have suitable terrestrial habitat for long-term viability are also important to consider when screening release sites for the captive breeding program (see Table 4). Germano and Bishop (2009) found that the primary reported cause of failure for release of translocated amphibians was poor habitat quality at the release sites. From 2018–2020, SCLTS larvae were successfully translocated to Willow Canyon Pond (Kasteen et al. 2021), which has since become a self-sustaining population on preserved land that, based on our estimate, provides suitable and accessible habitat for 78% of the adult population. For future releases, we suggest targeting ponds with > 65% of the SCLTS population projected to occur within the suitable and accessible habitat buffer as this is greater than the current range-wide average (see Appendix S1: Table S2 for the percentage of each SCLTS population expected to be supported at each pond). Fortunately, 6 of the 9 release sites that are currently under consideration are above this terrestrial habitat threshold.

While our analyses provide a thorough status assessment of terrestrial habitat across the range of SCLTS, there are some limitations. First, terrestrial habitat quality provides only half the story in a biphasic species like SCLTS, and aquatic habitat (e.g., depth, area, salinity, vegetation, prey density) needs to be of sufficient quality to support population persistence as well (Marchand and Litvaitis 2004; Cook et al. 2023, Stemle and Searcy 2024). Second, the National Land Cover Database layer does not differentiate between forest comprised of primarily native species (e.g., oak woodland) and those comprised of primarily invasive species like Eucalyptus, which are prevalent throughout the SCLTS range. Impacts of invasive Eucalyptus on amphibians include weaker immune responses, low nutrient leaf litter, and the presence of its toxic detritus/leachates can have notable stress-related consequences for the critical early stages of development in anurans (Iglesias-Carrasco et al. 2022). While data on the distribution of Eucalyptus is not available across the entire range of SCLTS, within Santa Cruz County Eucalyptus make up an average of 17.1% of all habitat currently counted as suitable (median 9.6%; GIS layer from Santa Cruz and Santa Clara County Enhanced Lifeform Map; Appendix S1: Table S3). Previous reports have raised concerns about Eucalyptus based on both SCLTS being captured more frequently in oak woodland than in Eucalyptus and on oak woodland supporting significantly more burrowing mammal activity (Biosearch Associates 2016). Third, all land use types counted as unsuitable in this analysis are not equivalent, with some likely allowing greater permeability to SCLTS movement than others. For example, grassland, which accounts for 17% of all upland habitat adjacent to SCLTS breeding ponds (see Appendix S1: Table S4), can be used by adult SCLTS for temporary cover during migration, sometimes for several days, since above ground movements only occur during rain events (Laabs and Allaback unpublished data). Furthermore, a percentage of post-metamorphic juveniles are expected to settle in grassland that is adjacent to breeding locations, and those that survive emigrate farther with the onset of winter rains in an effort to reach appropriate upland. Finally, migration distances may vary between breeding ponds. Our estimate is taken from a single site and then applied across the whole range. The drift fences in this study were in a mixture of forest, scrub, and herbaceous/pasture habitat that had limited upland outside of the study area due to a residential neighborhood and perimeter roads. This could have reduced migration distances since open canopy habitats often have higher resistance to amphibian movement (Rothermel and Semlitsch 2002; Lee-Yaw et al. 2015). Alternatively, this habitat context could have increased migration distances since salamanders might cross the grassland to settle in forest habitat at the far side (Nadorozny 1997).

Finally, while for this study we are focusing on the buffer width needed to contain 95% of the SCLTS population, as this is where the majority of salamanders are found, there are salamanders travelling even greater distances from the pond shoreline (at least 838 m in this dataset and with the top 1% estimated to travel ≥ 847 m) as the tail of the dispersal kernel extends out long past that of 95% of the population. For example, during an upland study near the eastern edge of their extant range in Santa Cruz County, seven adult SCLTS were captured at pitfall traps situated 908–975 m from the nearest known breeding pond, four heading toward the pond in reproductive condition at the beginning of the breeding season and three returning in the opposite direction at the end of the season (Allaback and Laabs personal observation). Given its Endangered status, “take” of this species at any distance is not allowed.

# Conclusions

Based on our range-wide assessment of terrestrial habitat quality, we have generated a list of ponds that should be prioritized for different types of habitat management given the nature of their most poignant stressors (see Table 3). We have similarly applied our methodology to constructed ponds that are being considered as release sites for captive-bred animals and find that many on Elkhorn Slough Foundation lands are in high quality terrestrial habitat with higher elevations, suitable land use types, and without major roads. To make the approach even more proactive, a list of sites where new pond construction is being considered could be pre-screened using the above methods in order to generate a ranked list of where the initiation of new metapopulations would be most promising.

Overall, animals with complex life cycles are faced with a plethora of different threats in their terrestrial habitats (urbanization, roads/fragmentation, sea level rise); thus, management plans need to consider all these threats in tandem. It is also critical to understand the spatial scale at which threats are relevant to individual species being managed. Here, we calculated the spatial scale that is relevant for the terrestrial habitat management of SCLTS and linked it with geospatial information from the most prominent threats to their habitat. A similar multifaceted approach could be used to guide management and suggest actionable conservation measures to protect other imperiled species.

# Declarations

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### Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

# Author Contribution

LS, DL and CS did conceptualization, data curation, validation, review & editing. LS and CS did formal analysis, methodology, and software. LS completed visualization and original draft writing. CS supervised.

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# Data Availability

Due to the sensitive nature of the species in this study, complete raw data on each pond's location can only be provided upon request and latitude and longitude aren't on the maps. Much of the data is available in the tables and supplemental materials but some GPS points are not shown or available due to sensitive locations. Extra habitat data and excel files are located on GitHub https://github.com/lstemle/SCLTS_buffer_Paper.

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# Tables

Table 1

Ponds with the most and least amount of suitable and accessible terrestrial habitat. Ponds in bold are in Santa Cruz County, while ponds not bolded are in Monterey County.

| Most suitable habitat within 598 m | Most suitable and accessible habitat within 598 m | Least suitable habitat within 598 m | Least suitable and accessible habitat within 598 m |
|---|---|---|---|
| Milsap 1 * (94.9%) | Tucker (91.5%) | McClusky (13.9%) | Valencia (2.0%) |
| Milsap 2 * (94.6%) | Buena Vista (90.8%) | Central (26.6%) | McClusky (13.9%) |
| Tucker (93.5%) | Greens (88.2%) | North Moro Cojo (28.3%) | Howell (17.0%) |
| Buena Vista (90.8%) | Racehorse Lane (86.5%) | Zmudowski (28.7%) | Central (20.3%) |
| Suess * (88.5%) | Delaney (84.9%) | South Moro Cojo (32.2%) | Hix (21.6%) |

Table 2
Breeding ponds with sufficient suitable and accessible habitat to support long-term viability of SCLTS. Ponds are ranked by the percentage of the SCLTS population projected to occupy the suitable and accessible habitat within migration distance (598 m) of the pond shoreline. *concern for eucalyptus dominance

| Pond | % SCLTS population supported | Breeding? |
|---|---|---|
| Tucker | 98.29 | Yes |
| Buena Vista | 97.65 | Yes |
| Shadowmere Lane | 96.88 | Yes |
| Buena Vista 2 * | 94.89 | Yes |
| Winterwind Way | 87.63 | Assumed |
| Greens | 84.92 | Assumed |
| Racehorse Lane | 84.86 | Yes |
| Delaney | 84.58 | Yes |
| Calabasas * | 84.40 | Yes |

Table 3
Priority list for terrestrial habitat management within the 598 m buffer.

| Priority rank | Vegetation improvement (% suitable habitat available from PVA) | Roads (% suitable habitat accessible) | Protection (% habitat protected) |
|---|---|---|---|
| 1 | Central (15.9%) | Valencia (2.0%) | Merk (0%) |
| 2 | McClusky (31.3%) | McClusky (13.9%) | Shadowmere (0.15%) |
| 3 | Zmudowski (36.0%) | Howell (17.0%) | Racehorse Lane (2.5%) |
| 4 | Pond X (36.4%) | Central (20.3%) | Zmudowski (2.6%) |
| 5 | Valencia (49.9%) | South Moro Cojo (26.3%) | South Moro Cojo (3.67%) |
| 6 | Seascape 3 (51.6%) | North Moro Cojo (28.3%) | Daniel’s Pond (5.9%) |
| 7 | Seascape 2 (55.1%) | Zmudowski (28.7%) | Valencia (6.6%) |
| 8 | North Moro Cojo (55.9%) | Upper Cattail (28.8%) | Winterwind Way (7.08%) |
| 9 | Alba J (59.5%) | Pond X (36.1%) | McClusky (7.07%) |
| 10 | South Moro Cojo (59.9%) | Seascape 3 (36.7%) | Tucker (12.95%) |

Table 4
Potential translocation sites ranked by percent of the SCLTS population expected to occur within the suitable and accessible habitat buffer.

| Pond Name (weighted habitat percentage PVA) | Possible Buffer Flooding (%) | Rank (categories) |
|---|---|---|
| Pig (84.4%) | 0 | 1, High habitat suitability, no predicted flooding, no roads in buffer |
| Rush (79.5%) | 0 | 2, High habitat suitability, no predicted flooding, no roads in buffer |
| Wallis/Cecil (77.8%) | 11.24% | 3, High habitat suitability, minimal predicted flooding, no roads in buffer |
| Hidden (75.5%) | 0.02% | 4, High habitat suitability, very minimal predicted flooding, no roads in buffer |
| Cattle Dip (74.8%) | 0 | 5, High habitat suitability, no predicted flooding, no roads in buffer |
| Long Valley (72.0%) | 2.94% | 6, High habitat suitability, some predicted flooding very close to pond |
| Swimming Pool (58.3%) | NA, Pond inundated | 7, Do not recommend, pond predicted flooded, near major road |
| Visitors Center (53.4%) | 8.12% | 8, Decent habitat suitability but immediately surrounded by grassland, minimal predicted flooding, near major road |
| Hix (42.7%) | 6.05% | 9, Decent habitat suitability, some predicted flooding very close to pond, adjacent to major road |

## Figures

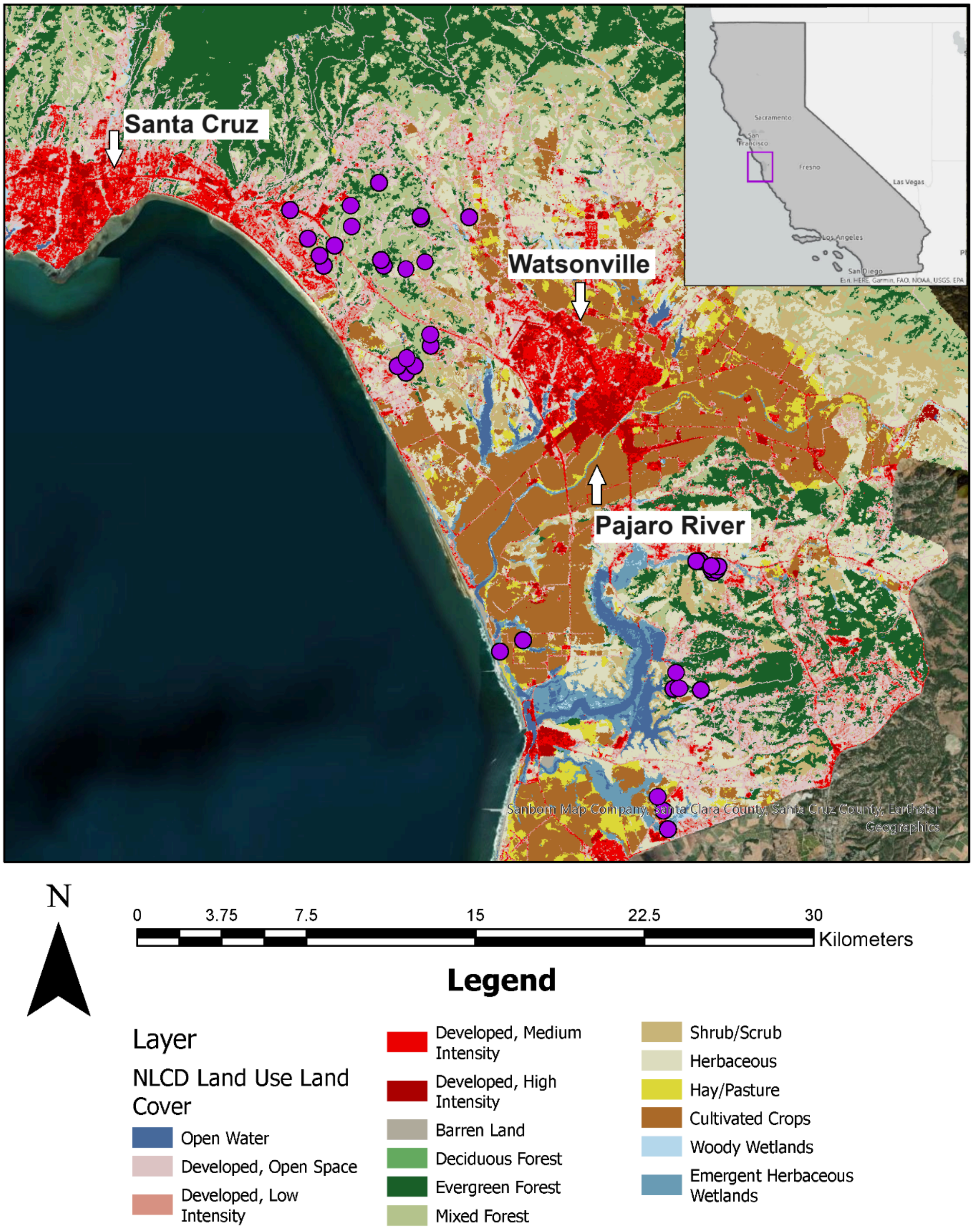



**Figure 1**

Map of all the current (2019-2023) SCLTS breeding sites, with breeding ponds (n = 37, one other not disclosed) denoted as purple circles. Land use is clipped by the SCLTS range extent as defined by the California Department of Fish and Wildlife GIS portal (https://lab.data.ca.gov/dataset/santa-cruz-long-toed-salamander-range-cwhr-a003a-ds2843). Note the gap in the middle of the range created by intensive agriculture along the Pajaro River

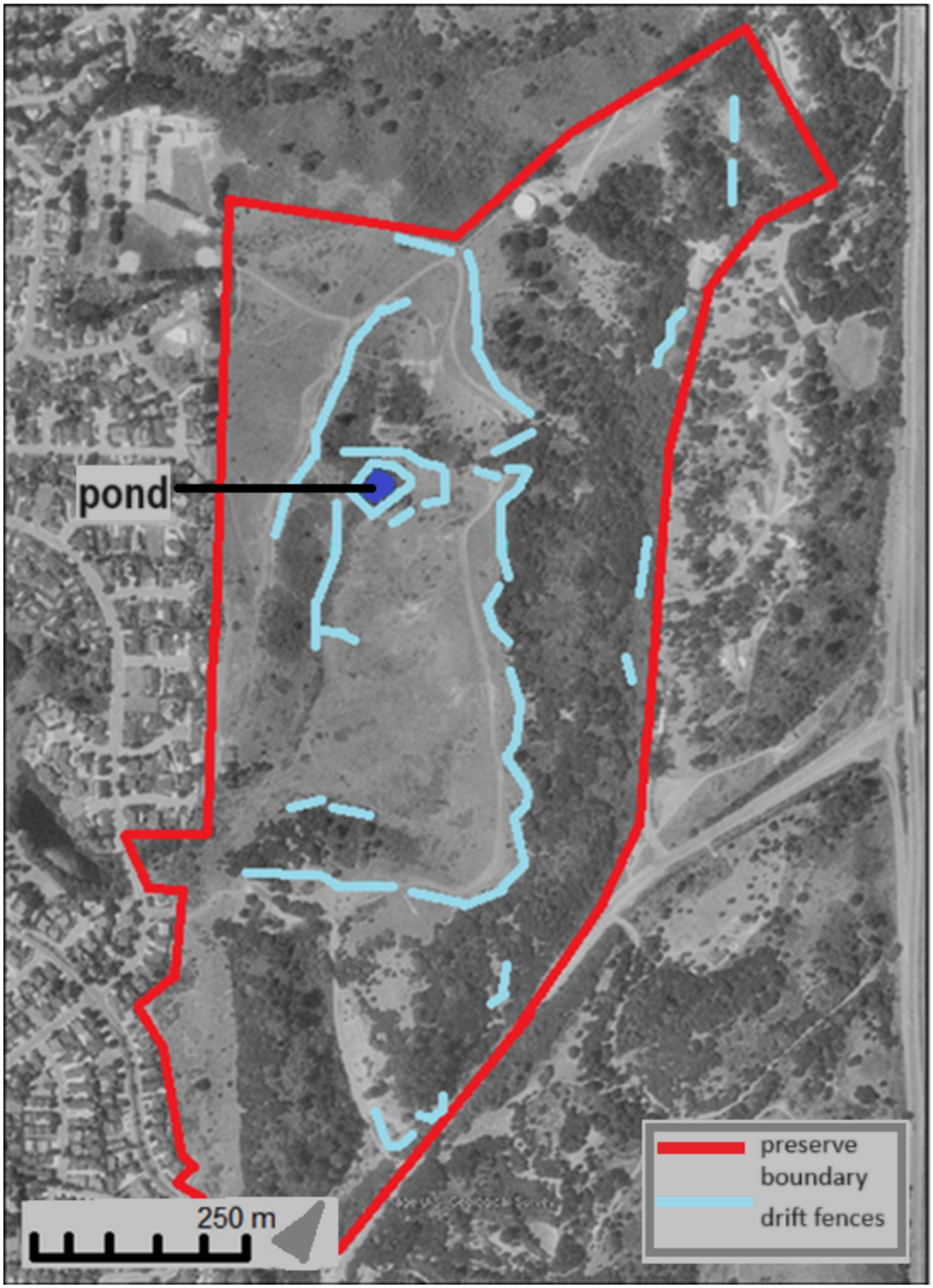



**Figure 2**

Blue lines represent the drift fence locations digitized from the Ruth 1986-87 survey. Red lines indicate the boundary of Seascape Uplands Preserve, Santa Cruz County, California. Dark blue indicates the pond location in the middle.

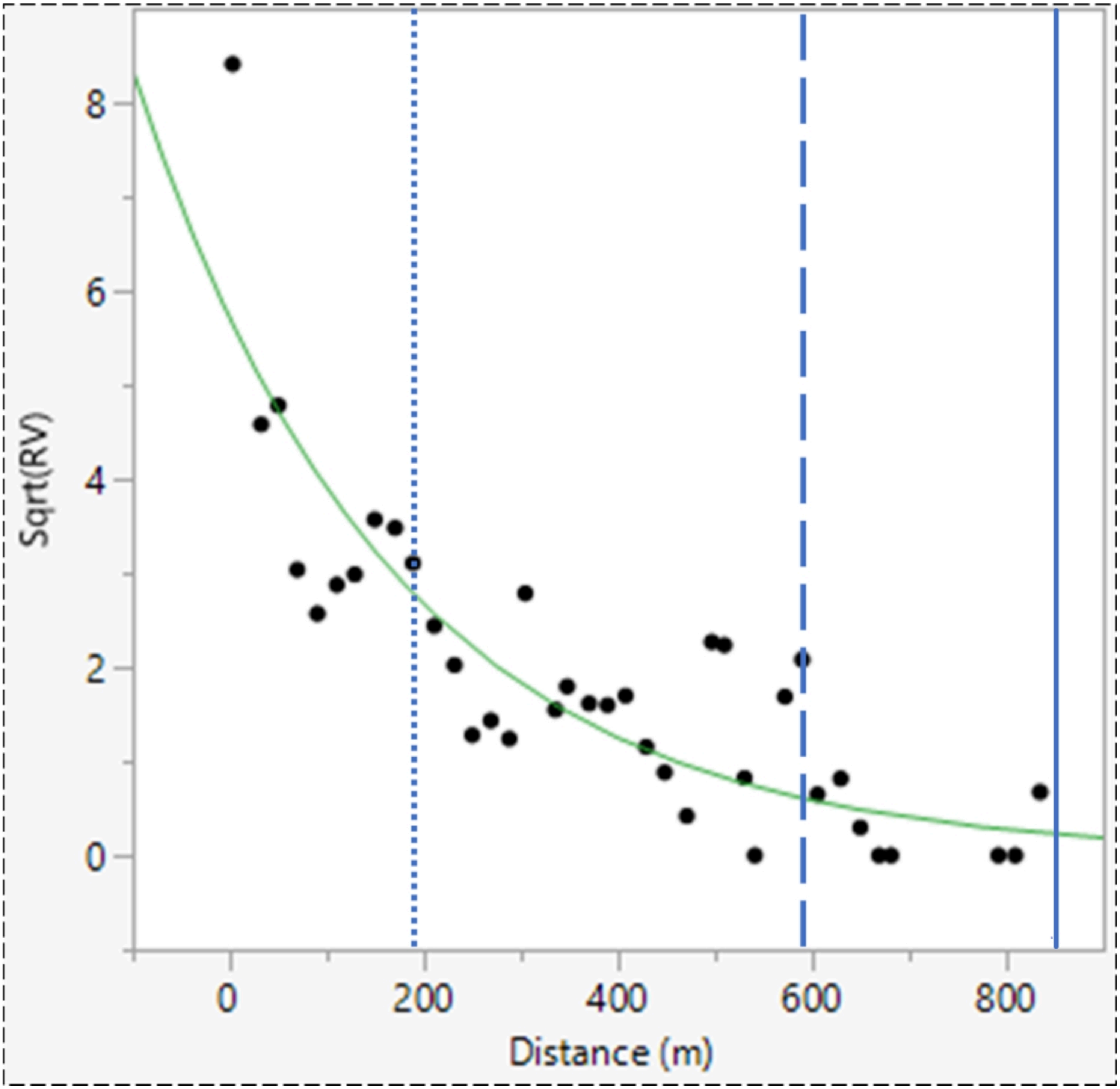



**Figure 3**

SCLTS density (summarized as reproductive value – RV – of the different age classes) as a function of distance from the breeding pond. The exponential decay function accounts for 75% of the variation in the observed capture densities. By integrating this function, it is possible to determine the mean migration distance (dotted line) and the terrestrial buffer width needed to include 95% (dashed line) or 99% (solid blue line) of the SCLTS population

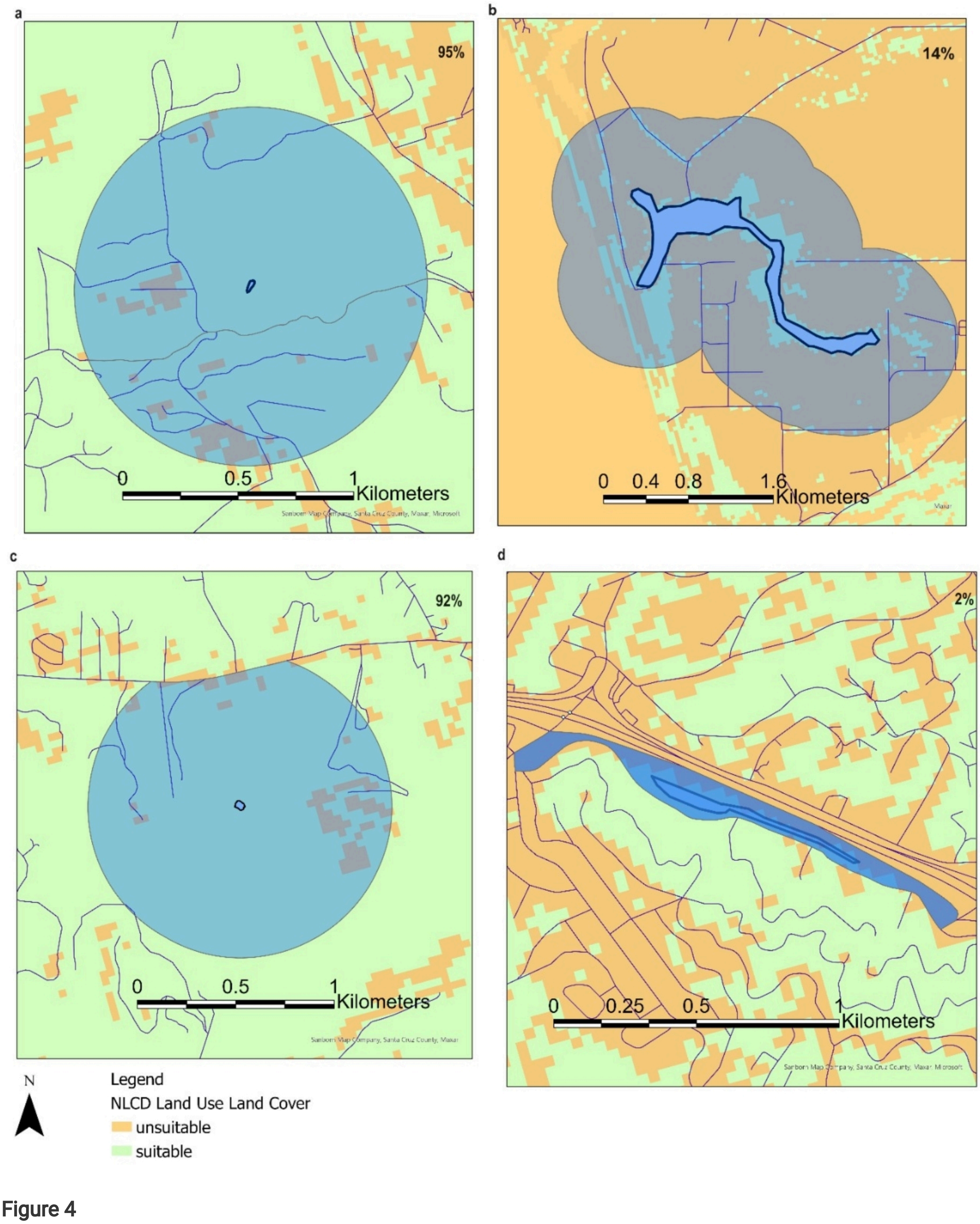
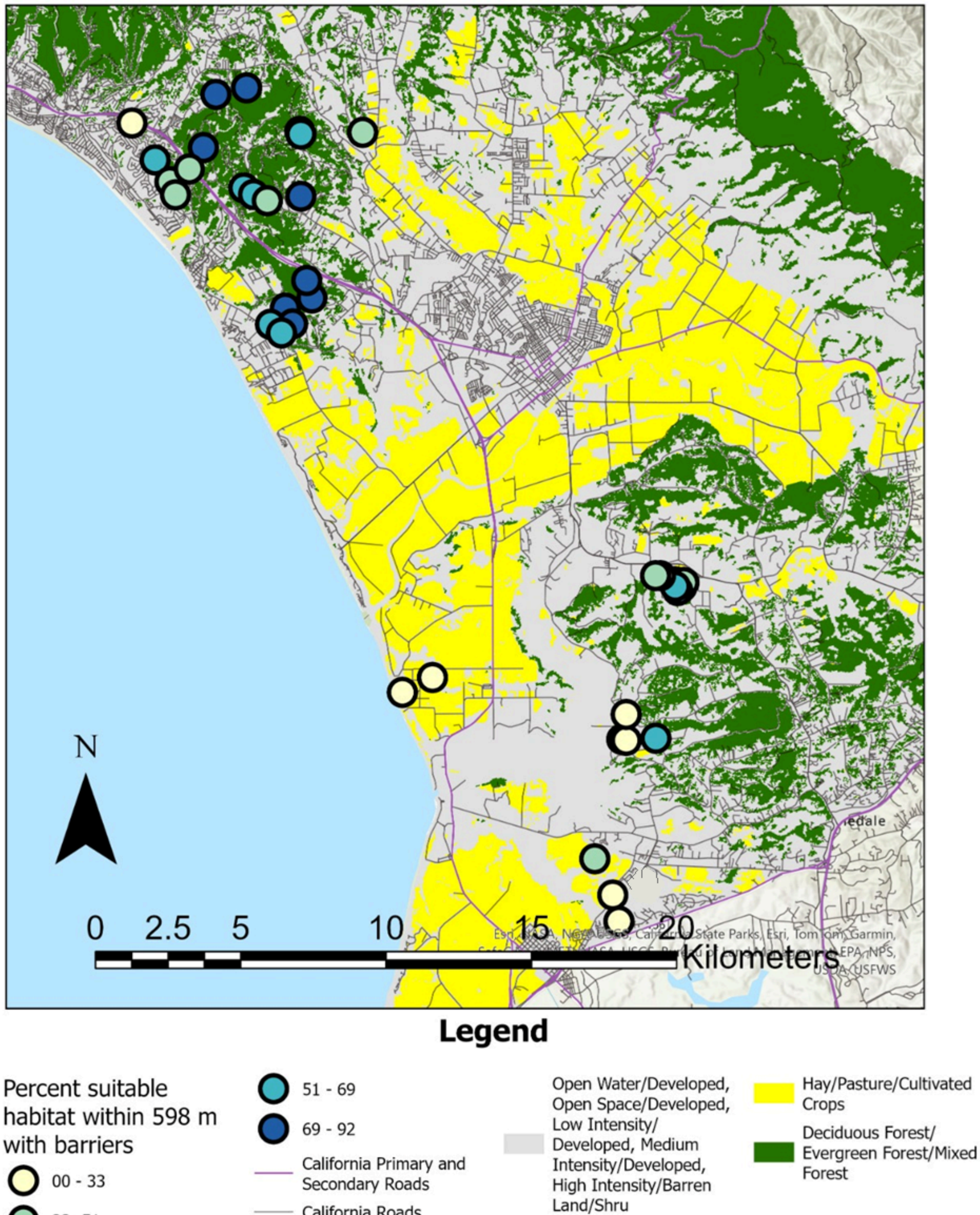



**Figure 4**

Maps of the breeding ponds with the greatest and least amounts of suitable and accessible terrestrial habitat to illustrate the huge variation across SCLTS' range. All suitable land uses are shown in light green and all unsuitable land uses are shown in tan. Panel A presents the pond with the greatest amount of suitable habitat (in this case primarily mixed forest) within 598 m (95%), while Panel B presents the pond with the least amount of suitable habitat (in this case primarily due to cultivated crops) within 598 m (23%). Panels C and D take the additional step of accounting for roads that act as barriers to dispersal, with Panel C presenting the pond with the most suitable habitat (again primarily mixed forest) that is also accessible (92%) and Panel D showing the pond most impacted by roads (only 2% of terrestrial habitat both suitable and accessible). These extreme cases illustrate the importance of prioritizing where to implement mitigation (most impacted ponds) and where to release captive-bred animals (least impacted ponds). All roads are traced with a purple line, but only those with a volume >1,000 cars/day cut the terrestrial buffers




## Figure 5

Variation in the proportion of suitable and accessible terrestrial habitat across the range of the Santa Cruz Long-toed Salamander. There is a positive correlation between suitable and accessible habitat and latitude ($R^2$ = 0.28, p = 0.0007), largely driven by a gradient in agricultural development

# Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- Supplementarymaterial.docx