CHAPTER 2

Distribution of Migrating Adults Related to the Location of Remnant Grassland Around an Urban California Tiger Salamander (*Ambystoma californiense*) Breeding Pool

Peter C. Trenham[1] and David G. Cook[2,3]

Abstract —In 2004, the U.S. Fish and Wildlife Service listed the California Tiger Salamander as threatened throughout its range. Habitat loss due to residential development was the primary threat cited in their decision to list this species. To improve efforts to conserve this species we have been studying several populations in a landscape that is becoming increasingly urbanized. We report the results of a two-year drift fence census of adults at a large breeding pool in Southwest Park in Sonoma County, California, an area surrounded by varying levels of urban development. Currently, the upland landscape in most directions around this breeding pool is developed or blocked from migrating salamanders by high-density development; the largest contiguous area of accessible grassland remaining is east of the pool. Even with this extensive development, in 2002–2003 and 2003–2004 we estimated the populations of breeding adults at 107 and 90, respectively. In both years, most adults were captured entering and exiting the pool in traps along the eastern shoreline, suggesting that they primarily occupy the grassland habitats east of the pool. Most of this grassland habitat is >100 m from the shoreline. Distribution of capture totals among traps within eight 45° wide sections of drift fence was most strongly correlated with the area of grassland habitat within those same 45° wide regions >100–700 m the pool. For individuals captured as they entered and exited the pool in a given breeding season, the compass heading of entry and exit traps differed by 64° on average, with males deviating significantly more than females. From the perspective of reserve planning, this result suggests that habitat corridors could be valuable, but that broad contiguous sections of undeveloped shoreline will be needed to minimize straying into unsuitable habitats (e.g., >30% of the total perimeter). Although this study suggests that California Tiger Salamanders may persist in landscapes with substantial development, additional studies are needed to understand the impacts of upland habitat conversion on population sizes and especially how individuals navigate these complex landscapes.

Key words — Ambystoma californiense, Breeding Migration, Drift Fence, Orientation, Pond-Breeding Salamander, Spatial Distribution, Urbanization

As the most populous U.S. state, California supports many reptiles and amphibians threatened by urbanization. In 1973, due at least partly to urban expansion, the San Francisco Garter Snake (*Thamnophis sirtalis tetrataenia*) and the Santa Cruz Long-Toed Salamander (*Ambystoma macrodactylum croceum*) were among the first species included on the federal list of endangered species. As California's urban areas have continued to expand, so has the list of threatened and endangered species. In 1994, 1996 and 1997, respectively, the Arroyo Toad (*Bufo microscaphus*), the California Red-legged Frog (*Rana aurora draytonii*) and the Alameda Whipsnake (*Masticophis lateralis euryxanthus*) were added to the federal list. In August of 2004, the California Tiger Salamander (*Ambystoma californiense*) became the most recent addition to this list (USFWS 2004).

[1]*Section of Evolution and Ecology, University of California, 1 Shields Avenue, Davis, CA 95616 USA*
[2]*Biology Department, Sonoma State University, 1801 East Cotati Avenue, Rhonert Park, CA 94928 USA*
[3]*Present Address: 3003 Magowan Drive, Santa Rosa, CA 95405 USA*

Although the bulk of California Tiger Salamander habitat was lost decades ago to agricultural conversion, the decision to list this species as threatened cites planned and projected low and high density residential development as the primary threat to the salamander's future status. Davidson et al. (2002) also found that landscapes within 5 km of historically known populations averaged 7% urbanized for currently extant populations and 22% urbanized for extirpated populations. California Tiger Salamanders in Sonoma County, isolated at the northern terminus of the species' range, are increasingly impacted by urbanization.

Sonoma County California Tiger Salamanders (SCCTS) are separated from the nearest other populations of this species by 72 km. An analysis of mitochondrial DNA variation revealed the SCCTS to be genetically distinct from populations elsewhere in the state, having been naturally isolated and evolving independently for an estimated one million years (Shaffer et al. 2004). All remaining populations of this disjunct population are found within roughly 15 km by 5 km of the Santa Rosa Plain and adjacent lowlands of the Petaluma River watershed, an area of rapid urban expansion (USFWS 2003). Three cities currently delimit the eastern boundary of occupied habitat. The northernmost of these is Santa Rosa which between 1980 and 1997 grew by 66%, with urban and industrial development eliminating at least three breeding populations in the process (USFWS 2002). As a result in 2002, the SCCTS was emergency-listed as an endangered distinct population segment (USFWS 2002). We have been conducting studies on eight preserves near Santa Rosa since 1999 to assist plans for the conservation of the SCCTS.

California Tiger Salamanders require aquatic breeding habitats, upland areas with suitable underground refuges, typically mammal burrows, and barrier-free migratory pathways between breeding and upland habitats (Shaffer and Trenham 2005). Although SCCTS breeding activity has been documented recently on all eight preserves, the long-term viability of these populations remains in question due to the small size of the preserves and adjacent land uses (D.G. Cook pers. obs.). Mean size of the eight SCCTS preserves is 19.7 ha (1.2–70.4 ha) and seven are bordered by urban or low-density rural-residential development. This is less than the 121 ha estimated to be required to encompass 95% of upland movements from a single breeding pool (Trenham and Shaffer 2005). Thus, it appears likely that many of these preserve populations use upland habitats on both preserve and adjacent non-preserve lands. To better understand how SCCTS interact with and navigate these increasingly complex landscapes, we have been studying breeding migrations of SCCTS at one breeding pool surrounded by an increasingly urbanized landscape.

Encircling breeding pools with drift fences and pitfall traps has been valuable tool in the study of amphibian breeding migrations for at least four decades (Shoop 1965; Dodd and Scott 1994). Drift fences allow accurate estimation of population sizes and reflect the spatial distribution of animals entering and leaving pools. The resulting spatial data have allowed researchers to gain insights into species preferences for certain types of adjacent upland habitat and their capacity for orientation (Shoop 1965, 1968; Douglas 1981; Stenhouse 1985). We used a drift fence surrounding a single breeding pool at Southwest Park to characterize the spatial distribution of SCCTS captures and determine if their distribution is associated with the amount of remaining undeveloped grassland habitat in the surrounding landscape. We also evaluated deviation between entry and exit points to assess the degree to which individual animals may wander randomly or use consistent tracks for their migrations. We discuss our findings in the context of planning for the long term conservation of SCCTS in a landscape increasingly fragmented by development.

Materials and Methods

Study Area — Southwest Park is situated within the western edge of the city of Santa Rosa in Sonoma County, California (Fig. 1). The park supports a single large vernal pool used by SCCTS as breeding habitat. When full, the pool has a surface area of 0.75 ha and a maximum depth of 1.2 m. In recent years much of the upland habitat near the breeding pool has been converted from disturbed non-native grassland habitat suitable for SCCTS to urban land uses. Southwest Park was developed in 1986, converting lands immediately east and northeast of the pool to manicured lawns, a baseball field, and other paved surfaces, devoid of the mammal burrows that SCCTS require. City of Santa Rosa data indicate that Hearn Avenue, to the immediate north, supports an average of >12,000 cars daily; Hels and Buchwald (2001) estimated that roads with this level of traffic are essentially 100% lethal to migrating amphibians. Remaining grasslands north of Hearn Avenue are blocked by
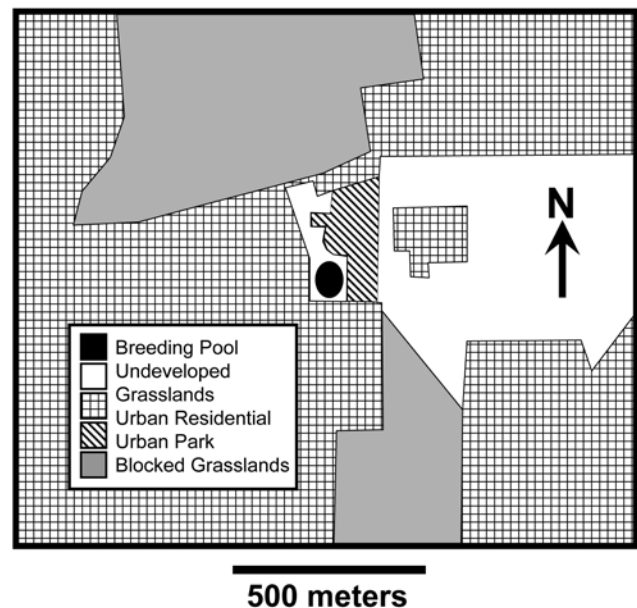

Fig. 1. Map of the landscape around Southwest Park, Sonoma County, California, USA. Map is centered on our study pool. Created from aerial photographs taken in 2002.

this road that also has storm drains and vertical curbs that salamanders cannot climb.

In 1999, a residential subdivision eliminated most grassland habitat to within 10 m of the south and west shorelines of the pool. This high-density development (0.04–0.07 ha lots) was built on a recontoured landscape of imported fill, eliminating all previously existing upland habitat. This development and its associated roads, with 15 cm tall curbs and storm drains, also block direct access to remaining grasslands to the southwest. East of Southwest Park is a mosaic of grasslands, rural residences, and high-density development. Currently the region within 100 m of the pool contains just 0.97 ha or 15.4% suitable grassland habitat (Fig. 1). Within the larger landscape, from the pool out to 700 m in all directions, 18.0% is grasslands accessible to CTS. Although there is some suitable grassland immediately north-northwest of the pool, 94% of directly accessible grassland habitat within 700 m is east of the Southwest Park. The manicured grounds of Southwest Park do not provide burrows, but migrating salamanders can traverse the area (D.G. Cook pers. obs.).

In 2000, the city of Santa Rosa implemented measures to protect the breeding pool at Southwest Park. A 1.2 m tall wire mesh fence now protects a 1.25 ha preserve area, including the pool, from human disturbance. A 60 cm-high drift fence, extending 90 m east and 150 m north from the southwest corner of the preserve, reduces salamander access to the adjacent roads.

Field Surveys — Our studies spanned two breeding seasons, 2002–2003 and 2003–2004, hereafter 2002 and 2003. To capture salamanders entering and exiting the breeding site, we constructed a drift fence with pitfall traps completely encircling the breeding pool (Dodd and Scott 1994). Our drift fence, constructed of plastic silt fencing, was 30 cm-high with the lower edge buried >5 cm deep. Pitfall traps were 3.7 and 7.3 L plastic cans buried with the lip flush to the ground, and spaced at 10 m intervals along both the interior and exterior of the drift fence. Each trap was equipped with an elevated cover for shade and a damp sponge to prevent desiccation of captured salamanders.

In both years, we opened the traps immediately prior to the first forecasted autumn rains in November and operated them continuously until several weeks after breeding activity ended and no more salamanders were captured (February in both years). We checked traps at sunrise each day, measuring captured salamanders and uniquely toe clipping each one. For each capture we recorded the date, trap number, toe clip number, sex, snout-vent length, and for females whether or not they appeared gravid (i.e., swollen with eggs). We then released salamanders on the opposite side of the fence at the point of capture.

Analysis Methods — We determined the coordinates of each trap using a Trimble GeoExplorer IIIc global positioning system (GPS) and mapped these points on an orthorectified aerial photograph of the region in a geographic information system (GIS). The accuracy of this unit is 1–5 m after base station correction. We adjusted some visibly erroneous trap locations based on the underlying aerial photograph. These locations are all accurate to within 5 m. We determined the compass direction of each trap as a vector from the center of the pool through the trap location.

We used the same aerial photograph and GIS to map the remaining accessible grassland habitats within 700 m of the pool. The 700 m distance was chosen based on work elsewhere showing CTS to move this far (Trenham et al. 2001). For these calculations we divided the landscape into eight 45° wide wedges starting at 0° (north) and centered on the breeding pool. Then within each wedge we determined the area of accessible (i.e., to which straight-line access is not blocked by a high traffic road or dense residential development; see Fig. 1) grassland remaining within 100 m reaches (bands) out to 700 m (e.g., 0–100 m, >100–200 m, etc.) from the edge of the breeding pool.

Descriptive statistics were calculated using Microsoft Excel, and circular statistics with Oriana 2.0. In all statistical tests α = 0.05.

Results

Over the course of two field seasons, we captured 171 individual SCCTS at least once at the breeding pool. After correcting for trespasses, an estimated 49 females and 55 males bred in 2002, and 44 females and 46 males bred in 2003 (Cook et al. 2006). Figure 2A summarizes the spatial distribution of incoming captures. Captures of incoming adults were not uniformly distributed; they were concentrated east and to a lesser degree northwest of the pool (Rayleigh Test for Uniform Distribution (RTUD): Z = 18.4, n = 146, P < 0.001). The majority of both sexes were captured entering in traps along the eastern shoreline; 95% confidence intervals on their mean vectors overlap broadly. Relatively small numbers of adults were captured entering along the isolated band of remnant upland habitat south and west of the pool; traps along this habitat strip cover roughly 40% of the pool shoreline but accounted for just 15.7% of total incoming captures. Although 53% of all incoming captures were males, the minor concentration of captures along the northwest shoreline was composed of 74% males (Fig. 2).

Salamanders departed the pool with an even stronger eastward bias (RTUD: Z = 53.9, n = 145, P < 0.001; Fig. 2B). Nearly 90% of departing salamanders were captured in traps between 0° and 180° including 69 of the 70 females captured. Although departing females were more strongly concentrated along the eastern shoreline, the mean exit vectors for males and females again had overlapping 95% confidence intervals.

Distribution of adjacent grassland habitat within 100 m of the breeding pool was not positively correlated with the distribution of incoming or outgoing captures of males or females (Fig. 3). Increasing the buffer width used to calculate
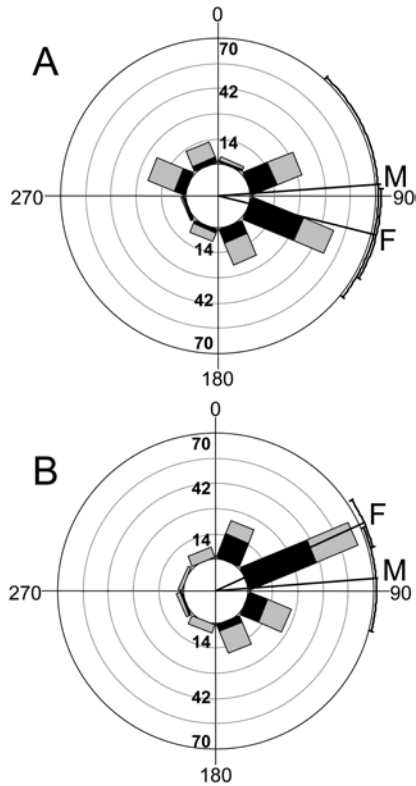
Fig. 2. Spatial distribution of incoming (A) and outgoing (B) captures of California tiger salamanders around the Southwest Park breeding pool during 2002 and 2003. Bars represent captures in traps between 0°-<45°, 45°-<90°, etc. Black portions of bars represent females and grey portions represent males. Mean vectors and 95% confidence intervals are also represented. Because our main interest was to understand where salamanders were arriving from and departing to, for these analyses we excluded individuals first captured inside the drift fence or last captured on the outside.

Fig. 3. Correlations between the spatial distribution of captures at the drift fence (represented in Fig. 2) and the area of accessible grassland habitat in the surrounding landscape. For these calculations both the traps and the upland habitats were divided into eight 45°-wide sections centered on the breeding pool. Correlations were calculated between captures in each section and the area of grassland in the same direction within 100, 200, 300, 400, 500, 600 and 700 m of the breeding pool. Positive correlation indicates correspondence between the number of salamanders captured and the amount of grassland remaining in the adjacent uplands.

areas of accessible grassland to 200 m and greater, however, we found consistently positive correlations between the distribution of captures and this upland habitat metric. For incoming captures of females and males, this correlation was maximized using buffers 400 and 200 m wide, respectively. The spatial distribution of outgoing captures of both males and females were most strongly correlated with grassland areas within 700 m of the pool.

The stronger directional bias among salamanders exiting versus entering the pool suggests that individuals may not follow consistent paths of travel as they move towards and away from this breeding pool. We found that for individuals captured both upon their initial arrival and final departure in 2002 or 2003, their apparent direction of travel, as indicated by the trap heading, differed by an average of 64.0° between entry and exit (95% CI = 55.3°–72.7°, n = 106). This is significantly less than the 90° mean that would result if movement were completely random, but far greater than the 10° mean difference between adjacent traps (range = 5°–19°). Figure 4
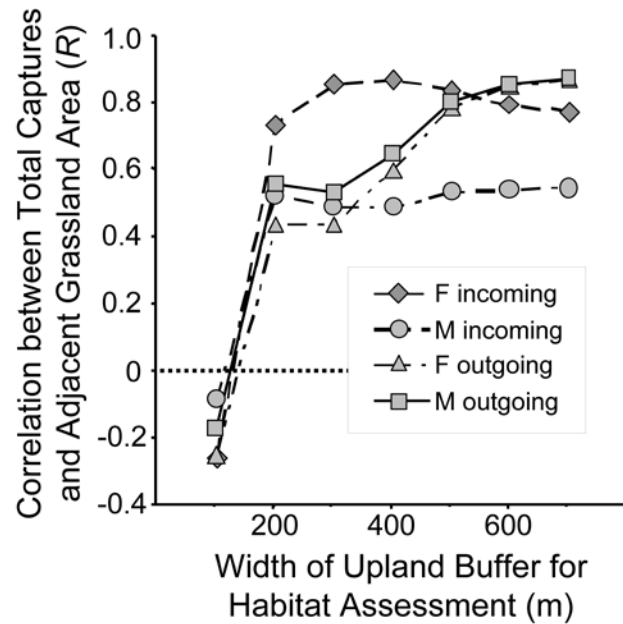
reflects a major dichotomy between animals captured entering in western versus eastern traps. SCCTS captured entering the pool in western traps, with headings between 180° and 360°, exited essentially randomly (95% CI = 82.1°–111.3°), while those entering between 0° and 180° deviated by an average of just 49.2° (95% CI = 40.2°–58.3°). The exit headings of animals entering from both the west (95% CI = 44.4°–84.8°) and east (95% CI = 62.2°–86.9°) were similarly focused eastward. Finally, comparing males and females, on average males exited significantly farther from their entry points than did females (Males: mean = 70.6°; Females: mean = 50.1°; Watson-Williams test: F = 5.55, df = 1, P = 0.02).

DISCUSSION

Modification of native wetland and upland habitats commonly results in the decline or loss of local amphibian populations (Gibbs 1998; Davidson et al. 2002; Rubbo and Kiesecker 2005). In cases where factors such as disease or climate do not appear to drive declines, maintenance of viable populations depends first on the preservation of sufficient appropriate habitat (Semlitsch 2002). Protecting wetland breeding habitats is often relatively simple. At Southwest Park, the city of Santa
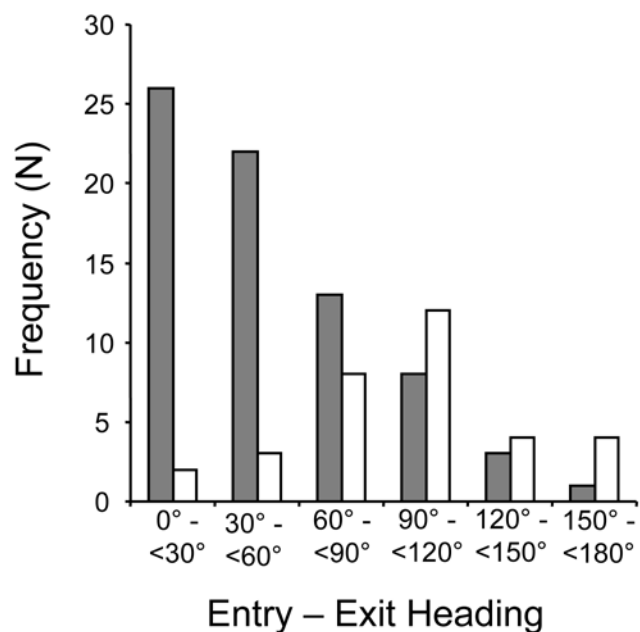
Fig. 4. Histogram representing the angular differences between capture locations for salamanders upon their initial entry and last departure from the pool in 2002 or 2003. Bars to the left indicate entry and exit along the same section of the drift fence. The maximum possible difference is 180° for an animal exiting on the exact opposite side of the pool from where it entered. Gray bars represent salamanders initially captured in eastern traps between 0° and 180° (n = 73); open bars represent salamanders initially captured in western traps between 180° and 360° (n = 33).

Rosa installed a barrier fence, at a modest cost, to minimize disturbance to the breeding pool. Determining upland requirements, not to mention adequately protecting these areas, is considerably more challenging. Our study adds to a growing body of work attempting to elucidate the upland habitat needs of aquatic-breeding amphibians (Loredo et al. 1996; Madison and Farrand 1998; Semlitsch and Bodie 2003).

As California's human population continues to grow, rural and natural areas like the lands of the Santa Rosa Plain will come under increasing development pressure. Often our ability to conserve amphibians and reptiles in these urbanizing landscapes is challenged simply by our incomplete knowledge of basic natural history (Semlitsch 2002). The fact that a substantial breeding population of California Tiger Salamanders remains at Southwest Park is encouraging because it suggests that populations may persist in landscapes that are not completely preserved. However, to put this information to use we must better understand how species manage to persist at this and other urban sites. The main findings of our two seasons of drift fence censuses are: 1) that the spatial distribution of captures along the pool shoreline appears to be tied to the distribution of upland grassland habitats >100 m from the pool, and 2) that most salamanders exit the breeding pool along the same general section of shoreline where they entered.

Based on our calculations, <20% of the upland landscape

surrounding the Southwest Park pool remains accessible and suitable for SCCTS, and most of this is concentrated east and to a lesser degree northwest of the pool. Similarly, adult captures were highest in traps along the eastern and northwestern shorelines. Correlation analysis revealed that captures along each segment of shoreline were roughly proportional to the area of grassland habitat remaining between >100 and 700 m from the pool in the same direction (Fig. 3). Because California Tiger Salamanders require small mammal burrows to survive in the uplands, the strong correlation between shoreline distribution and accessible undeveloped upland habitat is not surprising (Loredo et al. 1996; Trenham 2001). The absence of any positive correlation between distribution and area of grassland <100 m from the pool may seem unexpected, but this result is consistent with two studies showing that most California Tiger Salamanders migrate >100 m from breeding pools (Trenham 2001; Trenham and Shaffer 2005). Although the non-random distribution along the shoreline could result from factors other than the location of suitable upland habitats, repeated visual inspection of the shoreline area failed to reveal any heterogeneity that might suggest local habitat selection.

Admittedly, the relative heading from the pool center to a capture location does not provide strong inference as to an animal's origin, migratory track, or ultimate destination. Animals may not fall into the first trap they encounter and many likely deviate from the path suggested by traps located within 5 m of the pool shoreline. However, California Tiger Salamanders radio-tracked emigrating after breeding generally followed a compass heading similar to that suggested by the trap-based heading as they left the breeding pool, deviating by <30° on average (P.C. Trenham pers. obs.). Other amphibians have also been observed to follow roughly consistent paths as they move towards and away from breeding pools, supporting a relationship between shoreline and upland distributions (Shoop 1968; Semlitsch 1983; Madison and Farrand 1998).

Studies of the upland ecology of this and other wetland-breeding amphibians indicate that core upland habitat traversed and occupied by a substantial portion of a local population extends hundreds of meters beyond the aquatic habitat. Based on a review covering 32 amphibian species, Semlitsch and Bodie (2003) determined that core upland habitat essential for migration, foraging and sheltering extends 159 to 290 m from the edge of the breeding habitat. In a recent study of California Tiger Salamander upland distribution in Solano County, California, adult densities declined approximately exponentially with 90% of adults estimated to remain within 490 m of the breeding pool (Trenham and Shaffer 2005). These studies suggest that few SCCTS will remain in the narrow bands of grassland habitat south and west of the Southwest Park pool. Our results support this prediction.

Due to the relatively small amount of adjacent upland habitat northwest of the pool, the concentration of captures along this shoreline is worthy of additional attention. Assuming shoreline distribution reflects upland distribution, 23% of

the total incoming captures came from the ~70 m wide strip of grassland extending 200 m northwest of the pool. However, only 5% of captures exited in this direction, suggesting that this habitat may be suboptimal for year-round occupancy. Sex ratios along this shoreline were also strongly male biased, with males representing 74% of entering and 100% of exiting captures, suggesting that this grassland area supports a male biased subset of the population. The apparent male bias for this small patch of habitat could result from a general tendency of males to migrate shorter distances from breeding pools. This pattern has been documented recently for several related species (Faccio 2003; Regosin et al. 2003a,b). In our correlation analysis, incoming female and male captures were most strongly correlated with grassland areas within 400 m and 200 m of the pool, respectively, lending support to this interpretation (Fig. 3). Sex-biased upland habitat use remains worthy of additional study and potential consideration in reserve design.

Another plausible explanation for the concentration of incoming captures along the northwest shoreline is that landscape elements influence paths of travel. In this case, salamanders migrating westward encounter the road or the drift fence blocking access to the road, and then head south towards the pool. This would require that animals wander during migration to the pool. The greater variance, for both males and females, in the capture distributions of entering versus leaving salamanders may also indicate the tendency of immigrating adults to stray off target. If salamanders can sense the dense development south and west of the pool or the relatively suitable habitats to the east, this might explain the strong eastward departure bias; however, experiments with juvenile *A. maculatum* and *Bufo boreas* showed no strong tendency to move from pools towards nearby forest habitat (Rothermel 2004). In urban landscapes, studies to better understand how animals orient themselves and locate suitable habitat would assist reserve design.

In addition to a consistent association between the distribution of shoreline captures and the area of adjacent grassland, we also found that individuals tended to enter and exit the pool along the same section of shoreline. This tendency may increase the capacity of incompletely preserved landscapes to support populations in urban areas. At Southwest Park, because the bulk of individuals arrived from and returned to the east, they are less likely to stray towards nearby roads and other potentially lethal habitats. The degree of deviation between entry and exit capture locations varied in several important ways. First, although entry and exit points were significantly closer than would be expected if movement were completely random, an average deviation of 64° strongly suggests that most individuals do not immigrate and emigrate along exactly the same pathway. As a result, broad areas of suitable habitat adjacent to breeding pools will be needed to minimize losses due to the tendency to wander. Second, regardless of the location of an animal's entry it was most likely to exit eastwards towards the largest area of remnant grassland, reinforcing the importance of that region for this population. Third, females

deviated less between their entry and exit points than males. Although we know that males spend more time at breeding pools (Loredo and van Vuren 1996; Trenham et al. 2000; Cook et al. 2006) we found no correlation between days between captures and directional deviation.

Other authors interpreting similar data from drift fenced pools emphasized the degree to which movement was less than random and suggested this as evidence of a capacity for orientation. Shoop (1965) invoked complex orientation to explain an average deviation of 49° (95% CI = 40.1°–57.8°) between entry and exit points for *A. maculatum*. Although in those years any demonstration of orientation capacity in "lower" animals was impressive and surprising, from the perspective of designing preserves, recognizing the degree of imperfection in orientation is at least as important. In our dataset and all other similar studies, although significantly nonrandom, orientation appears consistently imperfect (Shoop 1965, 1968; Shoop and Doty 1972; Douglas 1981; Stenhouse 1985). These observations suggest that unless preserve designs encompass uplands adjacent to and beyond at least 30% of contiguous shoreline, most individuals will stray into unprotected areas. In urbanized landscapes, these data could be used to design experimental habitat corridors with the goal of connecting breeding pools to available upland habitats and other pools.

The substantial breeding population at Southwest Park and the tendency of these adults to orient towards open grasslands and away from roads and development suggest that the landscape as currently configured may support a viable population. No data exist on the size of this breeding population prior to recent habitat losses. Assuming that the loss of 82% of grassland habitat within 700 m of the Southwest Park pool has resulted in a proportional population reduction, historic breeding aggregations could have topped 500. These numbers are conceivable for a breeding pool of this size. Whereas the Southwest Park pool has a surface area of 7,000 m², several ponds with surface areas of just 700 m² or less, but in undeveloped landscapes, supported populations of 50–240 breeding adults (Loredo and van Vuren 1996; Trenham et al. 2000, 2001). More than 300 adults bred on average in one 3,660 m² pond (Trenham et al. 2001). Thus, although it may be possible to maintain populations in landscapes with development, the effects of habitat loss should not be underestimated.

Conversion of upland areas to unsuitable habitat will almost certainly result in population declines, but if pools are sufficiently productive and adequate uplands are protected they may maintain viable populations (Trenham and Shaffer 2005). Our findings suggest a few guidelines and strategies that may be applied to conserving this species in complex and rapidly developing landscapes. First, in addition to breeding pools, undeveloped grassland habitat appears essential to maintaining California Tiger Salamanders in a landscape. Our results support the observations of earlier studies showing that California Tiger Salamanders commonly move 100–700 m from breeding pools to grassland burrow sites (Trenham et al. 2001; Trenham and Shaffer 2005). Available data indicate

that pools with just 100 m of fringing grassland are unlikely to support populations with long-term viability. Unsuitable habitats, like the 75–100 m wide area of lawns and recreational fields of Southwest Park, do not appear to represent barriers to movement, and thus could possibly be incorporated into preserve designs. A recent study by Marsh et al. (2005) showing that narrow forest roads substantially reduced the ability of displaced salamanders to return to their home sites, however, suggests that migration across such novel habitats may be reduced. Because individuals tended to enter and exit along the same general section of pool shoreline, but with apparent deviation in their exact path of travel, pools set aside for this species should have at least 30% of contiguous shoreline abutting undeveloped uplands which extend at least several hundred meters from the pool. Ultimately, monitoring population sizes before and after construction is needed to record the effects of habitat conversion. Additionally, we suggest that application of radio tracking or similar methods could greatly improve knowledge of how individuals interact with complex urbanized landscapes.

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