
MOVEMENT PATTERNS AND MIGRATION DISTANCES IN AN UPLAND POPULATION OF CALIFORNIA TIGER SALAMANDER (*AMBYSTOMA CALIFORNIENSE*)

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Abstract.—During five winter breeding seasons (October–April, 2000–2005), I investigated the migratory movements of an upland population of California Tiger Salamander (*Ambystoma californiense*) in Contra Costa County, California. I used a drift fence and pitfall trap array to partially enclose a proposed 27 ha housing project and capture migrating adult and juvenile salamanders. The study objective was to assess movement patterns and migration distances for upland life stages during an effort to translocate all captured salamanders and reduce their mortality from future development at the study site. I recorded substantial numbers of adult and juvenile *A. californiense* (90–417 annually) farther from breeding ponds than previously reported. The majority of salamanders were captured at least 800 m from the nearest breeding pond while a smaller number of salamanders were captured as far as 2.2 km from the nearest breeding pond. The study indicates that recent recommendations to protect 630 m of upland habitat adjacent to breeding ponds may leave large portions of upland life stages at risk. Adults appeared to exhibit fidelity to upland habitat, returning close to the initial point of capture. In situations where translocation is used to remove salamanders from upland habitats subject to development, results suggest it may take several years to successfully relocate a high proportion of individuals in the population.

Key Words.—*Ambystoma californiense*; buffer zones; California Tiger Salamander; conservation; pitfall trap; migration distance; terrestrial movements; upland ecology.

INTRODUCTION

Conserving terrestrial habitat surrounding wetlands is essential for maintaining populations of many pond-breeding amphibians (Semlitsch and Jensen 2001; Semlitsch 2002; Semlitsch and Bodie 2003). Upland habitat is critical for feeding, refuge, and migratory movements of juvenile and adult life stages (Semlitsch 1998; Semlitsch and Jensen 2001). Recent studies emphasize that amphibian population viability can be extremely sensitive to survivorship of upland life stages (Biek et al. 2002; Trenham and Shaffer 2005). Further, the importance of specific areas of upland habitat and preferences for a particular migratory route have been reported for several species of ambystomatid salamanders (Shoop 1968; Stenhouse 1985; Trenham and Cook 2008).

Despite research documenting the biological importance of terrestrial habitat for amphibians, the extent and location of appropriate areas required to sustain viable populations are poorly understood. Several recent studies estimated the area of terrestrial habitat needed to adequately protect amphibian populations, based on migration distances from multiple studies and species. Semlitsch (1998) estimated that a 164 m “buffer zone” would encompass 95% of most ambystomatid salamander populations (based on six species). Semlitsch and Bodie (2003) estimated that “core terrestrial habitat” for 13 species of salamanders

ranged from 117 to 218 m from the wetland. Rittenhouse and Semlitsch (2007) found that 95% of the adult breeding population for six species of salamanders occurs within 245 m of the wetland boundaries. However, because these studies were primarily of eastern species that typically inhabit forest or woodlands, the resulting recommendations may not be well suited to western *Ambystoma* species associated with grasslands. Although much remains to be learned regarding the appropriate size of buffer zones, it is clear that identifying and protecting upland habitat should be a management priority, especially for rare and endangered species (Marsh and Trenham 2001; Semlitsch 2007; Harper et al. 2008).

The California Tiger Salamander, *Ambystoma californiense*, is listed as a threatened species by the U.S. Fish and Wildlife Service (2004) and the state of California (California Fish and Game Commission 2010). The range of this species is restricted to grasslands and foothills of central California (Storer 1925). Adults spend the majority of their life cycle in small-mammal burrows in upland habitat (Loredo et al. 1996). With the onset of winter rains, adults emerge from underground terrestrial retreats and migrate to ponds for reproduction (Loredo and Van Vuren 1996). The importance of maintaining upland habitat adjacent to breeding ponds for *A. californiense* has only recently been emphasized (Trenham 2001; Trenham and Shaffer 2005). A more detailed under-

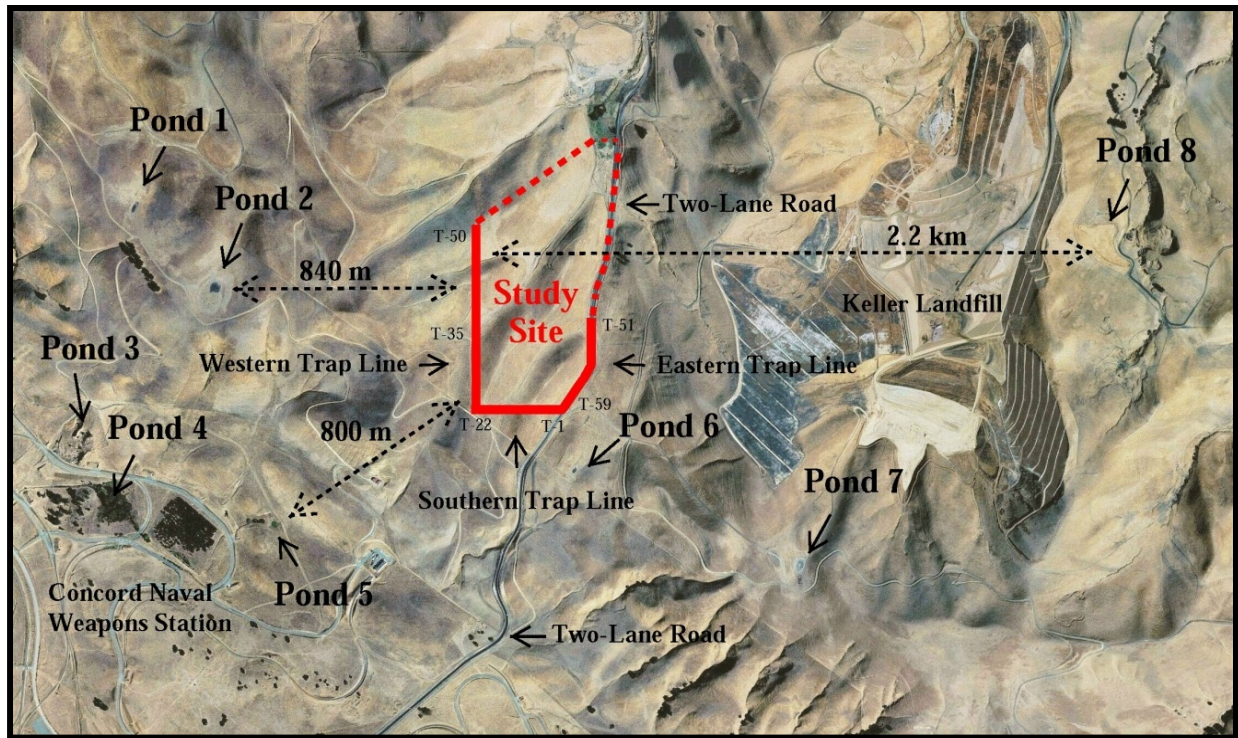


FIGURE 1. Aerial photograph showing the closest breeding ponds to the study site in Contra Costa County, California, USA (from <http://www.terraserver.com>; [Accessed 1 August 2002]). Bold red solid lines indicate trap line segments (western, southern, and eastern) along boundaries of the study site, T represents trap number, and dashed lines with arrows at both ends indicate distances from the western trap line to nearest breeding ponds. Ponds 1–5 are located on Concord Naval Weapons Station (CNWS) and Ponds 6–8 are located on a landfill adjacent to the study site

standing of migratory movements and activity patterns in upland habitats is fundamental to managing this species (Trenham and Shaffer 2005).

This paper presents findings of a five-year study investigating the migratory movements of upland life stages of a population of *A. californiense* at a proposed housing development. The primary objectives of the study were (1) to characterize movement patterns and timing of movements during the breeding season, (2) to measure distances from capture locations to closest known breeding ponds, and (3) to test for relationships between the timing of migratory movements and environmental parameters. An additional objective of the study was to reduce direct mortality from future development at the study site by translocating all captured salamanders outside the study site and restricting reentry. Conservation strategies involving translocations are a common wildlife management tool (Griffith et al. 1989; Fischer and Lindenmayer 2000; Dodd 2005). Although the effectiveness of translocation strategies has been subject to controversy (e.g., Dodd and Seigel 1991; Seigel and Dodd 2002; Trenham and Marsh 2002), a recent review has shown improved success rates for some species of amphibians when a critical minimum number of individuals are translocated (Germano and

Bishop 2008). Relatively few translocation studies have been conducted on amphibians (Germano and Bishop 2008) or addressed human and wildlife conflicts (e.g., Cooke and Oldham 1995; Rathbun and Schneider 2001), and none have assessed the efficacy of translocating adult amphibians within upland habitat.

MATERIALS AND METHODS

Study site.—The proposed housing development is located on the northern edge of the San Joaquin Valley in northeastern Contra Costa County, California. The 27-ha area consists of grazed annual grasslands on rolling to steep hills (elevation range = 213–274 m; Fig. 1). Two primary drainages traverse the site but amphibian breeding ponds are not present. Lands surrounding the site are primarily grazed grasslands. The Concord Naval Weapons Station (CNWS) is located to the west and south of the site and a privately owned, active landfill is located to the east and southeast.

Eight breeding ponds are known to occur near the study site (Fig. 1). To the west and southwest, the closest ponds are on CNWS (Ponds 1–5) and are the primary breeding ponds on CNWS lands (Stitt and Downard 2000; Shawn Smallwood, pers. comm.). To

the east and southeast, the closest ponds are located on the adjacent landfill (Ponds 6–8). To the north, no known breeding ponds occur within 2.5 km. I examined aerial photographs from several years (1999, 2000, 2004, and 2005) and USGS topographic maps, and found no other potential breeding ponds closer to the study site. Before the trapping study began, I conducted four night surveys during winter rain events to determine if *A. californiense* was present at the study site. During these initial surveys, I observed four adults at burrow entrances of California Ground Squirrels (*Spermophilus beecheyi*) and thus commenced an intensive translocation effort.

Trapping techniques.—My field team and I (hereafter we) installed a drift fence and pitfall trap array along a partial perimeter (1.3 km) of the study site. The drift fence bordered the boundaries most likely to be used as movement corridors, and included the western, southern, and a portion of the eastern border of the study site (Fig. 1). We installed 118 pitfall traps (59 pairs of 7.5 L plastic buckets) located every 15 to 30 m along the inside and outside of the drift fence. We used a 0.9 m tall commercial quality silt fence buried 0.3 m underground, stretched taut, and secured by both wooden and steel fence posts. We placed elevated covers over the traps to provide shading and minimize predation, and placed a damp non-cellulose sponge in each trap to maintain moisture for captured salamanders. We replaced the drift fence and pitfall traps (i.e., trap line) each year of the study and repaired the fence line as needed to maintain its integrity as a barrier to movement.

Our surveys encompassed five winter breeding seasons, from October 2000 to April 2005 (hereafter, years 2000 to 2004). In 2001 and 2002, we increased the length of the trap line by installing nine pairs of pitfall traps along the eastern border of the study site. While the trap line encompassed over half the total perimeter of the proposed development, the entire area was not completely enclosed due to the large area of the site. We opened all traps at dusk on nights when the chance of rain was predicted to be 40% or greater and checked at dawn the following morning. Because amphibians are often active on the night after a heavy rain (Gibbons and Bennett 1974), we left the traps open on nights after a rain event that exceeded 0.6 cm, even when no rain was predicted for that night. At all other times the traps were closed. We immediately translocated individuals captured inside the trap line to small mammal burrows 15 to 100 m outside the development. We kept individuals captured outside the trap line outside and translocated them in the same manner.

For each capture, we recorded date, trap number, trap line side (inside or outside), sex (adults only), reproductive condition (reproductive or non-reproductive), snout-vent length (SVL), total length, and age class (adult or juvenile). We identified individuals

as adults if they had at least one of the following characteristics: keeled tail, swollen vent (reproductive males), gravid condition (reproductive females), or large body length (≥ 75 mm SVL; Trenham et al. 2000). We identified juveniles based on small body length (usually < 75 mm SVL; Loredo and Van Vuren 1996) and the absence of adult characteristics. Males were distinguished from females by the presence of a keeled tail, swollen vent, or proportionally longer tail (Petranka 1998; Searcy and Shaffer 2008). We recorded adult-sized salamanders without other distinguishing characteristics as adults; these salamanders may have been subadults (≥ 1 year of age but not sexually mature) or salamanders returning from the ponds post breeding (i.e., non-reproductive). Because juvenile body lengths vary considerably (46–114 mm; Loredo and Van Vuren 1996) and can overlap adult sizes, we may have mistakenly classified some larger juveniles as adults in non-reproductive condition. In addition, we acquired two photographs of the dorsal surfaces of each captured salamander for individual identification.

Environmental variables.—In 2000 and 2001, I measured precipitation using a manual rain gauge located on site; the gauge was read and emptied when traps were opened at dusk and checked again at dawn the next morning. For the remainder of the study years, I used an automatic rain gauge (Hobo event logger, Onset Inc., Pocasset, MA., USA) to record hourly rain events (2.5 mm intervals). Air temperature was manually recorded on each morning traps were checked. I used additional data on hourly and yearly rainfall near the study site from California Department of Water Resources, California Data Exchange Center (available from <http://www.cddec.water.ca.gov> [last accessed 21 September 2006]).

Analyses.—I pooled daily capture data by week, year, sex, age class, and location (inside/outside trap line and trap line segment) as measures of salamander activity. I used the location of captures to infer likely movement patterns (i.e., attempting to leave or enter the study site, and directionality). To evaluate movement patterns within a breeding season, I divided capture data into early season (presumably migrating to breed) and late season (presumably returning from breeding) based on the temporal distribution of captures for all five study years combined.

To standardize for the variability in trapping effort (i.e., different number of traps per line segment and nights of trapping each year), I calculated capture rates (number of captures per 100 trap nights) for analyses. Distance calculations were measured as presumed straight line travel. Within each study year, I compared dorsal patterns in photographs to determine the number of intra-annual recaptures. Individual identification

using photography has been employed successfully with amphibians that have unique patterns of coloration; unlike invasive marking techniques, this causes no harm to the animal (e.g., Donnelly et al. 1994; Doody 1995; Bailey 2004).

I used parametric statistics when data were normally distributed and non-parametric tests when data were not. To determine if recaptured individuals returned to a similar point from which they were initially trapped, the observed mean number of traps between initial and returning trap locations was compared with the expected mean number of traps under a uniformly random scenario (Shoop and Doty 1972). For this analysis, I pooled data from all five study years to obtain an adequate sample size and used only those individuals that were initially trapped early in the breeding season on the inside of the western trap line and then recaptured later in the season outside that same trap line segment (i.e., presumably returning to the study site after breeding). I used the western trap line data because it had the majority of returns and traps along this segment were evenly spaced providing the most accurate distance measurements between initial and returning trap locations.

I tested for annual and seasonal variation in capture numbers among all five study years. I used chi-square tests to determine if annual sex ratios differed significantly from an expected 1:1 ratio. I evaluated the association between seasonal rainfall (both early and late season) and the proportion of males and females captured both inside and outside the trap line using Pearson's correlation coefficient. I used the sign test to compare annual adult capture rates early in the season on the inside of the western trap line and capture rates later in the season outside that same trap line segment, and to compare annual rainfall between early and late seasons. I used Pearson's correlation coefficient to assess whether there was a negative association between translocation efforts and annual capture rates over time based on the proportions of inside versus outside captures, and to test for a relationship between annual on-site rainfall and annual capture rates.

I also analyzed within-year associations between environmental parameters and the number of *A. californiense* captured. To assess the influence of precipitation and temperature prior to capture, I used Spearman's rank correlation. This analysis used rainfall amounts 12 h prior to opening traps (i.e., day prior to capture), 12 h prior to checking traps (i.e., night of capture), and within 24 h prior to checking traps (total of day and night). In addition, I used Wilcoxon two-sample rank sum test to assess if rain at dusk on the night of capture or the night prior to opening the traps was associated with the number of captures. Precise measurements of rain using the automatic rain recorder (which allowed for analysis of rain amounts in intervals less than a 24-h period) were available only in 2002, 2003 and 2004. Of these three

TABLE 1. Adult and juvenile *Ambystoma californiense* captured inside and outside the trap line during five winter breeding seasons at the study site in Contra Costa County, California. Totals include recaptured individuals. Unique captures exclude recaptured individuals and are shown in parentheses.

Year	Adult Total No. (Unique No.)	Juvenile Total No. (Unique No.)	Adult & Juvenile Total No. (Unique No.)
2000–2001			
Inside trap line	59 (58)	3 (3)	62 (61)
Outside trap line	76 (37)	62 (47)	138 (84)
Totals	135 (95)	65 (50)	200 (145)
2001–2002			
Inside trap line	184 (182)	4 (3)	188 (185)
Outside trap line	215 (158)	14 (13)	229 (171)
Totals	399 (340)	18 (16)	417 (356)
2002–2003			
Inside trap line	63 (61)	3 (3)	66 (64)
Outside trap line	120 (96)	34 (33)	154 (129)
Totals	183 (157)	37 (36)	220 (193)
2003–2004			
Inside trap line	37 (36)	0 (0)	37 (36)
Outside trap line	52 (37)	1 (1)	53 (38)
Totals	89 (73)	1 (1)	90 (74)
2004–2005			
Inside trap line	23 (22)	0 (0)	23 (22)
Outside trap line	72 (61)	86 (81)	158 (142)
Totals	95 (83)	86 (81)	181 (164)

years, I chose 2002 for analysis because it was least affected by translocation efforts and barrier fencing.

I excluded recaptures from the analysis of some data sets (i.e., capture distribution, movement patterns, sex ratios, and annual reductions). However, except for sex ratios, these analyses did include those individuals first captured during the early season inside the trap line and then later recaptured outside the same trap line during the late season. For annual comparisons of capture numbers, I deleted data on additional traps installed in 2001 and 2002 from the analyses. For all statistical tests, results were considered significant at $\alpha = 0.05$.

RESULTS

Capture numbers and movement patterns.—The annual number of *A. californiense* captured varied from 90 to 417 salamanders over the five year study period (Table 1). Recaptured individuals represented between 9–28% of annual totals, with 96% of these individuals captured on the outside of the trap line. Eight recaptured individuals were captured on or translocated to the outside of the trap line and then later captured on the inside, but these eight represented less than 1% of the total captures. Adult recaptures returning to the study site (presumably after breeding) were found

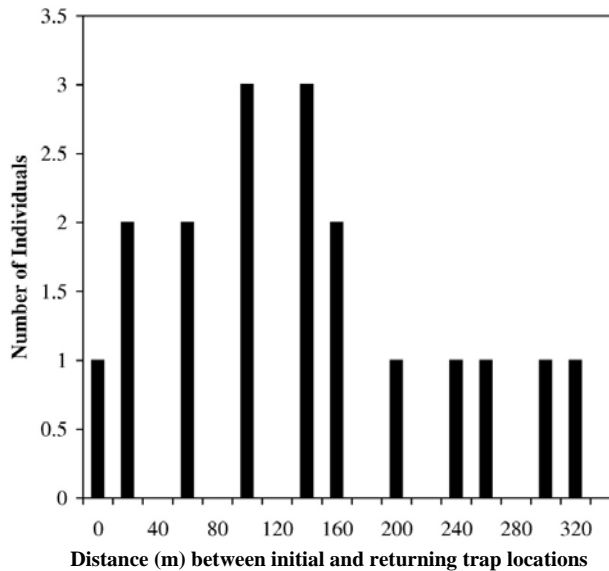


FIGURE 2. Frequency distribution of the distance between initial and returning trap locations for individual *Ambystoma californiense* for all five study years combined (2000–2005). Results include only those salamanders first trapped early during the breeding season inside the trap line and then recaptured outside the same trap line later in the season. Early season = late October to December 31; Late season = January 1 to end of March. Zero on the x-axis represents individuals that returned to the same trap location where they were initially captured.

significantly closer to where they were initially captured inside the trap line than would be expected by random ($Z = -2.92$, $P = 0.003$). Forty-four percent of adult recapture locations were within five traps (≤ 100 m) of the initial inside trap location (Fig. 2). Several individuals were recaptured more than once outside the western trap line, presumably attempting to reenter the site. One male returned to the site five times.

Capture rates from all five study years combined indicate that males and females migrated to the breeding ponds from late October to the end of December (early season) and returned to their upland habitat from the beginning of January to the end of March (late season) (Fig. 3). Annual sex ratios differed significantly from 1:1 in 2002, with females outnumbering males by 2:1 ($\chi^2 = 20.46$, $df = 1$, $P < 0.001$). By contrast males outnumbered females by 1.5:1 in 2000 ($\chi^2 = 3.80$, $df = 1$, $P = 0.051$). Sex ratios were near 1:1 in the other three study years (2001: $\chi^2 = 0.02$; 2003: $\chi^2 = 0.00$; and 2004: $\chi^2 = 0.11$; all $df = 1$, all $P > 0.70$). Among all study years, the proportion of each sex in the population captured early in the season on the inside of the trap line (Table 2) was associated with early season rainfall (negatively associated for males: $r = -0.808$; positively associated for females: $r = 0.808$; $P = 0.049$ for both). However, there was no significant association between the proportion of each sex captured early in the season outside the trap line and early rainfall (males: $r = -0.340$;

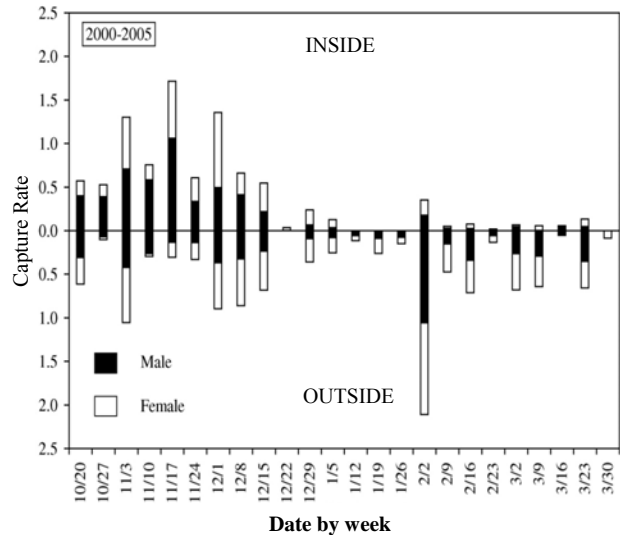


FIGURE 3. Weekly capture rates (no. per 100 trap nights) of male and female *Ambystoma californiense* inside and outside the trap line for all five study years combined (2000–2005). Early season = late October to December 31; Late season = January 1 to end of March. Dates on x-axis represent the beginning of each week. Recaptured individuals were excluded except for salamanders first captured during the early season inside the trap line and then recaptured outside the same trap line later in the season.

females: $r = 0.340$; $P = 0.288$ for both) or captured late in the season outside the trap line and late rainfall (males: $r = -0.494$; females: $r = 0.494$; $P = 0.198$ for both).

Within each survey year, the capture rates of adults and juveniles were generally highest along the western trap line (Fig. 4). Analysis of early season capture data, when most salamanders presumably migrated to the ponds, indicated highest adult capture rates on the inside of the western trap line (Table 3). By contrast, analysis of late season data, presumably when most salamanders returned from the ponds, indicated highest adult capture rates outside the western trap line (Table 3). Capture rates for juveniles were highest outside the western trap line primarily in the early season (Table 4). Among all study years, more adults were captured early in the season inside the western trap line than were captured later in the season outside that same trap line segment (sign test, $P = 0.031$). Early and late rainfall was not significantly different among years (sign test, $P = 0.50$).

Migration distances.—The shortest distances from inside the western trap line, where the majority of adults were captured in the early season, to the closest breeding ponds to the west were 800 to 840 m (Ponds 5 and 2 on CNWS, respectively; Fig. 1). A smaller number of adults captured early in the season on the outside of the western trap line may be migrating east (Table 3). The closest breeding pond from the western trap line to the east is Pond 8 at 2.2 km. A few adults captured early in

TABLE 2. Proportions of male and female *Ambystoma californiense* captured during the early and late winter breeding seasons on the inside and outside of the trap line. Parentheses indicate the number of each sex captured and N = the total number of adults captured. Early season = late October to December 31; Late season = January 1 to end of March. Results exclude all recaptured individuals.

Season/ Trap Line Side	2000– 2001	2001– 2002	2002– 2003	2003– 2004	2004– 2005
Early/Inside					
Male	0.76 (41)	0.50 (86)	0.39 (23)	0.68 (23)	0.52 (11)
Female	0.24 (13)	0.50 (87)	0.61 (36)	0.32 (11)	0.48 (10)
N =	54	173	59	34	21
Early/Outside					
Male	0.42 (8)	0.55 (46)	0.28 (23)	0.43 (13)	0.41 (15)
Female	0.58 (11)	0.45 (38)	0.72 (58)	0.57 (17)	0.59 (22)
N =	19	84	81	30	37
Late/Outside					
Male	0.33 (6)	0.45 (52)	0.33 (11)	0.36 (5)	0.43 (12)
Female	0.66 (12)	0.55 (64)	0.66 (22)	0.64 (9)	0.57 (16)
N =	18	116	33	14	28

the season along the inside of the eastern trap line may have been traveling east as well. The closest known breeding pond is only 225 m from the southeast corner the study site (Pond 6). I captured relatively few adults along the inside of either the southern or eastern segments of the trap line in the early season.

Migratory movements and environmental parameters.—Based on trapping data adults began moving with the first night of substantial rain of the season (≥ 1 cm). Smaller amounts of nightly rain (≤ 0.5 cm) at the beginning of the breeding season did not appear to initiate movement. In all survey years, the earliest dates adults were captured ranged from 20 October (2004) to 11 November (2001). Most adult captures occurred between early November and mid-December with fewer more temporally dispersed captures later in the season. Juveniles began arriving at the boundaries of the study site each year within six nights of measurable rain. The earliest dates juveniles were captured ranged from 29 October (2000) to 22 November (2001).

Both the amount of rain within 12 h (night of capture) and 24 h prior to checking traps were positively correlated with number of *A. californiense* captured ($r = 0.626$ for night rain; $r = 0.603$ for 24 h; $P < 0.001$ for both). Rain 12 h prior to opening traps was also correlated with captures ($r = 0.375$, $P = 0.012$). In addition, rain at dusk (Wilcoxon $Z = 2.66$, $P < 0.005$) and temperature ($r = 0.363$, $P < 0.015$) were positively associated with number of captures. Rain the night prior to opening traps was not associated with number of captures (Wilcoxon $Z = 0.31$, $P = 0.378$).

TABLE 3. Capture rates of adult *Ambystoma californiense* (no. per 100 trap nights) along the western, southern, and eastern trap lines during the early and late winter breeding seasons of the five study years. Early season = late October to December 31; Late season = January 1 to end of March. Data represent captures inside/outside each trap line. Recaptured individuals were excluded except for salamanders first captured during the early season inside the trap line and then later recaptured outside the same trap line during the late season. Total number of adults captured is indicated by N.

Season/Trap Line	2000– 2001	2001– 2002	2002– 2003	2003– 2004	2004– 2005
Early Season, N =	71	251	136	65	59
Western	8.6/2.5	28.4/6.7	9.8/12.3	4.4/2.1	3.5/4.5
Southern	1.0/1.0	4.8/5.9	1.9/3.4	1.0/3.1	0.5/2.7
Eastern	—	4.2/22.7	1.4/6.3	2.9/3.5	1.3/2.6
Late Season, N =	34	146	46	21	29
Western	0.8/4.8	1.9/19.7	0.5/4.6	1.5/3.3	0.4/3.2
Southern	0.0/1.9	0.7/2.6	0.7/2.2	0.4/1.7	0.0/0.6
Eastern	—	5.3/1.5	0.0/2.9	0.0/0.0	0.0/0.0

Annual reduction in captures.—Over the five study years, the proportion of adults captured inside the trap line decreased ($r = -0.845$, $P = 0.036$) and adult capture rates were not associated with on-site rainfall for those five years (Fig. 5, $r = -0.753$, $P = 0.071$). In 2000 and 2001, the capture rate of adults was higher inside than outside the trap line (Fig. 5). However, during 2002–2004 the capture rate was higher outside than inside. By 2004 the ratio of adult captures inside the trap line (versus outside) was much lower (0.35) than in previous years (0.62–1.2).

DISCUSSION

Successful conservation for *Ambystoma californiense* requires protection of both breeding sites and adequate surrounding uplands (Petranka 1998; Semlitsch 1998). Knowledge of terrestrial movement patterns and migration distances is essential to establishing appropriate upland protection zones adjacent to breeding ponds. My study expands the current understanding of upland habitat use for *A. californiense* and should better inform management for this species. The most important findings of my study are that *A. californiense* appeared to exhibit fidelity to upland habitat locations and occurred in relatively large numbers farther from breeding ponds than previously reported.

Study limitations.—The present study has certain limitations that should be taken into account when interpreting my findings. The partial drift fence may have affected my results in the following ways: 1) capture rates may have over- or under-estimated the actual number of salamanders entering or leaving the study site, 2) distribution of captures was limited to

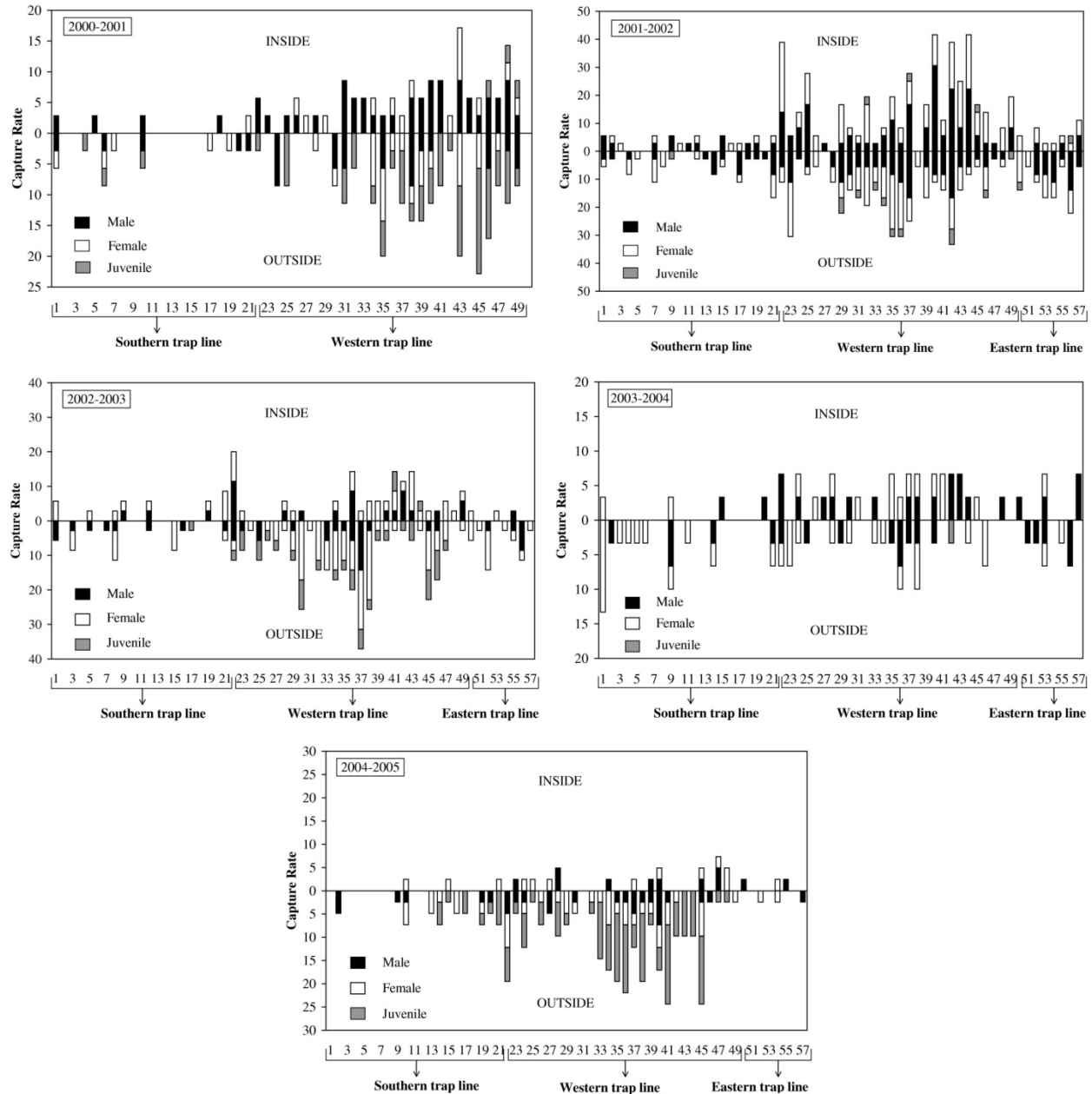


FIGURE 4. Capture rates (no. per 100 trap nights) of *Ambystoma californiense* inside and outside the trap line by sex, age class, and trap line for each of the five study years. Trap number for each trap line segment is indicated on the x-axis. Recaptured individuals were excluded except for salamanders first captured during the early season inside the trap line and then recaptured outside the same trap line later in the season.

certain sections of the study site, and 3) trespass rates for the study site could not be determined (i.e., when a salamander exits or enters a site without being captured). These limitations may have influenced my analysis of patterns of movement, sex ratios/proportions, and annual reductions in number of individuals captured.

In addition, translocating salamanders and restricting their entry into the study site may have altered the age class distribution for those remaining within the site. Studies of *A. californiense* and other *Ambystoma* species

have shown that age classes may differ in their use of habitat (Rothermel 2004; Trenham and Shaffer 2005) and vary in activity in response to environmental cues (Semlitsch 1983). This may have influenced my analysis of patterns of movement, and migratory movements with applicable data sets. Lastly, my findings are also limited by having only one study location. Although my results are directly applicable to this site, it may not be representative of other grassland areas that support *A. californiense*.

TABLE 4. Capture rates of juvenile *A. californiense* (no. per 100 trap nights) along the western, southern, and eastern trap lines during the early and late winter breeding seasons of the five study years. Early season = late October to December 31; Late season = January 1 to end of March. Data represent captures inside/outside the trap lines. Recaptured individuals were excluded except for salamanders first captured during the early season inside the trap line and then later recaptured outside the same trap line during the late season. Total number of adults captured is indicated by N.

Season/Trap Line	2000–2001	2001–2002	2002–2003	2003–2004	2004–2005
Early Season, N =	36	14	29	1	45
Western	0.5/5.3	0.2/2.4	0.6/5.2	0.2/0.0	0.0/8.0
Southern	0.0/0.7	0.0/0.0	0.0/0.3	0.0/0.0	0.0/1.1
Eastern	—	0.8/0.0	0.0/0.0	0.0/0.0	0.0/0.0
Late Season, N =	14	2	7	0	36
Western	0.0/2.7	0.2/0.0	0.0/1.1	0.0/0.0	0.0/3.8
Southern	0.0/0.3	0.0/0.2	0.0/0.2	0.0/0.0	0.0/1.7
Eastern	—	0.0/0.0	0.0/0.0	0.0/0.0	0.0/0.0

Capture numbers and movement patterns.—Adults tended to return to a location close to where they were initially captured, which suggests fidelity to specific areas of upland habitat. Although several other studies have indicated *Ambystoma* species tend to follow the same nonrandom pathways as they move toward and away from breeding ponds (Stenhouse 1985; Phillips and Sexton 1989; Trenham and Cook 2008), these results were typically inferred from the distribution of captures around ponds, not from distant upland habitat capture data.

In all study years more adults were captured early in the season (presumably going to breed) than were captured later in the season along the same trap line segment (presumably returning from breeding). Rainfall amounts during the early and late seasons did not appear to account for this decrease in captures. The lower number of returning animals may be partly due to mortality, or salamanders straying off path when returning from their natal ponds or dispersing to different ponds (Trenham et al. 2001; Trenham and Cook 2008).

A higher proportion of migrating males than females has been correlated with low rainfall years in other studies of *A. californiense* (Loredo and Van Vuren 1996; Cook et al. 2006). My findings are consistent with this pattern. Apparently more females forego breeding in dry years than males (Loredo and Van Vuren 1996; Trenham et al. 2000). My results contrast with previous studies of *A. californiense* and other *Ambystoma* species that suggest a female bias at greater distances from breeding ponds (Regosin et al. 2003; Trenham and Cook 2008). The distances from the nearest breeding ponds in my study were considerably greater than these previous studies, yet my annual sex ratios were only female biased in one of the five study years.

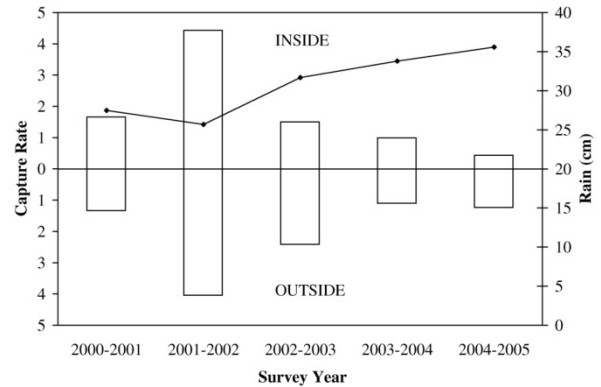


FIGURE 5. Annual capture rates (no. per 100 trap nights) of adult *Ambystoma californiense* inside and outside the trap line (bars) and on-site rainfall amounts (October–April; solid line) for the five study years. Recaptured individuals were excluded except for salamanders first captured during the early season inside the trap line and then recaptured outside the same trap line later in the season.

Migration distances.—I captured large numbers of *A. californiense* farther from breeding ponds than has been previously documented. In early studies of migration distances, maximum distance ranged from 130 m during one night of visually tracking (Loredo et al. 1996) to 248 m using radio tracking (Trenham 2001). However, these studies only examined movements during initial dispersal into the terrestrial habitat and thus may not be representative of the total distance adults may travel (Trenham and Shaffer 2005). In a more recent study using variable trap line distances from a pond, Trenham and Shaffer (2005) found that 50–95% of adults were trapped between 150 to 620 m from the pond, respectively. Continuing work at this site has documented a few individuals moving up to 1000 m from the most likely breeding pond (Peter Trenham, pers. comm.). *Ambystoma californiense* has also been observed up to 2.1 km from breeding ponds (U.S. Fish and Wildlife Service 2004); however, this was thought to be only a small number of individuals. Even in light of these studies showing a few individuals making longer distance movements, the large numbers of adults and juveniles I captured at least 800 m from the closest breeding ponds is noteworthy.

Current estimates that 95% of adult *A. californiense* occur within 620 m of the breeding pond (Trenham and Shaffer 2005) do not appear applicable to my study site. If this estimate were applied to my study site, which is greater than 620 m from the closest breeding ponds on CNWS, the large number of captures would represent less than 5% of the adult upland population. This would result in an exceedingly high extrapolated number of adults using the ponds on CNWS (~5,000 to 10,000 adults). However, Loredo and Van Vuren (1996) found an average of only 141 adults at their study pond on CNWS (Pond 5, Fig. 1), which is typical for other sites (Trenham et al. 2001; Cook et al. 2006). It is more likely that a greater percentage of the breeding population at

CNWS is moving farther away from the breeding ponds than previous research would have predicted.

Migratory movements and environmental parameters.—Movement patterns in my study area were influenced by the distribution of rainfall within the 24-h period prior to capture, with both rain at dusk and on the night of capture (12-h prior) strongly correlated to captures. Although several studies of *A. californiense* or other *Ambystoma* species also found adult migration to be positively associated with rainfall (Semlitsch 1983; Beneski et al. 1986; Trenham et al. 2000), these studies measured daily (24-h periods) or weekly rainfall, not rainfall within less than a 24-h period.

The majority of *A. californiense* adults were captured from early November to mid-December, which is earlier than other study sites where peak migration occurred in January in Monterey County (Trenham et al. 2000) or December and January in Sonoma and Contra Costa counties (Loredo and Van Vuren 1996; Cook et al. 2006). Unlike these other studies, which were conducted at study ponds and recorded only the date of arrival at those ponds, my data presumably represent the actual initiation of migration from upland emergence. Therefore, the discrepancy in peak migration periods may be because my study site was at least 800 m away from the closest probable breeding ponds, and it may have taken several rainy nights to reach the ponds.

Reduction in numbers.—My findings suggest that it takes multiple years of trapping and translocating animals to substantially reduce the number of adults within a project site. This is consistent with other research that has shown *A. californiense* typically spend up to four to five years in their upland burrows before they reach sexual maturity and migrate to breeding ponds for the first time (Trenham et al. 2000). The reduction in annual captures found over my five study years could have been affected by variables other than removal trapping. For example, rainfall has been shown to affect both the number of migrating adults and reproductive success among ambystomatids (e.g., Semlitsch 1983). However, my annual capture numbers were not correlated with on-site rainfall. In addition, I examined local annual rainfall data for the five years prior to my study and found no patterns that might have affected past reproductive success and subsequently influenced capture numbers during my study. It is important to note that because the drift fence was not a closed system, it was not possible to determine whether individuals captured inside or outside the trap line were resident to those sides of the study site.

The costs and benefits of amphibian translocation strategies have been debated and establishing criteria for success is difficult (Seigel and Dodd 2002; Trenham and Marsh 2002). Because my study only involved moving

animals to adjacent grassland habitat a short distance from the capture point (≤ 100 m), some of the more critical problems typically associated with translocation projects were not applicable, including the availability of suitable habitats, disease transmission, and genetic considerations (Dodd and Seigel 1991). However, because a portion of my translocated animals were recaptured presumably trying to return to the study site, they could have been subject to additional stress which reduced their survival (Matthews 2003; Germano and Bishop 2008). In addition, I do not know if the resources of the adjacent area were adequate to sustain an increase in population size (Petranka 1989).

Other options for managers to reduce the number of salamanders in a proposed construction area include passive relocation using wooden ramps with barrier fencing or excavating salamanders from their burrows. Although I have observed *A. californiense* using ramps to exit a project site, there are no published reports on the success of this passive relocation technique. Excavation is time consuming (Pittman 2005), difficult due to the complexity of burrow systems, and potentially hazardous to the salamanders.

Management implications.—My findings have several implications for future conservation and management of this species. First, the current suggested buffer zone of 630 m around breeding ponds for long-term preservation of individual *A. californiense* populations (Trenham and Shaffer 2005) may not protect a substantial portion of some upland populations. Second, the method proposed by Searcy and Shaffer (2008) for calculating mitigation value for *A. californiense*, which is based on the exponential decrease in salamander density with increased distance from breeding ponds, may not be applicable in all cases. Other factors could be influencing the density distribution around ponds, such as uneven distribution of resources and presence of other species (Rittenhouse and Semlitsch 2007; Searcy and Shaffer 2008). The results of my study underscore the need to consider other relevant biological factors in establishing buffer zones or mitigation credits. Third, trapping may be the most reliable means of predicting habitat value or detecting occurrence in uplands. I found that the number of salamanders observed during winter night surveys was not a reliable indication of population size. The limited number of salamanders I observed was probably due to few being above ground at the burrow entrances during the night surveys. Fourth, efforts to remove *A. californiense*, via trapping or passive relocation, from a proposed project site for only one year (to reduce impacts from development) may miss a large portion of the population. My findings suggest that multiple years are required to substantially reduce the abundance of adult life stages in upland habitat.

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