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Orientation and Land Use Influences on Migrating California Tiger Salamanders (*Ambystoma californiense*)

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Abstract.—**Fragmented landscapes can potentially disrupt biphasic amphibians that migrate between terrestrial and aquatic habitats. The endangered California Tiger Salamander in Sonoma County (SCTS; *Ambystoma californiense*) is primarily relegated to preserves situated adjacent to properties fragmented by various anthropogenic land uses. We captured migrating adult SCTS using a pitfall trap array that encircled a breeding pool and identified individuals using spot pattern analysis. We assessed the movement and orientation of SCTS in relation to land uses within 100-m wide buffers ranging 100–500 m around the breeding pool. Our land use analyses included Cattle Grazed Preserve, Rural Mixed-Use, and Preserve lands. We found that many breeding SCTS used this pool, and we captured 585 individuals over 2 y. Individual SCTS moved nonrandomly at the pool with a weak tendency to move back toward the upland areas from which they originated. The spatial distribution of incoming SCTS capture rates differed significantly from outgoing capture rates. Adults entering from regions containing Rural Mixed-Use lands 200–500 m from the pool exited significantly farther from their points of entry, relative to those entering from Cattle Grazed Preserve and Preserve lands. In contrast, we found no detectable difference in orientation between Cattle Grazed Preserve and Preserve.**

Key Words.—amphibians; grazing; land use; migration; movement patterns; orientation; spot analysis; urban land uses

Introduction

Anthropogenic land use changes impact amphibian migrations, potentially limiting population growth, connectivity, and genetic diversity (Trenham and Cook 2008; Scheffers and Paszkowski 2012; Cordier et al. 2021). Habitat loss has led to significant amphibian declines particularly affecting biphasic amphibians (Davidson et al. 2002; Hamer and McDonnell 2008; Trenham and Cook 2008). Biphasic amphibians are especially vulnerable to altered landscapes because adults often require habitat connectivity between aquatic breeding and terrestrial non-breeding habitats (Pope et al. 2000). Determining how species adjust their movement and orientation in altered landscapes is especially important for conserving declining species with low vagility that migrate seasonally (Davidson et al. 2002; Cushman 2006; Trenham and Cook 2008; Simon et al. 2009; Lavin et al. 2021).

The California Tiger Salamander (CTS; *Ambystoma californiense*), a native biphasic amphibian, is in steep decline throughout their range primarily due to habitat loss and fragmentation (California Department of Fish and Game [CDFG] 2010; U.S. Fish and Wildlife Service [USFWS] 2016). California Tiger Salamanders are endemic to the lowland areas of California, where urban and agricultural development has reduced suitable habitat (USFWS 2016). In response, federal and state agencies have listed CTS as Threatened or Endangered throughout their range (CDFG 2010; USFWS 2016). This species is fossorial, inhabiting small mammal burrows within grassland or oak savannah habitats (Loredo and Van Vuren 1996; Loredo et al. 1996; Trenham and Shaffer 2005). Adult CTS move overland from these burrows during winter rains to aquatic sites (historically vernal pools), where they breed and then return to terrestrial habitat (Loredo et al. 1996; Trenham et al. 2000; Trenham and Shaffer 2005). Their movement ecology provides a model to examine anthropogenic influences on amphibian breeding migrations (Storer 1925; Trenham et al. 2000; Searcy et al. 2013; Pittman et al. 2014).

In Sonoma County, a population of CTS is designated as a Distinct Population Segment (DPS), as it is genetically distinct and isolated from other CTS (CDFG 2010; USFWS 2016). Sonoma CTS (SCTS; Fig. 1) mainly occur on the Santa Rosa Plain, which was historically a 32,800-ha grassland and oak

Figure 1. Sonoma California Tiger Salamander (*Ambystoma californiense*) at Alton Preserve in Sonoma County, California, USA. (Photographed by Victoria Brunal-Byrd).

savannah vernal pool complex, but is now fragmented by urban, rural, and agricultural development (Trenham and Cook 2008; USFWS 2016; Stokes et al. 2021). Researchers have estimated loss of vernal pool habitat on the Santa Rosa Plain to be as high as 85% (Debra Ayres and Christina Sloop, unpubl. report). Much of the remaining habitat is now managed as preserves, which are limited in size, have no connectivity, and are often bordered by human land uses (Stokes et al. 2021). Because uses of land around these preserves may alter migratory movements of SCTS, determining how they navigate through fragmented landscapes is of particular interest to resource managers (Trenham and Cook 2008; Stokes et al. 2021).

Outside of Sonoma County, researchers have documented CTS moving long distances, with their median migration distance estimated at 556 m (Searcy et al. 2013). Established SCTS preserves are limited in size and range from 1.2–69.6 ha, indicating that SCTS may commonly migrate beyond preserve boundaries and are likely to encounter habitats that have been variously altered (Stokes et al. 2021). Trenham and Cook (2008) found that the spatial capture distribution of SCTS coming into a breeding pool at a 1.2 ha urban preserve was positively correlated with the area of grassland habitat 100–700 m away from the pool. They also found that adults that entered the pool from areas closer to urbanized land departed in random directions, whereas those entering from areas with more grassland exited closer to their entry points. This research provided insights into the effects of urban land use on adult SCTS; however, most preserves in Sonoma County are bordered by agriculture and rural residential areas (Stokes et al. 2021). We investigated SCTS adult orientation based on their entry and exit points around a breeding pool surrounded by a mix of grassland and rural residential development. Our goals were to determine if SCTS adults showed nonrandom orientation between their entry and exit points at the breeding pool, and to identify differences in orientation that may be associated with sex, body size, or surrounding upland land uses, such as rural residential areas and grazed grasslands.

Materials and Methods

Study site.—Our study site was located at Alton Preserve, approximately 7 km northwest from the city center of Santa Rosa, Sonoma County, California (Fig. 2). This preserve, situated on flat terrain, contained more than 50 vernal pools, which were constructed in phases in the late 1980s (Cook et al. 2022). The study site habitat was comprised of primarily non-native annual grassland with small stands of oaks (*Quercus* spp.) and shrubs, such as Coyote Brush (*Baccharis pilularis*) and Poison Oak (*Toxicodendron diversilobum)*. We studied SCTS at Pool 2, the largest, deepest, and one of the oldest constructed pools at the preserve (Ted Winfield, pers. comm.). This pool had a maximum depth of 105 cm, a surface area of 0.47 ha, and is in the northwest corner of the preserve (Fig. 2). Pool 2 is surrounded by a grassland understory with oak woodland and sparse shrubs, in an approximately 50-m radius around the pool. Beyond that, the dominant habitat was non-native grassland that was comprised primarily of Oat Grass (*Avena* spp.), Ripgut Brome (*Bromus diandrus*), and Italian Ryegrass (*Festuca multiflorum*), with only minor elevation change (Cook et al. 2022).

Pitfall trapping.—To study movement and orientation of SCTS, we installed a pitfall trap array around Pool 2. We buried black drift fencing (woven plastic fabric) approximately 15 cm below ground, with 30 cm of taut fencing secured above ground with vertical stakes (Heyer et al. 1994; Cook et al. 2006; Lewis et al. 2023). We located the fencing 2–3 m away from the estimated maximum shoreline of the pool, which resulted in a 202 m long fence encircling the pool. To create the pitfalls, we buried 4-L canisters (16.5 cm diameter and 19 cm height) on opposing sides of the fence at 10 m intervals, with minor adjustments made for obstructions, such as trees. We installed 42 traps (21 trap pairs), each equipped with elevated lids for shade, and a

Figure 2. Satellite view of the study site for Sonoma California Tiger Salamander (*Ambystoma californiense*) depicting the surrounding land uses and study pool, in Sonoma County, California, USA. The white circle is centered on the study pool and has a radius of 500 m.

wet sponge to prevent amphibian desiccation. We monitored the traps daily beginning with the onset of winter rains from November 2020 to February 2021 (Winter 2021) and from October 2021 to March 2022 (Winter 2022); thus, we gathered data during two breeding seasons. To track local weather patterns, we obtained rainfall data from the Charles M. Shultz Sonoma County Airport weather station, located 1.8 km from Alton Preserve. The long-term average annual rainfall at this station from 2000 to 2022 was 78.9 cm ± 6.7 standard error (SE).

Surrounding land use.—We categorized surrounding land uses within 500 m of Pool 2 (See below) and identified three land use categories: Cattle Grazed Preserve (CGPR), Rural Mixed-Use (RURE), and land inside Alton Preserve (PRES; Fig. 2). We defined CGPR as a non-native grassland habitat containing a complex of vernal pools subjected to seasonal cattle grazing. We defined RURE lands as primarily single-family private homes, located in a low-density setting (i.e., ≤ five houses/ha), which included a section of country road, landscaped areas, and fields actively maintained or altered by the private property owner (Fig. 2). We included small portions of agricultural land uses, including a vineyard, in our RURE land use category. We did not consider the country road a barrier to SCTS movement or source of significant mortality, as it was an uncurbed low-profile roadway that was a dead-end street with low residential traffic. For the PRES land, we defined the area as a non-native grassland containing sparse oak woodlands with a complex of vernal pools and no cattle grazing.

Using Google Earth, we categorized predominant land uses in 100-m buffers ranging from 100–200 m, 200–300 m, 300–400 m and 400–500 m from Pool 2 by drawing a straight line transect extending perpendicular from the shoreline from each trap pair. We did not consider land uses within 0–100 m of Pool 2 because there is no significant land use variation at this scale. We focused on habitat within 500 m of the pond based on previous research on CTS outside of Sonoma County (Searcy et al. 2013). We determined the land use in which each trap resided (CGPR, RURE, and PRES) at each distance based on a composition of > 60% of the linear transect (Fig. 2). Dominant land uses within the buffers differed, with 100–200 m including CGPR and PRES, 200–300 m and 300–400 m including CGPR, PRES, and RURE, and 400–500 m only including PRES and RURE (Table 1).

Salamander processing.—We collected morphological data on all captured and recaptured adult SCTS (sex, weight, and snout to vent length); however, we only used the first capture measurement data of each individual for analyses. Researchers weighed each salamander using spring-loaded scales and measured their snout-vent length using handheld rulers. To identify recaptured SCTS, we marked individuals with a tail clip by snipping 3–4 mm from the end of the tail. We identified adults as male if their cloaca was swollen and they had laterally compressed tails; whereas we identified adults as female if their abdomen was swollen, an indication of gravidity, and their tails were rounded and relatively short (Stebbins 1951). We did not include juveniles (n = 7), identified by their small size and non-breeding condition (Stebbins 1951; Searcy and Shaffer 2008), in our analyses.

To identify individuals, we analyzed spot patterns from dorsal and ventral photographs with the program I3S Pattern+ (Brehme et al. 2021). Photographic matches were confirmed by two researchers by visually inspecting spot patterns and reviewing morphological measurements. Spot analysis was only conducted within seasons, not between them. All SCTS were released on the opposite side of the fence from where they were captured, either into the pool or a rodent burrow.

Trap recapture deviation.—To evaluate SCTS patterns of movement, we calculated a Trap Recapture Deviation (TRD) value, determined as the number of traps between the entry point into the pool and their last capture for each individual, within a single breeding season (Shoop and Doty 1972). We assigned a TRD value as zero if a salamander entered and departed the pool at the same trap pair, while a TRD of ± 1 indicated the salamander was captured one trap away from their original entry point, increasing consecutively in either direction up to ± 10. We designated movements counterclockwise from an entry point as negative TRD values, while clockwise movements were positive TRD values. Because the traps were spaced 10 m apart, a TRD of ± 1 indicated a movement of approximately 10 m.

We excluded individuals from the analysis that trespassed (caught consecutively on the same side of the fence; n = 57) or could not be identified due to poor photographic image quality (n = 76). To avoid potential escape or drowning, during the Winter of 2022, we closed four traps for 18 days (of 165 trapping days) because they were inundated with water (Alvarez et al. 2022); we reopened the traps once water levels receded. We adjusted the TRD value as needed; if a salamander departed the pool when a trap was closed, we did not include the trap in the TRD because it was not an option for a salamander exiting the pool.

Statistical analyses.—We used R Studio v. 4.4.1 (R Core Team 2024) for all statistical analyses. We assessed model residuals for approximate normality and homoscedasticity using the plot() function, where we checked Residual vs. Fitted plots to confirm that residuals did not follow a distinct pattern and that the Q-Q residuals followed an approximately straight line. We also assessed Scale-Location plots for indications of homoscedasticity and Residual vs. Leverage for significant outlier points.

Orientation analyses.—Following Shoop and Doty (1972), we evaluated individual orientation using points of capture expressed as TRD values within a winter trapping period. We used this method to compare the spread of movement data (TRD) centered around zero (i.e., the entry location) by comparing the observed TRD variance (σ_o^2) to a random variance (σ_r^2), where exit location is independent of entry. To calculate the random variance (σ_r^2), we squared each possible TRD value (1–10), summed these values, and doubled the total to account for equal probability to move in clockwise or counterclockwise directions. We then divided this value by the total number of trap pairs. We calculated *σo2* based on the observed TRD data using the var() function in R and calculated a F ratio (σ_r^2 / σ_o^2) to assess random or directional orientation. Finally, we compared the F ratio value to a F critical value, determined by (n - 1), and evaluated at a significance level of $P < 0.0001$.

To compare the overall distributions of incoming and outgoing SCTS capture rates, we conducted a Mardia-Watson-Wheeler Test using the circular package in R. We calculated capture rates per trap by dividing the total number of all SCTS captures for both trapping seasons by the number active trapping days. In addition, we categorized trap pairs by cardinal direction from the pool center (e.g., headings between 315° to 45° = North) and calculated mean capture rates for each direction.

To assess variables influencing the absolute value of TRD (TRD_{abs}), we used a General Linear Model for each land use buffer from 100–500 m. We used TRD_{abs} because we did not expect a difference in orientation based on clockwise or counterclockwise

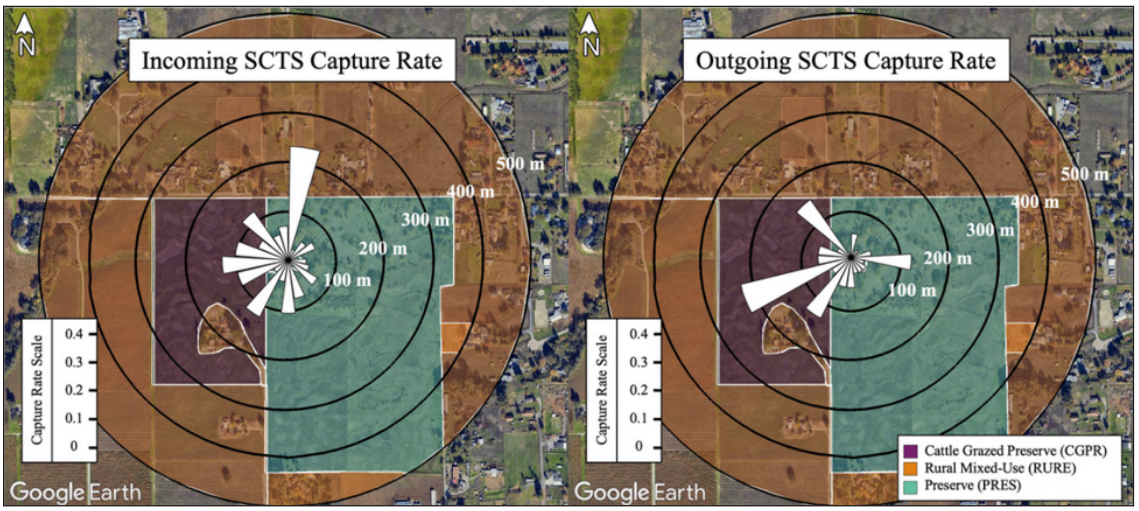

Figure 3. Incoming and outgoing capture rates of Sonoma California Tiger Salamander (SCTS; *Ambystoma californiense*) at Pool 2 in Sonoma County, California, USA. Circles mark the boundaries of each 100-m buffer used to determine predominant land use for each trap pair, ranging from 100–500 m. The SCTS capture rate scale per trap (Total SCTS captures/number of active trapping days) is shown in the bottom left corner depicting the increase in capture rate values by bar height.

movement, relative to our fixed effects. Each model also included sex, trapping year, and the initial body weight of a salamander. We square-root transformed TRD_{abs} to approximate normality and combined data for the two study years for all analyses. To remove nonsignificant effects from the final models, we conducted a reverse stepwise selection. We reported one standard error (SE) ± for mean TRD_{abs}. We analyzed significant results from final models *post hoc* using the emmeans package to make pairwise comparisons between TRD_{abs} and land uses at each distance buffer. To control for Type 1 errors, we used a Tukey correction at an alpha level of 0.05.

Results

Capture totals.—We marked 585 SCTS and recaptured 372 during Winter 2021 and 2022. We captured fewer SCTS in Winter 2021, marking 80 salamanders (12 females and 68 males) and recapturing 61; compared to Winter 2022, where we marked 505 SCTS (227 females and 278 males) and recaptured 311. During Winter 2021 rainfall was 32% of average, and Pool 2 only partially filled to a depth of 25 cm. Winter 2022 rainfall was 75% of average, and Pool 2 reached a maximum depth of 105 cm. Through spot analysis, we identified 242 recaptured individuals including 133 males and 109 females across both seasons, of which 185 met the criteria for orientation analysis.

Although we captured SCTS at Pool 2 in all cardinal directions, the distribution of incoming and outgoing capture rates differed significantly (W = 42.29, $P < 0.001$; Fig. 3). We found that the overall capture rates of incoming salamanders had a mean directional bearing of 275°, compared to outgoing salamanders with a mean bearing of 234° (Fig. 3). When grouping traps by cardinal direction, we found that north traps had the highest number of incoming captures with a mean capture rate of 0.13 ± 0.01, whereas the outgoing north capture rate was only 0.02 ± 0.004. We found that outgoing capture rates were concentrated to the west, with a mean capture rate of 0.14 ± 0.01 (Fig. 3).

Adult movement and orientation.—We found an observed variance in TRD (σ_o^2) of 18.15 for identified SCTS movements and calculated a random variance (σ_r^2) of 36.7, providing an F ratio (σ_r^2/σ_o^2) of 2.02. The F critical value is 1.27, significantly lower than the F ratio value (2.02; $P < 0.001$), signifying nonrandom movement. We found a mean TRD of -1.71 ± 0.31 indicating a minor counterclockwise deviation bias on departure (Fig. 4). For TRD_{abs}, we found a mean of 3.80 ± 0.19.

Trap recapture deviation.—We found no significant difference in TRD_{abs} between PRES and CGPR traps at any distance (Fig. 5; Table 1). In contrast, RURE traps had the highest average TRD_{abs} at all distances (Fig. 5), except at 100–200 m, where

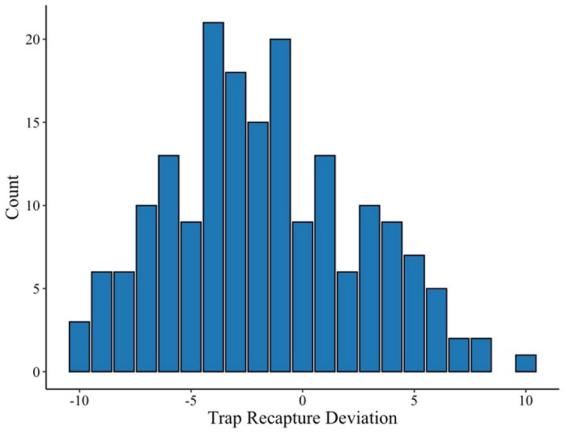

Figure 4. Distribution of observed Trap Recapture Deviation (TRD) values for individual Sonoma California Tiger Salamanders (*Ambystoma californiense*) captured entering and exiting the study pool in Sonoma County, California, USA. Directional values are centered at zero with negative and positive values representing the number of traps, counterclockwise and clockwise, respectively, separating entry and exit points.

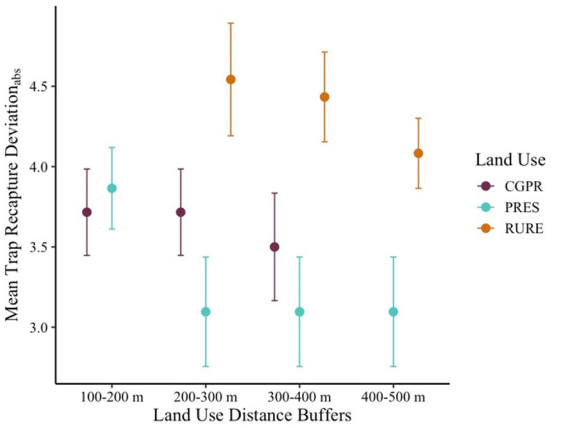

Figure 5. Mean absolute Trap Recapture Deviation (TRD_{abs}) of Sonoma California Tiger Salamanders (*Ambystoma californiense*) for each dominant land use category in 100 m wide buffers upland from each trap ranging from 100–500 m in Sonoma County, California, USA. Land use categories include Cattle Grazed Preserve (CGPR), Rural Mixed-Use (RURE), and Preserve (PRES). Bars are (±) one standard error of the mean.

land use was nonsignificant ($F_{1,181} = 0.004$, $P = 0.95$). At 100–200 m only year significantly affected TRD_{abs} ($F_{1,181} = 5.05$, $P = 0.03$). For the 200–300 m buffer, we found that year ($F_{1,180} = 6.88$, $P = 0.009$) and land use ($F_{2,180} = 5.55$, $P = 0.004$) were significantly associated with TRD_{abs}, while weight ($F_{1,180} = 3.95$, $P = 0.048$) was not significant. The TRD_{abs} values were significantly smaller for PRES than RURE traps, and marginally lower in CGPR than RURE traps (Fig. 5; Table 1). At the 300–400 m scale, we found that year ($F_{2,180} = 7.47$, $P = 0.007$), body weight ($F_{1,180} = 2.17$, $P = 0.040$), and land use ($F_{2,180} = 6.47$, $P = 0.002$) were significant; with TRD_{abs} lower for both PRES and CGPR than RURE traps (Fig. 5; Table 1). For both the 200–300 m and 300–400 m models, we found that body weight generally increased with TRD_{abs}. Finally, at 400–500 m, we found that only land use had a significant effect, with TRD_{abs} significantly lower in PRES traps than RURE traps (Table 1). For all models, TRD_{abs} was generally higher in 2021 than 2022 (Fig. 5). Sex was not a significant factor in any model.

Discussion

Despite conducting this study at an isolated preserve located on the edge of a developed city and surrounded by fragmented uplands, we captured 585 individual SCTS. At similarly sized pools in undeveloped landscapes, the maximum numbers of adults captured were 140 males and 100 females over 8 y (Trenham et al. 2000) and 65 males and 81 females over 2 y (Loredo and Van Vuren 1996). Cook et al. (2006) and Trenham and Cook (2008) reported 171 SCTS adults, but that population was on the edge of urban development and has since gone locally extinct (Stokes et al. 2021). Determining how SCTS successfully navigate through remnant habitats could help shape management decisions to ensure long-term persistence (Trenham and Cook 2008).

Our findings that SCTS adults tend to enter and leave the breeding pond in the same direction should increase the probability that they return to suitable upland habitat. We did find that return movements lacked precision, however, with SCTS entering from areas dominated by Rural Mixed-Use lands exhibiting even greater deviations in their return orientation. This increased deviation may indicate that Rural Mixed-Use areas contain less suitable upland habitat compared to less disturbed areas such as preserve lands, causing some SCTS to stray farther while searching for more suitable terrestrial habitat.

Individual orientation.—Several other species of ambystomatid salamanders in the eastern U.S., including Spotted Salamander (*A. maculatum*), Marbled Salamander (*A. opacum*), and Jefferson Salamander (*A. jeffersonianum*) have demonstrated nonrandom movement. These species tend to use similar exit routes to those used when entering breeding pools (Shoop and Doty 1972; Stenhouse

Table 1. General Linear Model results relating TRD_{abs} to the surrounding upland habitat in 100-m wide buffers out from the incoming capture trap. Buffers range from 100–500 m. Only two predominant land use types were found with the 100–200 m and 400–500 m buffers. The number of traps and number of Sonoma California Tiger Salamander (SCTS; *Ambystoma californiense*) in each land use category per model are listed. Pairwise comparisons are adjusted using a Tukey correction, and the estimate values (β) and Standard Errors (SE) are reported. Significant differences in TRD_{abs} among land uses are denoted with an asterisk (*).

Buffer Distance (m)	No. of Traps	No. of SCTS	Mean TRD_{abs}	*F*	*P*	Pairwise Comparison	β	SE	*P* (adj)
100–200	PRES (16)	PRES (111)	3.86	0.004	0.95	PRES × CGPR	-0.04	0.11	0.74
	CGPR (5)	CGPR (74)	3.72	–	–	–	–	–	–
	RURE (0)	RURE (0)	–	–	–	–	–	–	–
200–300	PRES (10)	PRES (52)	3.10	5.55	0.004*	PRES × CGPR	0.21	0.13	0.24
	CGPR (5)	CGPR (74)	3.72	–	–	CGPR × RURE	-0.26	0.13	0.09
	RURE (6)	RURE (59)	4.54	–	–	RURE × PRES	-0.47	0.14	0.002*
300–400	PRES (10)	PRES (52)	3.10	6.47		PRES × CGPR	0.09	0.14	0.77
	CGPR (3)	CGPR (62)	3.50	–	–	CGPR × RURE	-0.36	0.13	0.015*
	RURE (8)	RURE (71)	4.43	–	–	RURE × PRES	-0.46	0.12	< 0.001*
400–500	PRES (10)	PRES (133)	3.10	8.25	0.005*	PRES × RURE	-0.33	0.12	0.006*
	RURE (11)	RURE (52)	4.08	–	–	–	–	–	–
	CGPR (0)	CGPR (0)	–	–	–	–	–	–	–

1985; Phillips and Sexton 1989; De Lisle and Grayson 2011). Newly metamorphosed SCTS re-orient away from their natal pool, even after experimental disruption to their initial dispersal direction (Lewis et al. 2023). In adult SCTS, Trenham and Cook (2008) also found movements to be non-random, yet highly imprecise, with an average angle between entry and exits of 64°, compared to 90° that would indicate random movement. In their case, however, the broad orientation pattern seemed to be influenced by nearby urban development (Trenham and Cook 2008). We found an average TRD_{abs} of 3.8 indicating a deviation of 38 m from their entry points, or if applying the directional bearing methods of Trenham and Cook (2008), an average angle deviation of 62º. In both studies, deviation between entry and exit was greater for adults entering from human-altered uplands.

Compared to small adults, we also found that larger adult SCTS exhibited a higher average TRD when exiting the study pool. These results may be associated with greater movement capabilities of larger individuals as seen in other studies (Gutierrez et al. 2018; Murphy and Boone 2022); however, body size is likely only one of many factors that influence variation in individual movement patterns (Straus et al. 2022).

Land use effects.—Although Rural Mixed-Use areas are typically less treacherous to salamanders than high traffic roads (Bain et al. 2017) and housing developments (Trenham and Cook 2008), individuals coming from these areas may be re-orienting more often as they return to uplands. Altered upland habitat around breeding sites likely influences SCTS movements into the upland, as CTS have the longest known migratory distance among ambystomatid salamanders (Searcy et al. 2013) and have been documented up to 2.2 km away from breeding pools (Orloff 2011). While we found no significant effect of land use at 100–200 m, this is likely because this area only contained preserve lands, whereas buffers from 200–500 m indicated an effect of land use on SCTS orientation and contained Rural Mixed-Use lands. This was most obvious at the 300–400 m

buffer, where SCTS coming from Rural Mixed-Use lands deviated significantly further than both preserve land categories. It should be noted that uplands at our site > 400 m are highly fragmented and contain < 1% grassland, appearing to be marginal habitat for SCTS. Currently, large-scale unfragmented grasslands like those where other CTS movement studies were conducted (Loredo et al. 1996; Trenham 2001; Orloff 2011; Searcy et al. 2013) do not occur in Sonoma County.

The subtle increased deviation of approximately 1 TRD (or about 10º) during return orientation from Rural Mixed-Use areas may suggest that these areas contain less suitable habitat. An alternative interpretation could be that SCTS are temporarily reorienting at the pools just prior to returning toward their initial trajectory. The difference in incoming and outgoing capture rates indicates a bias toward preserve lands, however, as we observed a large shift away from the north where there is a high concentration of Rural Mixed-Use lands. Individuals that originally came from the north, but did not return toward those areas, may represent naïve individuals who settled in those areas during their initial dispersal as juveniles (Pittman et al. 2014).

Several studies have demonstrated impacts of land use on amphibians (Johnston and Frid 2002; Jacobs and Houlahan 2011; Connette and Semlitsch 2013; Bendik et al. 2014; Cordier et al. 2021; Murphy and Boone 2022). Types of human land uses that have impacted amphibian populations include areas such as urban housing (Trenham and Cook 2008; Bendik et al. 2014), logged forests (Johnston and Frid 2002; Connette and Semlitsch 2013), and roads (Jacobs and Houlahan 2011; Bain et al. 2017), among others (Cordier et al. 2021). As our site is located on the outskirts of a highly developed city, this study provides insights into the impacts of rural residential land uses. Future research should consider land use features conducive to movement such as burrow densities, vegetation type, moisture corridors, and anthropomorphic barriers (Vos et al. 2007; Scheffers and Paszkowski 2012).

The SCTS leaving the pool toward Cattle Grazed Preserve did not significantly differ from those leaving from areas associated with non-grazed Preserve land, supporting the idea of CTS being compatible with cattle grazed lands (Pyke and Marty 2005; Stokes et al. 2021). While cattle grazing can have differential impacts on amphibian species (Burton et al. 2009), this likely also varies with grazing practices (such as intensity and rotation practices). Pyke and Marty (2005) found that seasonally grazed ephemeral wetlands had longer hydroperiods on average than non-grazed ephemeral wetlands; benefitting CTS that require enough time for aquatic larvae to develop and metamorphosis before a pool dries. Historically, vernal pool ecosystems were grazed by native ungulates, indicating that native species are adapted to some level of large herbivore disturbance (Marty 2005). Our results further support the compatibility of grazing lands, as salamanders at our site that originated from seasonally grazed lands allowed for similar upland orientation to non-grazed Preserve land.

Conclusions.—Urban land uses can negatively impact amphibian populations, but additional research into how these impacts vary among populations and land uses is critical for informed management decisions (Hamer and McDonnell 2008; Trenham and Cook 2008; Scheffers and Paszkowski 2012; Cordier et al. 2021). Breeding migrations of SCTS are influenced by proximity to urbanized land (Trenham and Cook 2008), including preserves established for this species in more rural areas, as seen here. Our study indicates that Sonoma preserves may be able to expand their sizes through the incorporation of agricultural areas that conduct sustainable grazing practices. The addition of these areas could better support the natural history needs of SCTS by expanding the available terrestrial habitat needed outside of the breeding season (Searcy and Shaffer 2011; Stokes et al. 2021).

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Committee Protocol of Sonoma State University (2025-71).

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