DEMOGRAPHY AND BREEDING PHENOLOGY OF THE CALIFORNIA TIGER SALAMANDER (*AMBYSTOMA CALIFORNIENSE*) IN AN URBAN LANDSCAPE

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ABSTRACT—The influence of urban development on populations of amphibians has received a significant amount of attention in the recent literature. However, few studies have attempted to obtain demographic data on amphibians in urban landscapes. To assess the influence of urbanization on amphibian life histories, we collected demographic and phenologic data on an urban population of the California tiger salamander (*Ambystoma californiense*) in Sonoma County, California. This population breeds in a single isolated vernal pool nested in a mosaic of urban land uses. We used drift fences with pitfall traps to capture adults migrating to and from the pool over the course of 3 breeding seasons. We estimated the breeding adults at between 65 and 107 annually, which was somewhat surprising given that only 17.5% of the grassland habitat surrounding the pool is currently undeveloped. The study population had similar temporal patterns of migration activity among years. Rainfall triggered migration to the breeding pool, and males remained at the pool longer than females. Migration activity began in November, but most breeding adults were captured in December and January, and captures in February were rare. The migration pattern associated with pool depth showed a tri-modal distribution; however, minimum pool depth for breeding occurred when the pool was approximately half full to completely full. Finally, we were able to stimulate colonization by gophers of areas near the breeding pool by constructing large mounds of soil. Our trapping records indicate that some salamanders over-summered in these areas where no suitable upland burrows existed prior to mound construction. Although developed landscapes are less than optimal for the long-term conservation of this species, our study shows that populations may persist with some degree of adjacent development.

Key words: California tiger salamander, *Ambystoma californiense,* demography, phenology, endangered species, urban population, Sonoma County, California

The influence of urban development on populations of amphibians has received significant attention in the recent literature (Stuart and others 2004; Young and others 2004). However, few studies have attempted to obtain demographic data on amphibians in urban landscapes. While some amphibian groups may be fairly resilient to adverse effects of urbanization, ambystomid salamanders appear to be sensitive to urban development (Rubbo and Kiesecker 2005). The California tiger salamander (*Ambystoma californiense*) is a relatively recent addition to the federal endangered species list, and urbanization is a primary reason for its recent decline (Jennings and Hayes 1994; Fisher and Shaffer 1996; Davidson and others 2002; USFWS 2004). Although the threat that urban-

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ization poses for this and other species is widely recognized, detailed studies of urban endangered species are needed to assess the long-term viability of populations and focus management appropriately.

Ambystoma californiense is endemic to the lowlands of central California, habitats that are also highly attractive areas for agricultural and urban development due to their flat to gently sloping terrain (Davidson and others 2002). Adult *A. californiense* breed in seasonal ponds or pools but spend most of their lives underground in the burrows of small mammals (Storer 1925; Jennings and Hayes 1994; Petranka 1998). In 2002, an isolated population of this species occupying vernal pools and uplands in Sonoma County was 'emergency listed' as endangered by the US Fish and Wildlife Service due to threats posed mainly by rapidly expanding residential development (Wooten 2002). This population is isolated by >60 km from other *A. californiense* (Wooten 2002; Stebbins 2003) and is estimated to have been evolving independently for approximately 1 million years (Shaffer and others 2004). Although a variety of studies of this species have characterized elements of the natural history and population ecology, all of those studies were conducted outside of Sonoma County and in landscapes lacking urban development (Loredo and van Vuren 1996; Trenham and others 2001; Trenham and Shaffer 2005).

Sonoma County differs in at least 2 important ways from other regions with *A. californiense.* First, an average of 76 cm of precipitation is recorded there annually. This is nearly twice the average recorded at well-known occupied areas in Monterey, San Mateo, and Contra Costa counties at 44 cm, 34 cm, and 39 cm, respectively. Second, the occupied areas of Sonoma County, more than any other region still supporting *A. californiense,* are highly subdivided. This area has a network of paved roads and a complex mixture of rural, agricultural, and increasingly dense residential developments. These differences suggest that data collected elsewhere may not be appropriate for guiding management in Sonoma County.

The data we present in this paper come from a 3-y drift fence study during which we captured migrating adults at a large breeding pool around which much of the upland habitat has been converted to dense residential development. Our primary objectives were to obtain data on 1) the demography and dynamics of this isolated breeding population, and 2) timing and triggers of breeding migrations. We compared these data with observations reported from other regions of the state and interpreted their implications for conservation. In addition, we also evaluated the potential for enhancing terrestrial habitat near this breeding site to improve its long-term probability of persisting.

Methods

Study Area

The study was conducted at Southwest Park in Santa Rosa, Sonoma County, California. The 0.75-ha breeding habitat where we captured *A. californiense* is a vernal pool with a maximum depth of 1.2 m. Several studies of upland habitat use indicate that individual *A. californiense* move from tens to hundreds of meters away from breeding habitats (Loredo and van Vuren 1996; Trenham 2001; Trenham and Shaffer 2005). Uplands occupied by *A. californiense* are most commonly grassland or savannah habitats with populations of small mammals providing underground burrows (Trenham 2001). Botta's pocket gopher (*Thomomys bottae*) burrows are the primary source of subterranean refugia available for *A. californiense* at Southwest Park and throughout the occupied range in Sonoma County (DGC, pers. obs.).

At the time of this study, most of the uplands within 700 m of the study pool had been converted to land uses less suitable for this species (Table 1; Fig. 1). Historically, most of the study area was covered in orchard and scattered low-density rural residences (USGS 1954). During the later half of the 20th century, orchards were either developed for urban land uses or reverted to grassland dominated by non-native annual grasses and forbs (USDA 1972; DGC, pers. obs.). Developed in 1986, Southwest Park converted most lands immediately east of the breeding habitat to manicured lawns, athletic fields, and recreational facilities. In 1999, a residential subdivision displaced the grasslands south and west to within 10 m of the breeding habitat. A small fragment of grassland remains north of the pool.

During fall 2000, several actions were taken to protect and enhance *A. californiense* habitat

TABLE 1. Captures of *Ambystoma californiense* and land use characteristics surrounding the Southwest Park breeding pool. Captures are from winter 2002 and 2003 trapping surveys and include 1st-time migrations to the pool. Numbers in parentheses are percentages.

	Direction				
Habitat or captures	North	East	South	West	Total
Immigration captures					
2002–2003	34 (22.5)	106 (70.2)	6 (4.0)	5 (3.3)	151 (100.0)
Grassland within 700 m of the pool					
Area, ha	3.9 (9.0)	26.8 (60.8)	0.03 (0.06)	0.06 (0.1)	30.8 (17.5)
Enhanced undeveloped habitat and small mammal burrow density					
Area, ha	—	—	0.03	0.03	—
Gopher burrow density (burrow/m^2)					
2000 (pre-enhancement)	—	—	0.00	0.00	—
2002 (enhanced)	—	—	1.00	0.89	—
2003 (enhanced)	—	—	0.43	0.36	—
Reference Site	—	—			0.24

at Southwest Park. To minimize human disturbance, a wire fence was installed encompassing a total area of 1.25 ha including the pool. To discourage salamanders from moving west or south toward adjacent roads and housing, a partially buried, 60-cm-high aluminum flashing barrier was installed along those portions of the wire fence. Finally, to encourage small mammal activity and enhance terrestrial habitat for *A. californiense,* linear mounds of friable soil were placed along the south and west borders of the pool. Mounds were approximately 1 m high, 6 m wide, and had a combined length of 94 m. Evidence of pocket gopher burrows was not detected in this area prior to enhancement.

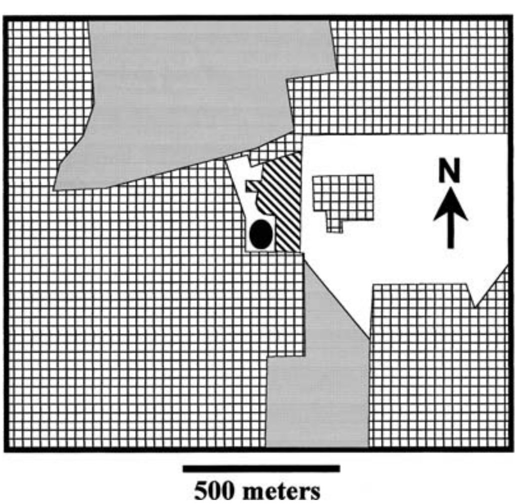

FIGURE 1. Map of the landscape around Southwest Park study area. Map is centered on our study pool, which is represented as a black oval. Uncolored areas are grasslands accessible to *Ambystoma californiense* breeding at the pool. Gridded sections currently support dense urban or residential development and associated infrastructure. The hatched area east of the breeding pool supports a city park. Gray areas are grasslands isolated by major roads and dense urban development. Created from aerial photographs produced in 2002.

Field Surveys

We used drift fences and pitfall trap arrays (Heyer and others 1994) to monitor *A. californiense* movements to and away from the study pool. We had opportunities to collect data during the 1999–2000, 2002–2003, and 2003–2004 breeding seasons (hereafter winters 1999, 2002, and 2003), with traps open from November through February of each season. We constructed ≥30 cm-high drift fences from plastic silt fencing and used 3.8 L and 7.3 L plastic cans for pitfall traps. In 2002 and 2003, our drift fence completely encircled the pool, but in 1999 we were only able to install eight 8-m-long drift fence sections randomly placed around the perimeter of the pool encompassing approximately 19.9% of the pool perimeter. In 1999, we installed pitfall cans at the ends of each fence section. In 2002 and 2003, interior and exterior pairs of pitfall cans were spaced 10 m apart along the fence. To determine if salamanders occupied burrows in the constructed mounds, we also isolated these areas with drift fences and pitfall traps. Each pitfall trap included an elevated cover for shade and a damp sponge to maintain moisture for captured salamanders.

We opened pitfall traps just prior to the 1st forecasted fall rains and trapped until several weeks after *A. californiense* breeding activity ended and no additional salamanders were captured. Traps were closed during periods when there was no rain and the study pool was completely dry. We checked traps daily at sunrise. Captured salamanders were measured, uniquely toe clipped in the field, and released on the opposite side of the fence at the capture location. Data recorded included date of capture, toe clip identification, sex, gravid condition (females), snout to vent length (SVL) measured to the posterior end of the cloacal opening, total length (2003 only), trap number, and drift fence side. Pool depth, measured with a staff gauge in the deepest part of the pool, was recorded daily. We obtained precipitation data from a permanent California Department of Water Resources weather station located on the Santa Rosa Plain. Average rainfall values were based on precipitation data collected at this station since 1905. Also, we obtained regional precipitation data from the National Oceanic and Atmospheric Agency, Western Regional Climate Center.

We quantified the Botta's pocket gopher digging activity on the constructed mounds and at reference sites. Reference sites were mounded soil areas located at Southwest Park where no ground disturbance had occurred for several years. To estimate digging activity we counted mounds of excavated soil plus plugged and open tunnels. Burrow surveys were conducted during winter when *A. californiense* were most active on the surface. Mound counts within areas with small mammal activity were used to calculate burrow densities and to estimate digging activity.

Analysis Methods

In 1999, our drift fences only encompassed 19.9% of the pool perimeter. Therefore we estimated the number of breeding adults by dividing the total number of individuals captured by 0.199. Although our continuous drift fences in 2002 and 2003 should have theoretically captured all breeding adults in 2002 and 2003, trespass of migrating individuals occurred and was accounted for in estimating population sizes (for details of these calculations see: Trenham and others 2000). Trespass is defined as an animal captured sequentially on the same side of the drift fence, thus having evidently evaded capture. The probability that animals evade capture completely is a function of both the probability of crossing the fence without being captured and the number of times they cross the fence. We assumed that individuals should be 1st captured outside the drift fence, last captured inside the drift fence, and on alternate sides in between. For each individual, we determined the total number of crossings and total number of captures. Then, for each year, and for males and females separately, we determined the average number of fence crossings and the average probability of crossing without being captured. We corrected breeding adult census totals for trespass using calculations detailed in Trenham and others (2000).

To examine associations with rainfall in 2002 and 2003, we used $\log_{10}$-transformed weekly capture totals and weekly rainfall totals for regression analysis preformed with DataDesk 5.0. We evaluated associations between capture totals and rainfall for each year separately. Also, descriptive and other statistics were calculated using Microsoft Excel, including mean ($\bar{x}$), standard deviation (s), Chi squared (χ^2), and Student's t-test (2-tailed).

We mapped and compiled information about the remaining accessible grasslands within 700 m of the study pool using orthorectified aerial photographs of the region from 2002. Grassland areas within 700 m but determined to be inaccessible to *A. californiense* were excluded from grassland calculations, including grasslands to the north of the park separated by a high traffic roadway with curbs and including grasslands to the south isolated by dense residential development bordered by curbed roads (Fig. 1).

RESULTS

Population Dynamics

We recorded 460 *A. californiense* captures in 16,772 trap-nights during our 3-y study. In winter 1999, we captured 3 female and 10 male *A. californiense* in our partial drift fence for an estimated breeding population of 65 (Table 2). In 2002 we captured 44 females and 55 males;

TABLE 2. Breeding population characteristics of *Ambystoma californiense* in Sonoma County, California, during 3 winter seasons. Numbers under breeding adults are population estimates. Actual captures are shown in parentheses.

	Breeding adults					
Year	Male	Female	Total	Previous recaptures	Mean SVL (mm)	Sex ratio M:F
1999	50 (10)	15 (3)	65 (13)	—	104.2 ± 6.5	1:0.30
2002	55 (55)	52 (44)	107 (99)	0	107.1 ± 4.8	1:0.95
2003	44 (44)	46 (46)	90 (90)	37	108.1 ± 5.2	1:1.05

trespass probability was 34.4% for females and 22.9% for males, and average number of fence crossings was 2.2 for females and 3.8 for males. In 2003 we captured 46 females and 44 males; improvements to the drift fence reduced trespass probabilities to 4.9% for females and 11.6% for males, and average number of fence crossings was 2.2 for females and 3.1 for males. We estimated that overall trapping efficiency, or the probability that we captured individuals that were present, was 84.8% for females in 2002, and was >99% for all other groups. Based on these data, adult breeding populations in 2002 and 2003 were 107 and 90, respectively (Table 2). None of the *A. californiense* captured in 2002 were recaptures from 1999 but in 2003 we recaptured 4 males marked in 1999, 12 males marked in 2002, and 21 females marked in 2002. Partial regrowth of a clipped digit was evident on 2 salamanders from 1999 and 29 from 2002. The survival to 2003 of at least 31% (4/13) of animals marked in 1999 translates to an annual probability of survival of >70%. At least 33% of salamanders marked in 2002 survived to and bred in 2003.

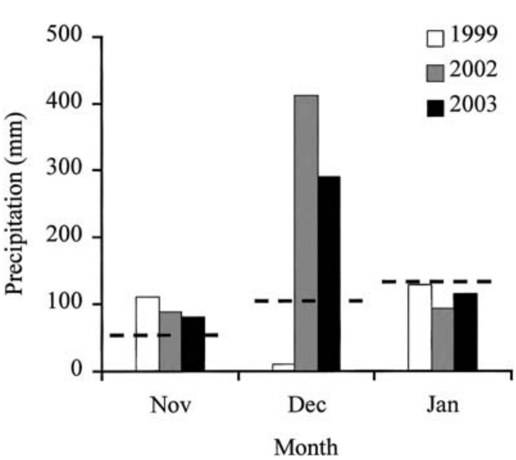

FIGURE 2. Monthly precipitation during winter breeding seasons of *Ambystoma californiense.* Dashed lines indicate weather station long-term averages.

The estimated number of breeding adults was highest in 2002 when winter rainfall was above normal and the highest during our study (Fig. 2). Sex ratios (Table 2) did not differ significantly from 1:1 in winter 2002 or 2003 (2002: $\chi^2 = 0.084$; df = 1; $P = 0.77$; 2003: $\chi^2 = 0.044$; df = 1; $P = 0.83$). The significant deviation from a 1:1 sex ratio during winter 1999 ($\chi^2 = 18.846$; df = 1; $P < 0.001$) may have been affected by the trapping method. However, the male-biased ratio is consistent with observations elsewhere in years with below-normal rainfall (Fig. 2; Trenham and others 2000; Loredo and van Vuren 1996). Adult SVL measurements were similar among years and ranged from 92 mm to 121 mm. Sexual dimorphism in tail lengths was evident in the significantly longer total body lengths of males ($\bar{x}_{\text{female}} = 199.8$, $s = 11.1$, $n = 46$; $\bar{x}_{\text{male}} = 227.8$, $s = 18.3$, $n = 32$; $t = -7.7$, df = 47, $P < 0.0001$).

Migration Patterns

Temporal patterns of migration differed among years and were strongly tied to the timing of rainfall (Figs. 3, 4, and 5). Adult activity at the pool lasted 9 to 14 wk, with 75.5% of captures concentrated in a period of <3 wk. Weekly capture totals for 2002 and 2003 were significantly associated with rainfall totals during the same periods (2002: $r^2 = 0.817$, $F = 35.8$, df = 8, $P < 0.0003$; 2003: $r^2 = 0.287$, $F = 5.22$, df = 13, $P < 0.0397$). Variation in the timing of rainfall among years affected the timing of salamander captures at the pool. In 1999, little rain fell prior to January and all 3 females were captured on January 21 (Fig. 3). By contrast, in 2002 and 2003, December rainfall was above average (307% and 217%, respectively), and in both years all but 1 or 2 females were captured exiting the pool by the end of December (Figs.

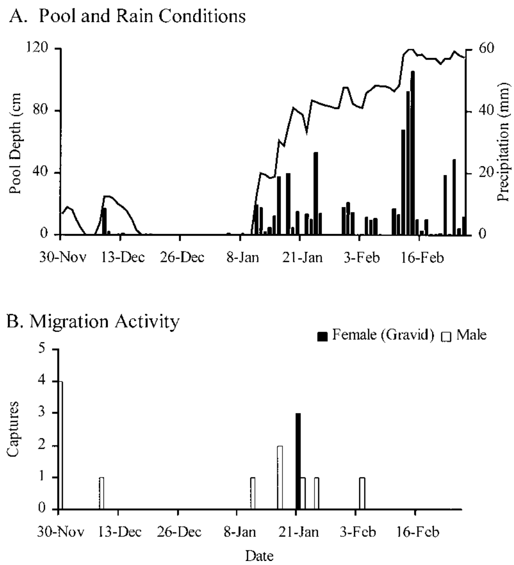

FIGURE 3. Movement phenology of breeding *Ambystoma californiense* during winter 1999. A. The relationship of rainfall and pool hydration. B. Migration activity based on pitfall trap captures. Captures are from a partial trapping array and include combined immigration and emigration captures.

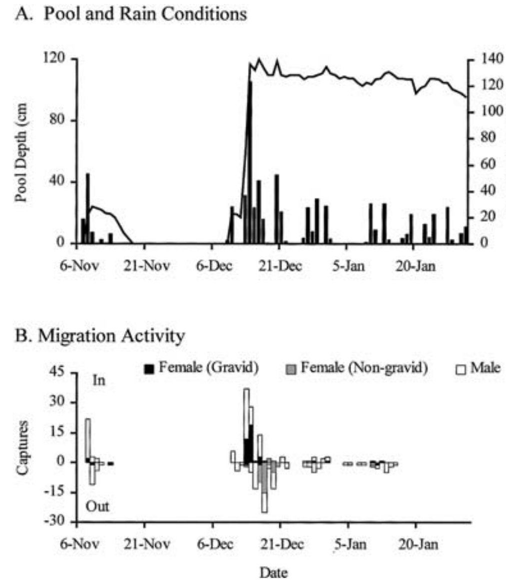

FIGURE 4. Movement phenology of breeding *Ambystoma californiense* during winter 2002. A. The relationship of rainfall and pool hydration. B. Migration activity based on pitfall trap captures.

4 and 5). In all years, the 1st males were captured in November. In 1999 and 2003, males were captured into February. In 2002, the last male was captured on January 15.

Although a few *A. californiense* migrated independently of measurable rainfall (the 3 females captured in 1999 were captured on a day when there was no recorded rainfall), most migrations resulting in breeding occurred with rainfall between 28 and 123 mm/d (Figs. 4 and 5). This was indicated by gravid females captured on the outside of the drift fence followed within a few days by inside capture of the same now non-gravid females. Although breeding occurred mainly during 1 or 2 annual events, some females arrived independently of the main migrations. The timing of peak captures of in-migrating gravid females differed among years by as much as 39 d (Figs. 3 and 4). Most breeding was completed within a few days of migration to the pool. For example, 31 females (70.5% of the total females captured) migrated to the pool on 13 and 14 December 2002, and 24 of these females, now non-gravid, were captured leaving the pool on 16 and 17 December 2002. A similar migration pattern occurred

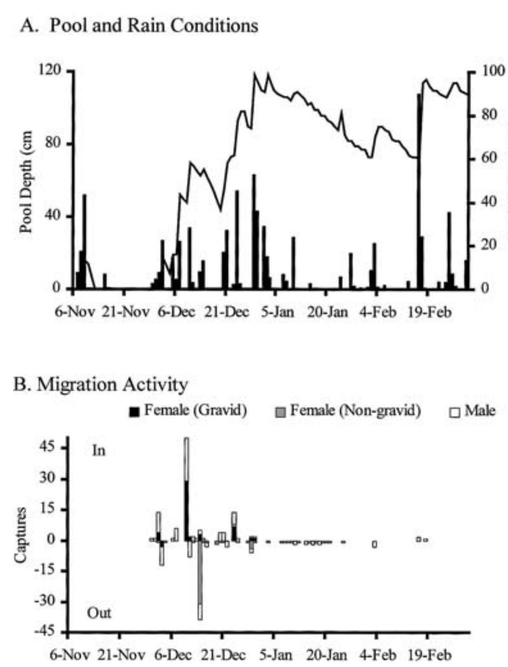

FIGURE 5. Movement phenology of breeding *Ambystoma californiense* during winter 2003. A. The relationship of rainfall and pool hydration. B. Migration activity based on pitfall trap captures.

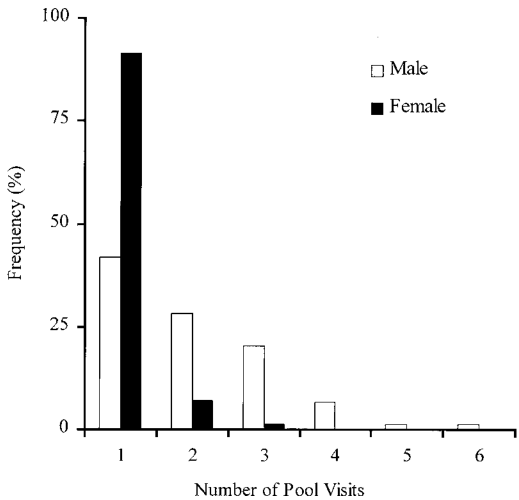

FIGURE 6. Frequency of pool visits by *Ambystoma californiense* during winter 2002 and 2003.

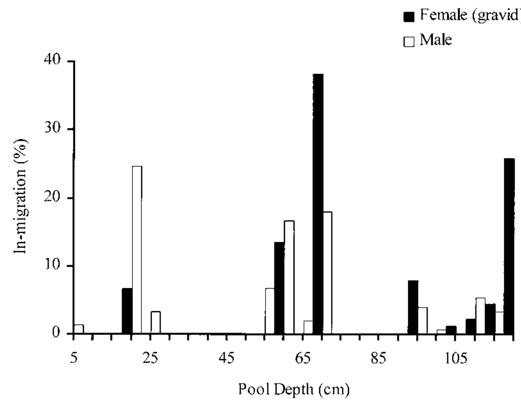

FIGURE 7. The relationship between pool depth and *Ambystoma californiense* migrating to the pool. Percent values are from trap captures during winter 2002 and 2003 and include 150 male and 89 gravid female immigration events and may include multiple visits by an individual.

during winter 2003 when over half the adults (n = 50) arrived on 10 December and then most departed 4 d later on 14 December coinciding with the next heavy rain event. The frequency of pool visits by *A. californiense* varied by sex (Fig. 6). Most females (91.5%) visited the pool once, whereas 58.1% of males visited the pool more than once.

The migration pattern of *A. californiense* and pool depth showed a tri-modal distribution with migrations occurring primarily during shallow, mid-level, and deep water depths (Fig. 7). Minimum pool depth for breeding varied by year, based on outward capture of non-gravid females. During 2002 and 2003, respectively, the pool was at maximum depth (120 cm) and at about half maximum depth (66 cm) when breeding began. Both males and females occasionally arrived before the pool had filled (Figs. 3, 4, and 5), but these individuals typically did not remain within the drift-fenced area. For example, 14 adults arrived on 2 December 2003 but water in the pool was only 17 cm deep. Twelve adults were captured exiting the pool the next day, and the others departed 2 and 11 days later (Fig. 5). Average depths (cm) were significantly greater when females were captured entering the pool ($\bar{x}_{male} = 63.1$, $s = 36.0$, $n = 149$; $\bar{x}_{female} = 82.4$, $s = 28.4$, $n = 90$; $t = 4.6$, df = 220, $P < 0.0001$).

Enhanced Terrestrial Habitat Use

Approximately 30.8 ha (17.5%) of the grasslands within 700 m of the study pool remains undeveloped or is accessible to *A. californiense* (Table 1; Fig. 1). Only 0.09 ha of undeveloped land remains to the south and west of the pool, which contains the enhanced terrestrial habitat mounds. Pocket gophers rapidly colonized the mounds (Table 1). We observed digging activity within a few months after mound construction. Two years after installation, pocket gopher tunneling activity was estimated to be 0.89 to 1.00 burrows/m^2, which is greater than the estimated level of activity at the reference site (0.24 burrows/m^2; Table 1). In 2002 and 2003, 11 (7.3%) of the *A. californiense* captured migrating to the pool entered from the area with the enhanced mounds. This enhanced area borders roughly 36% of pool shoreline. When departing the pool, most of these salamanders did not return to the area with the enhanced mounds (PCT and DGC, unpubl. data).

DISCUSSION

Although the future of *A. californiense* in Sonoma County remains uncertain, state, federal and local interests have been working to establish a conservation strategy to preserve this species. As the 1st ecological study of *A. californiense* in Sonoma County, the data presented here should assist that effort. Although we are hesitant to draw broad conclusions from this localized observational study, Sonoma County is an area of rapid habitat conversion where action cannot always wait for conclusive data. In situations like this, action based on logical interpretation of available data is preferable to actions based on anecdotal information. We see the main findings of the study showing that 1) a substantial population of breeding *A. californiense* persists in this area of extensive habitat conversion, 2) breeding migrations here occur earlier than in other parts of the species range, and 3) enhancing habitat for fossorial mammals may facilitate *A. californiense* survival in previously unsuitable upland habitats.

Considering the degree to which upland habitats in and around Southwest Park have been made unsuitable for *A. californiense,* the fact that we estimated approximately 100 adults bred there was somewhat surprising. Also surprising was that adult survivorship was comparable to observations from a completely rural area in Monterey County, California (Trenham and others 2000). We estimated at the time of this study that only 17.5% of the total area within 700 m of the Southwest Park pool was potentially suitable upland habitat for *A. californiense.* Our observations suggest that adult *A. californiense* are able to navigate to and from areas of suitable upland habitat without incurring substantially elevated mortality. Unfortunately we have no data on juvenile survivorship, and because *A. californiense* most often require 4 to 5 y to reach sexual maturity (Trenham and others 2000), many or most of the animals we captured may have been older than the adjacent urbanization. Continued monitoring of *A. californiense* at Southwest Park would provide valuable insight into the future of this population and those in similar situations.

The region of Sonoma County supporting *A. californiense* receives an average of 76 cm of rain annually, whereas Contra Costa (California) and Monterey counties, where breeding migrations of *A. californiense* were also studied (Loredo and van Vuren 1996; Trenham and others 2000), average 39 and 44 cm of annual rain, respectively. Although breeding phenology was generally similar across these studies, some differences were apparent. In all 3 studies, rainfall triggered migration to the breeding pool and males remained at the pools longer than females. At Southwest Park, most breeding adults were captured in December and January, and captures in February were rare. In Monterey County, over the course of 7 y, captures of males and females peaked in January and were higher in February than in December (Trenham and others 2000). Also, in Contra Costa and Monterey counties, adults were captured into March (Loredo and van Vuren 1996; Trenham and others 2000), and gravid females in Monterey County were commonly captured in February and even March (PCT, unpubl. data). Thus, in Sonoma County where rainfall is more abundant, breeding occurs earlier and is concentrated over a shorter period of time, possibly because pools consistently fill earlier. It would be especially interesting to know if earlier breeding in this area results in earlier metamorphosis, larger size at metamorphosis, or both. Even though breeding in Sonoma County occurs over a shorter interval, because males and females do not arrive synchronously and males generally outnumber females during breeding, *A. californiense* are best described throughout their range as 'prolonged' rather than 'explosive' breeders (Wells 1977).

Although breeding numbers and adult survivorship at Southwest Park remain encouragingly high, the future of this population is uncertain at best. Currently, urban development isolates the Southwest Park breeding habitat from other known occupied areas so, if the population were to become extirpated, natural recolonization would be extremely improbable (Trenham and Marsh 2002). In addition, residential developments are planned that will eliminate the remaining suitable upland habitat north and east of the Southwest Park pool where it appears most adult salamanders reside during the non-breeding season (Trenham and Cook, unpubl. data). Because adults captured during this study are most likely older than the recent urbanization and because juveniles occupy areas farther from breeding sites than do adults (Trenham and Shaffer 2005), the ultimate effects of urbanization in the surrounding landscape may be delayed several years. Although Trenham and Shaffer (2005) modeled the likely consequences of upland habitat conversion, we recommend that these effects be documented directly by continued monitoring at sites like Southwest Park.

Although we have no illusions about the long-term viability of our study population, the results of our upland habitat enhancement are encouraging. Captures of in-migrating *A. californiense* in 2002 and 2003 suggest that some adults survived through the summer in the narrow band of enhanced habitat south and west of the breeding pool. Before 2000, when we constructed the soil mounds, we detected no burrows where salamanders could survive the summer in this area. Pocket gophers naturally colonized these mounds and reached high densities by 2002. The relatively small proportion of total captures emerging from this area suggests that this is suboptimal habitat, but it is habitat. Mound creation may provide an opportunity for proactive enhancement of upland habitat, especially in areas with relatively few suitable burrows and is worthy of additional study. Data showing that most *A. californiense* move hundreds of meters away from breeding pools, even when available burrows are closer, indicate that providing a few mounds near breeding ponds should not be considered a long-term strategy for conservation (Trenham and Shaffer 2005). Yet, in an area like Sonoma County where conservation options are often few, mound creation is worth additional consideration and study.

Ambystoma californiense may not persist in Southwest Park over the long-term, but the data from our study should inform conservation planning for this federally listed animal. Because large areas of continuous undeveloped habitat are rare or non-existent in the areas occupied by *A. californiense* in Sonoma County, persistence of this population at Southwest Park despite substantial adjacent development and a long history of surrounding land use illustrates that pristine habitat is not essential for the conservation of this species. However, this conservation effort would benefit from a wide variety of further research. Regional variation in phenology almost certainly extends beyond the differences in patterns and timing of breeding migrations that we noted. Local studies may be needed to document the timing of other key life history events, such as metamorphosis and juvenile emergence from breeding pools. We are convinced that efforts to enhance breeding and upland habitats can be successful, but an adaptive management approach is needed if we hope to learn from both our successes and our failures.

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