Microhabitat use and migration distance of an endangered grassland amphibian

Christopher A. Searcy [a,*], Emilio Gabbai-Saldate [b], H. Bradley Shaffer [c,d]

[a] Department of Evolution and Ecology and Center for Population Biology, 1 Shields Avenue, University of California, Davis, CA 95616, USA
[b] Department of Biological Sciences, 78 College Street, Dartmouth College, Hanover, NH 03755, USA
[c] Department of Ecology and Evolutionary Biology, University of California, 621 Charles E. Young Dr. South, Los Angeles, CA 90095-1606, USA
[d] La Kretz Center for California Conservation Science, Institute of the Environment and Sustainability, University of California, La Kretz Hall, Suite 300, 619 Charles E. Young Dr. South, Los Angeles, CA 90095-14966, USA

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ABSTRACT

There have been many studies of microhabitat use in forest-dwelling amphibians, but very few for grassland specialists. This study examines habitat use of the endangered California tiger salamander (*Ambystoma californiense*), which inhabits grasslands in California's Great Central Valley. We used an extensive drift fence array to capture most of the surface-active salamanders over 2 years at two adjacent breeding ponds in a natural prairie ecosystem. Model selection using simultaneous autoregressive models was used to generate models describing the microhabitat use of each of three salamander age classes (adults, juveniles, and metamorphs). Adults tended to use microhabitats with flood intolerant vegetation and juveniles were most often found at higher elevation sites; both of these surprising results suggest that California tiger salamanders favor the driest microhabitats in the prairie. For certain comparisons, significant interaction terms indicated that there is both temporal and spatial heterogeneity in the distribution of *A. californiense* with respect to proximity to breeding ponds. A literature review indicated that *A. californiense* have the second longest migration distance reported for any salamander (median = 556 m) and the longest among ambystomatids. Our results emphasize the importance of replicating landscape ecological studies over sites and years, particularly for endangered taxa where effective management hinges on understanding the variability in habitat use across time and space. They also suggest that habitat use of grassland amphibians may be fundamentally different from that of forest-dwelling amphibians in that they require larger terrestrial buffers and use different microhabitats within those buffers.

1. Introduction

An essential element of any species' ecology is spatial aggregation and the associated habitat use driving that aggregation. The precise location of any species in a landscape is a property of multiple, often subtle factors including life history requirements, permeability of landscape features, and the distribution of environmental and biological resources (Mueller and Fagan, 2008). The resulting distribution patterns have important consequences for basic ecology and conservation and management of threatened taxa. From an ecological perspective, the spatial distribution of a species affects both interactions between individuals and population dynamics, at single population and metapopulation scales (Hanski, 1998). From a conservation perspective, it is critical to understand how a species is distributed across a landscape if one is to set conservation priorities for effective management. The more detailed the information concerning the microhabitat use of individuals

and the environmental contingencies that create spatial and temporal variation in distribution patterns, the more refined the eventual conservation recommendations can be.

It is a truism that aquatic-breeding amphibians require bodies of water to reproduce, and that their distribution across the landscape will thus be influenced by the location of breeding ponds/streams. Since the 1990s, there has been an increased recognition of the additional importance of uplands (land surrounding a breeding pond/stream) to these species, because many of them spend nearly all (>95%) of their lives in this terrestrial environment (Husting, 1965; Madison and Farrand, 1998; Shoop, 1965). However, the ways in which different aquatic-breeding amphibians use terrestrial microhabitats is extremely variable, making broad generalizations difficult. For example, mole salamanders (family Ambystomatidae) tend to rely on deep, persistent mammal burrows for protection from desiccation and as potential foraging grounds (Madison and Farrand, 1998; Regosin et al., 2003; Trenham et al., 2001). In contrast, stream-dwelling lungless salamanders (family Plethodontidae) avoid desiccation by utilizing habitats with deep leaf litter, high soil moisture, and high canopy cover instead of mammal burrows (Crawford and Semlitsch,

* Corresponding author. Tel.: +1 530 752 1925; fax: +1 530 752 1449.
E-mail addresses: casearcy@ucdavis.edu (C.A. Searcy), emilio.gabbai-saldate@darmouth.edu (E. Gabbai-Saldate), brad.shaffer@ucla.edu (H. Bradley Shaffer).

2008). As a final example, arroyo toads (*Bufo californicus*) specialize on sandy soils, but actively avoid areas with tall, dense vegetation, possibly because the associated roots interrupt their burrowing activities (Griffin and Case, 2001). Given this diversity of strategies to attain the same end goal (a cool, moist microhabitat), it is critical to understand the site-specific ecology of a wide array of species across a range of habitats before broader generalizations on upland habitat use can emerge.

Most studies examining amphibian upland distributions have been conducted in the eastern US, where most species are woodland specialists (Crawford and Semlitsch, 2008; Dillard et al., 2008; Rittenhouse and Semlitsch, 2006). Few studies have focused on either western US or grassland amphibians (but see Bulger et al., 2003; Wang et al., 2009). Unlike its eastern relatives, the endangered California tiger salamander (*Ambystoma californiense*) occupies prairies and oak savannahs, and it is unclear whether predictions concerning habitat use derived from eastern salamanders (deMaynadier and Hunter, 1999; Rittenhouse and Semlitsch, 2006) are likely to apply.

The California tiger salamander is endemic to California. It currently inhabits parts of the Great Central Valley and Coast Range, with outlier populations in Santa Barbara and Sonoma Counties (Shaffer and Trenham, 2005). Like other members of the Ambystomatidae, *A. californiense* spend most of their terrestrial life underground in the burrows of California ground squirrels (*Spermophilus beechyi*) or Bottae's pocket gopher (*Thommomys bottae*) (Loredo et al., 1996; Trenham and Shaffer, 2005). During winter rain events, adults travel over land to nearby ponds, where breeding occurs and females deposit eggs (Storer, 1925). Larvae grow and develop within these ponds, emerging as terrestrial metamorphs between May and August as ephemeral breeding ponds dry (Trenham et al., 2000). Primarily because of *A. californiense*'s fossorial nature while on land, until recently little was known about its terrestrial ecology. Unlike some other amphibian species whose declines may be due to multiple cryptic factors (Blaustein and Kiesecker, 2002), the decline of California tiger salamanders is largely due to habitat destruction (Davidson et al., 2002). Thus, a deeper understanding of its upland ecology is critical to successful management in its remaining habitat fragments.

Here, we use a multi-year, landscape ecological approach to quantify the relationship between California tiger salamander spatial distribution and physical and biological landscape characteristics across an intact prairie landscape. By examining these environmental factors simultaneously across sites and years, we present the most detailed, ecologically complete analysis to date of upland habitat use by any grassland amphibian. Previous studies have examined both spatial (Kovar et al., 2009) and temporal (Johnson et al., 2007) variation in amphibian distributions, but no previous study has examined both simultaneously and quantified their interaction. In constructing a model that considers both of these sources of heterogeneity in the distribution of this endangered amphibian, we develop species-specific conservation recommendations that should apply across a range of breeding ponds and climatic regimes utilized by this declining species, and form a foundation for comparative analyses with other grassland amphibians.

2. Methods

2.1. Study site

We studied two California tiger salamander breeding sites at the Jepson Prairie Reserve in Solano County, California: Olcott Lake (33 ha) and Round Pond (3 ha). Both are natural ephemeral pools separated by approximately 1 km of protected, uninterrupted grassland. The remaining 589 hectares of the preserve are predominantly grassland characterized by cool temperatures and extensive rains that often flood the prairie during the winter (November–April: 44.6 cm precip., high 17.6 °C, low 5.5 °C), and hot, dry summers (May–October: 0.9 cm precip., high 28.3 °C, low 12.7 °C). Although the prairie is heavily invaded by exotic grasses and forbs, there are still many native plants that co-occur with the exotics. Unlike most of the remaining California tiger salamander habitat, which is either in the inner Coast Range or the Sierra foothills (Shaffer and Trenham, 2005) and often has hundreds of meters of elevational relief, Jepson Prairie is essentially flat, with minor contours that reach a maximum height of approximately 2 m above Olcott Lake's high water mark. This low-lying valley ecosystem is similar to much of the species' ancestral habitat (Storer, 1925), and Jepson Prairie provides a model for the ecological conditions under which *A. californiense* probably evolved.

2.2. Trapping and sampling methods

We captured salamanders using an array of drift fences and pitfall traps (Fig. 1) around the northeast quarters of both Olcott Lake and Round Pond. The northeast quarter of Olcott Lake was selected because previous work found it to have the highest density of salamanders (Trenham and Shaffer, 2005), and the northeast quarter of Round Pond was chosen to replicate the sampling design at Olcott Lake. The trap array has two components: a continuous shoreline drift fence with pitfall traps every 10 m, and discontinuous trap lines consisting of 10 m drift fences separated by ~90 m of unfenced habitat. All trap lines were placed parallel to the shoreline, and form partially complete, concentric rings around the two breeding sites (Fig. 1). Traps at Round Pond consist of 100 m of continuous shoreline fence, and discontinuous trap lines 100, 200, 300, and 400 m from the pond edge. At Olcott Lake, the trap array consists of a 400 m continuous shoreline fence and discontinuous trap lines at 100, 200, 300, 400, 500, 600, 700, 850, and 1000 m from the pond edge. Each drift fence is made from a piece of silt cloth 30 cm tall, and buried ~6 cm into the ground. The shoreline drift fences have two associated pitfall traps, one at each end. These pitfall traps have a wooden divider in the center to separate immigrating and emigrating salamanders. Each upland drift fence has a pair of pitfall traps at each end, one on the side facing the pond and one of the side away from the pond.
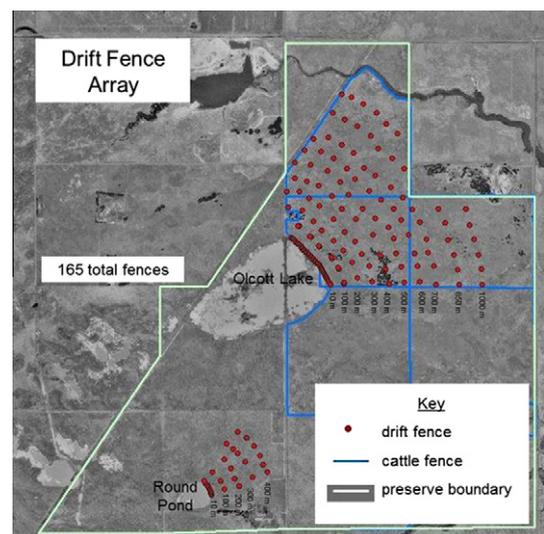

Fig. 1. Map of the drift fence array at the Jepson Prairie Preserve.

We trapped from November to March of 2005–2006 and 2006–2007 for the winter rainy season and also from May to July of 2006 for the spring metamorph emergence. We did not open the traps during the 2007 metamorph emergence because the 2006–2007 rain year was so dry (51% of average) that both ponds dried in mid-April and all larvae died – there was no metamorph recruitment. During the rainy season, all traps were open every night that was forecast to have a 30% or greater chance of rain, because adult and juvenile *A. californiense* are only surface-active during rain events (Trenham et al., 2000). We occasionally opened traps during non-rain winter nights, and confirmed that there was essentially no surface activity. During the spring metamorph emergence, traps ⩽200 m from the shorelines were open almost every night from date of first capture of a metamorph until the total number of captured metamorphs dropped below ten per night. All captured salamanders were weighed, photographed, and immediately released into a burrow on the opposite side of the drift fence from where they were initially captured. A subset were "marked" either with VIAT (visual implant alphanumeric tags) or by taking a digital photograph of the dorsal spot pattern (Searcy and Shaffer, 2011). We classified each individual as an adult, juvenile, or metamorph using the method described in Searcy and Shaffer (2008).

We measured microhabitat variables around each fence ⩽500 m from the shorelines of the ponds. Each 10 m section of fence had four 1 m² quadrats associated with it, each 1 m from a corner of that section of fence (Fig. S1). Quadrats were placed 1 m from the fences rather than adjacent to them to avoid the area that was disturbed while checking the pitfall traps. Within each quadrat, all plants (58 total species) were identified to species and their percent cover was recorded (Appendix A). Each plant species was assigned a visually-estimated percent cover irrespective of the presence of other species. We also counted the number of mammal burrows and mounds in each quadrat. Finally, we used Light Detection and Ranging data to determine the elevation at the midpoint of each fence with an accuracy of ±2.3 cm. All microhabitat variables were collected during July and August of 2006, between the two seasons of salamander activity.

2.3. Variables

We collected information on four dependent and 12 predictor variables (Table S1). The four dependent variables were the densities (individuals/10-m fence) of the three visually identifiable salamander age classes (ADULT, JUVENILE, and METAMORPH), and reproductive value (RV), which is a weighted sum of the three age class densities based upon their relative probability of reaching maturity (Searcy and Shaffer, 2008). Occasionally after heavy rains some traps were flooded and closed. We corrected for this by using that trap's average nightly trapping rate for that age class/year.

The 12 predictor variables included two nominal variables (YEAR: 2005–2006 and 2006–2007 and POND: Olcott Lake and Round Pond, Table S1) and ten continuous variables: DISTANCE of each fence to the shoreline, ELEVATION at the midpoint of each fence, and a single value for mammal activity assigned to each fence by averaging the number of gopher burrows and mounds (MML_B and MML_M) from the four quadrats surrounding each of the fences. The remaining variables described the average vegetation around each of the fences across its four associated quadrats. The dimensionality of the vegetation parameters was reduced by performing a principal components analysis (PCA) on the percent cover data of the 58 plant species. We used the covariance rather than the correlation matrix so that more common species would have a greater influence on the resulting PC axes. The first five axes (PC1–PC5) explained over 80% of the variance in plant cover and were used in further analyses. Finally, we calculated vegetation exoticness (EXOTIC) by summing the percent covers of the exotic species in each quadrat and then subtracting the percent covers of the native species in that quadrat.

2.4. Analysis

Our first goal was to identify subsets of the environmental parameters that best explained the distribution of salamanders across the landscape. Because our trap lines are in close proximity, we used simultaneous autoregressive models to correct for spatial autocorrelation. To select the optimal model for each dependent variable, we started with the full model and eliminated non-significant covariates as long as the simpler model was significantly better than the more complex one based on a likelihood ratio test (Beale et al., 2010). This model selection was conducted using SAM (Rangel et al., 2010). Using this procedure, we created four models describing the density of salamander captures, one for each of the three salamander age classes and one for RV. The dependent variables were log-transformed prior to analysis in order to increase normality. PC1 was included in one of the models, and we used logistic regression to test the hypothesis that this axis separated plant species according to flood tolerance based on plant habitat preferences drawn from the Jepson Prairie Annotated Plant List (nrs.ucdavis.edu/Jepson/species/jepson-plantlist.pdf). Plant species with habitat descriptions of marshes, playas, pools, or streamside were classified as flood tolerant, and all others were classified as flood intolerant. Finally, we used CANOCO 4.5 (Ter Braak and Šmilauer, 2002) to conduct a redundancy analysis (RDA) to create a single model that summarizes all four of the dependent variables; a Monte Carlo permutation test with 500 replicates was used to determine the significance of each independent variable in the resulting ordination model (Lepš and Šmilauer, 2003).

Our second goal was to examine the effects of spatial and temporal heterogeneity on the distribution of salamanders around the breeding ponds. We averaged the number of salamanders caught at each distance from the shoreline up to 1000 m at Olcott Lake and 400 m at Round Pond over all of the fences at that distance and used a repeated-measures ANCOVA with POND as the main effect, DISTANCE as the covariate, YEAR as the repeated measure, and RV as the response variable, including the POND ∗ DISTANCE interaction in the model. A second repeated-measures ANCOVA tested for temporal variation within each of the ponds, and a third ANCOVA examined spatial variation within each year.

Our final goal was to determine the distance from the pond shoreline that would include 50%, 90%, and 95% of the salamander population. We created a function relating salamander density to DISTANCE, rotated it around a vertical axis located at the center of the pond, and integrated to determine the volume of the resulting three-dimensional solid using Mathematic 5.1 (Wolfram Research Inc., 2004). This approach assumes that the migration distances we observed northeast of the ponds are representative of other directions, which appears to be reasonable. Then, the resulting volume represents the total estimated salamander population associated with a pond. Based on this model, one can determine how far from the shoreline one would have to go in order to include any given percentage of this volume. We used the combined parameter estimate for the distance term across ponds and based our calculations on a hypothetical pond with an area that is the average of Olcott Lake and Round Pond.

3. Results

We captured 10 042 *A. californiense* during 22 137 trap-nights: 957 adults, 3208 juveniles, and 5877 metamorphs. For all age classes Olcott Lake had higher capture numbers (878 adults, 3067

juveniles, 3146 metamorphs) than Round Pond (79 adults, 141 juveniles, 2731 metamorphs). Olcott Lake also had higher average capture rates for both adults and juveniles (6.5 (95% CI: 5.5–7.5) and 22.4 (95% CI: 19.8–25.0)/fence) than Round Pond (2.9 (95% CI: 2.2–3.7) and 5.3 (95% CI: 4.0–6.6)/fence), but Round Pond had a higher average metamorph capture rate (160.6 (95% CI: 94.4–226.9)/fence vs. 60.5 (95% CI: 47.1–73.9)/fence). Based on recaptures of "marked" individuals, 11.2% of capture events were actually recaptures. Recaptures were analyzed the same way as first time captures, because we felt that if a salamander stayed in an area long enough to be captured twice that it reflected a true propensity of salamanders to utilize that section of the habitat to a greater degree.

Habitat use models indicated that adult and juvenile salamanders seek out (or in the case of migrating adults pass through) the driest areas of the prairie. This was surprising given that amphibians generally select moist microhabitats, a tendency that we assumed would be even stronger in the seasonally arid environment of Jepson Prairie. This affinity for the drier areas of the prairie was revealed by the inclusion of PC1 (which differentiates between flood tolerant and intolerant plants) in the adult model and ELEVATION in both the juvenile and RV models (Table 1). Regardless of how the three plant species with unknown flood tolerance were classified (Appendix A), the correlation between flood tolerance and loadings on PC1 was significant (logistic regression: $0.0212 < p < 0.0364$). Adult densities were higher at fences surrounded by more flood intolerant plants, and juvenile densities were greater at higher (and drier) elevations. Together, these represent the areas of the prairie that are least likely to become inundated during winter rains.

Five other variables entered one or more of the habitat use models. All models included DISTANCE, but in different ways. Juvenile density increased from the shoreline to 500 m, whereas RV, metamorph and adult captures decreased with distance. YEAR also entered all of the models; all models had a negative coefficient, corresponding to the lower number of salamanders captured in 2006–2007 than in 2005–2006. For adults, juveniles, and RV, POND also entered the models, reflecting the lower density of salamanders at Round Pond than at Olcott Lake. Adults were the only age class showing a (negative) relationship with MML_B, and juvenile density and RV were both positively correlated with PC5.

The RDA (Fig. 2) corroborated what we found using model selection. DISTANCE, ELEVATION, POND, and YEAR were all important variables. Together they explained 86% of the variance in the age class densities (YEAR 44%, POND 20%, DISTANCE 14%, ELEVATION 8%), and they each had significant correlations ($p = 0.002$) with the age class densities (Table S2). The only other variable that was significantly correlated with the age class densities was PC5 ($p = 0.014$). However it only explained 1% of the variance and thus
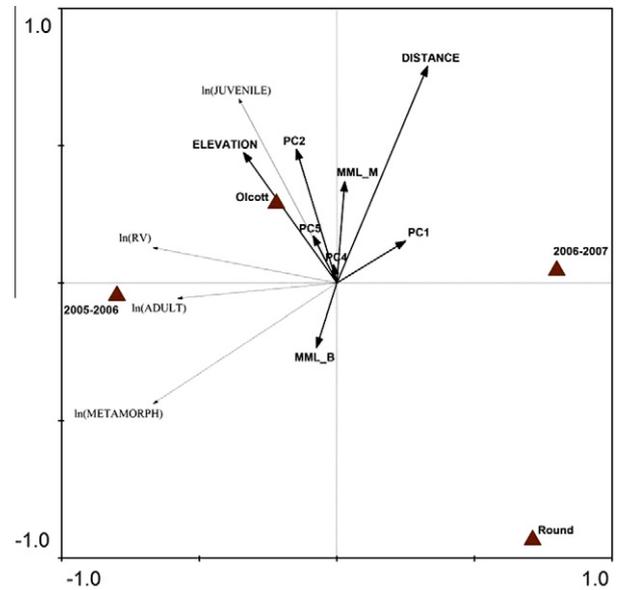

Fig. 2. Correlation biplot illustrating the redundancy analysis of the three age classes and reproductive value (RV) on the 12 predictor variables. Arrows that point in similar directions represent correlated variables. The length of arrows for dependent variables represents the proportion of variation in that variable explained by the graph. The length of arrows for predictor variables represents the percentage of variation explained by that variable. The two nominal predictor variables are represented by triangles rather than arrows, but each level of one of the nominal variables can be interpreted the same way as an arrow pointing to the center of its corresponding triangle.

was not a quantitatively important explanatory variable. PC2 explained the next most variance (5%) after ELEVATION, but was not significantly correlated with age class densities ($p = 0.23$).

Spatiotemporal variation had a significant effect on the distribution of *A. californiense* (Table 2). The three-way interaction term between DISTANCE, POND, and YEAR was significant ($p = 0.0302$), indicating that the distribution of reproductive value with respect to distance from the shoreline depends upon the particular pond * year combination (Fig. 3). This suggests that both temporal (year to year) and spatial (between pond) heterogeneity are important components of the system. When years were examined separately, the relationships between RV and distance for 2005–2006 (ln(RV) = 2.864 − 0.00431 * DISTANCE, $df = 11$, $p < 0.0001$, $R^2 = 0.88$) and 2006–2007 (ln(RV) = 1.498 − 0.000542 * DISTANCE, $df = 11$, $p = 0.637$, $R^2 = 0.54$) indicated that during the 2006–2007 season California tiger salamanders were dispersed farther from the pond edge than during the 2005–2006 season. The significant three-way interaction indicates that it is important to further examine this

Table 1
Simultaneous autoregressive models chosen through model selection to describe habitat use of each salamander age class and their weighted sum based on relative reproductive value (RV). Numbers are coefficients with standard errors.

Age classes Variables	Adult	Juvenile	Metamorph	RV
POND	−0.949 ± 0.134[***]	−1.731 ± 0.176[***]		−1.093 ± 0.121[***]
YEAR	−0.498 ± 0.072[***]	−0.559 ± 0.077[***]	−3.89 ± 0.204[***]	−0.911 ± 0.092[***]
DISTANCE	−0.002 ± 0.0003[***]	0.002 ± 0.0003[***]	−0.006 ± 0.0004[***]	−0.0006 ± 0.0002[**]
ELEVATION		0.847 ± 0.152[***]		0.582 ± 0.105[***]
MML_B	−0.176 ± 0.089[*]			
PC1	0.004 ± 0.001[**]			
PC5		0.005 ± 0.003[*]		0.004 ± 0.002[*]
Model R^2	0.465	0.603	0.916	0.462

[*] p-Values = $0.1 > p > 0.01$.
[**] p-Values = $0.01 > p > 0.001$.
[***] p-Values = $p < 0.001$.

Table 2
Repeated-measures ANCOVA examining spatial and temporal heterogeneity in the relationship between salamander density and distance from the breeding pond. Estimates are coefficients ± standard errors.

Term	Estimate	*p*-Value
Intercept	2.166 ± 0.0077	<0.0001
Distance	−0.00234 ± 0.0000858	0.0003
Pond	−1.569 ± 0.0281	<0.0001
Year	0.093 ± 0.00424	0.0007
Distance ∗ Pond	−0.00215 ± 0.000374	0.0354
Distance ∗ Year	0.00394 ± 0.000271	0.0029
Pond ∗ Year	−0.663 ± 0.0888	0.0195
Pond ∗ Year ∗ Distance	−0.00257 ± 0.000415	0.0302

effect at each pond separately since they may be contradictory. At Olcott Lake, salamanders were significantly more dispersed during the 2006–2007 season than during the 2005–2006 season ($p = 0.0099$), while at Round Pond there was no significant distance ∗ year interaction ($p = 0.1298$). However, the between year difference at Round Pond was even larger than at Olcott Lake, suggesting that the lack of significance was due to low power. Since neither of the simple distance ∗ year interactions contradict the main distance ∗ year interaction and since both simple interactions were in the same direction, the overall indication is that salamanders were more dispersed during the 2006–2007 season. The greater dispersion in 2006–2007 was largely due to the substantial number of metamorphs in 2005–2006, all of which were concentrated near the pond edge. The same trend toward greater dispersion in 2006–2007 was also present in adults ($p = 0.1158$) and juveniles ($p = 0.0833$) separately, indicating that the year effect was not entirely due to metamorphs.

The models for *A. californiense* captures at Olcott Lake and Round Pond separately were ln(RV) = 2.545 − 0.00127 ∗ DISTANCE ($df = 8$, $p = 0.0023$, $R^2 = 0.72$) and ln(RV) = 1.787 − 0.00341 ∗ DISTANCE ($df = 3$, $p = 0.0159$, $R^2 = 0.73$), respectively, indicating that California tiger salamander captures near Round Pond declined nearly three times more steeply with distance from the shoreline than did those at Olcott Lake ($p = 0.0354$). Again, the significant three-way interaction demands a closer examination of this effect separately within each year. In 2005–2006, salamanders were significantly more dispersed at Olcott Lake than at Round Pond ($p = 0.0023$), while in 2006–2007 the distance ∗ pond interaction was not significant ($p = 0.7864$). Thus, we cannot accept the overall trend that salamanders are more dispersed at Olcott Lake than at Round Pond, but must say that this effect only appears in one of the 2 years (2005–2006).

Based upon these models, we calculated the distance required to protect 50%, 90%, and 95% of the *A. californiense* population averaged across ponds, years and age classes. For the Jepson Prairie landscape, these distances were 556 m, 1486 m, and 1849 m from

the shoreline, respectively. Because every California tiger salamander breeding pond cannot be studied in this level of detail, we used the average of the distributions observed at the two study ponds as our best estimate of the upland habitat requirements for an "average" breeding site, although we fully admit that *A. californiense* might migrate differently in other habitats or regions.

4. Discussion

4.1. Habitat use

Perhaps the most surprising finding of this study is that California tiger salamander densities are positively correlated with environmental variables that are associated with the driest available microhabitat. Juvenile density was positively correlated with higher elevations (the regions of the prairie least subject to inundation) and adult density was positively correlated with flood intolerant vegetation. With few exceptions, other studies of amphibian habitat use have found that amphibian densities are positively correlated with environmental variables associated with moist microhabitats. Amphibians usually prefer deep leaf litter, dense canopy, moist substrate, and a high density of coarse woody debris (Blomquist and Hunter, 2010; Crawford and Semlitsch, 2008; Montieth and Paton, 2006). This general preference for moist microhabitats characterizes amphibian populations in regions with much higher annual rainfall (54–219% higher) than Jepson Prairie. Given the low annual precipitation at Jepson Prairie, we expected that California tiger salamanders would select the most mesic microhabitats. It is certainly true that they select rainy nights for their breeding migrations (Trenham et al., 2000), suggesting that high moisture levels are essential for surface activity. Their use of drier microhabitats presumably reflects the fact that surface activity of adults and juveniles is restricted to the wettest four months of the year, when parts of the prairie routinely flood. To avoid flooded burrows, they tend to frequent higher elevations areas with flood intolerant vegetation, presumably to find better drained refuge sites. This assumes that the areas with the highest surface capture rates are also the areas that salamanders most often use as refuge sites. Consistent with this assumption is our observation that metamorph densities are not correlated with elevation or flood intolerant vegetation, and metamorphs are the one age class that is not active on the surface during the rain season.

The relationship between salamander density and distance from the breeding pond also varies between age classes. Both adult and metamorph densities are negatively correlated with distance from the breeding site, while juvenile densities show a positive correlation (at least over the first 500 m). This presumably reflects the dependence of adults and metamorphs on the aquatic habitat. Most adults that are active on the surface are migrating to their
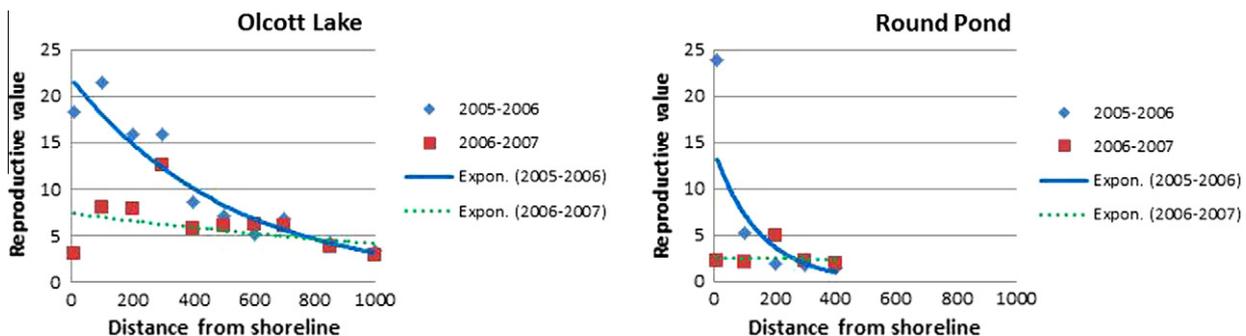

Fig. 3. Spatiotemporal heterogeneity in the distribution of salamanders with respect to distance from the breeding ponds. The rate of exponential decay depends on the exact pond ∗ year combination, but in general salamanders are more dispersed around the larger breeding pond (Olcott Lake) and in the drier year (2006–2007).

breeding site. Thus, regardless of where their home territory is located (if they have home territories), they must pass through the land adjacent to the breeding pond. Metamorphs by definition have recently emerged from the pond, and thus are concentrated in the terrestrial habitat at the pond edge. Juveniles are the only age class that is independent of the breeding pond, neither needing to visit it for reproduction, nor emerging from it at metamorphosis. Juveniles are therefore the only age class that presumably tracks the truly highest quality terrestrial habitat, and the observation that their density is positively correlated with distance from the pond suggests that this highest quality habitat is not at the pond edge. Whether terrestrial habitat farther from the breeding pond is higher quality by some absolute metric, or simply because it has lower densities of adults and metamorphs is an important question for future study.

Another area needing additional research is our observation that adult density has a negative correlation with the density of mammal burrows. Presumably, adult salamanders are not actually repelled by these burrows, which they rely on as refuge sites. Instead mammal holes are presumably correlated with other variables (e.g. hydrology, soil type, or prey density) that adult salamanders avoid. It should also be pointed out that in a simple linear regression adult density had no significant relationship with mammal hole density.

4.2. Population dynamics

Several aspects of habitat use were consistent across age classes. There were fewer salamander captures in all age classes during the drought year of 2006–2007 than during the preceding wet year of 2005–2006. This is similar to other amphibian populations, which often track annual precipitation (Pechmann et al., 1991; Daszak et al., 2005). This apparent change in population size may be a mixture of a true fluctuation in population size and a "catchability" issue. We can only capture salamanders when they are surface-active on rainy nights. Thus, in a dry year there are fewer opportunities to capture salamanders and one might predict fewer captures even if the population size remained constant. While a lack of surface activity may account for fluctuation in adult and juvenile numbers, it does not explain the difference in metamorph captures between 2005–2006 (>5000) and 2006–2007 (0). The drought in 2006–2007 was so severe that the breeding ponds dried up in mid-April, which was too early for successful metamorphosis. Across its range, the earliest date when metamorphs of A. californiense have been captured is May 13 (Loredo and Van Vuren, 1996; Trenham et al., 2000; Searcy and Shaffer, unpublished data). The difference in metamorph captures between 2005–2006 and 2006–2007 thus reflects a four order of magnitude difference in recruitment. While not unheard of for an amphibian population (Pechmann et al., 1991), this result emphasizes the importance of rainfall patterns, including future climate change scenarios, to the long-term survival of pond-breeding amphibians.

Another aspect of habitat use that was similar across age classes was the lower density of salamanders captured at Round Pond compared to Olcott Lake for adults and juveniles. Without additional replicate ponds it is impossible to say with certainty what caused this difference. Interestingly, Round Pond actually produced a higher density of metamorphs, suggesting that the limited number of adults and juveniles in the surrounding upland habitat is not driven by poor aquatic habitat or a lower production of young animals entering the local ecosystem. Rather, it appears that the difference is probably linked to the quality of the terrestrial habitat. The land around Round Pond has a lower average elevation, which our analysis suggests is less favored and probably of lower quality, at least for juveniles. Round Pond also has lower average burrowing mammal activity, which may limit refuge site

availability. While our analysis did not indicate that any of the age classes favor drift fences with greater surrounding mammal activity, it is possible that this factor is unimportant at the drift fence scale, but important at the pond scale (Homan et al., 2004). This is the scale at which Trenham et al. (2001) found a correlation between burrow density and average mass of California tiger salamanders, and it makes biological sense that the overall density of upland retreat sites should correlate with terrestrial carrying capacity.

4.3. Spatiotemporal heterogeneity

We found an effect of year and pond not only on the total number of salamanders captured, but also on how those salamanders were spatially distributed. This distance * year interaction suggests the somewhat non-intuitive result that salamanders were more concentrated near the breeding pond during the wet year, when there was greater overall surface activity, than during the dry one. Again, the explanation presumably lies in the greater prevalence of breeding adults and metamorphs during the wet year, as both these groups tend to be concentrated near the shoreline. This is similar to the result found by Johnson et al. (2007) that gray treefrog (Hyla versicolor) males are concentrated closer to the breeding pond during the breeding season than during the non-breeding season. We observed the same effect on a larger scale (between good and poor breeding years rather than between breeding and non-breeding seasons within a year). We also found a distance * pond interaction for one of our two study years. This interaction indicated that during 2005–2006 salamanders were concentrated closer to the shoreline at Round Pond than at Olcott Lake. Kovar et al. (2009) found a similar distance * pond interaction among populations of the common toad (Bufo bufo). They attributed the interaction to either population size, with larger populations being more dispersed, or to terrestrial habitat type, with toads more dispersed in meadow than in forest habitat. Virtually identical grassland habitat surrounds both Olcott Lake and Round Pond, but Olcott Lake is much larger than Round Pond, and supports a larger salamander population. It is therefore quite possible that the greater dispersion of the population at Olcott Lake is due to that pond's larger population size, although our documentation of this effect in only one of the 2 years suggests that data from additional years are necessary to better characterize the pattern of this interaction through time.

Given the significance of both distance * pond and distance * year interactions, multi-year and multi-site investigations are clearly required to fully understand the distribution of amphibian populations around breeding ponds. This is particularly true if the ultimate goal is to determine habitat conservation strategies at the population level (Semlitsch, 1998; Semlitsch and Bodie, 2003). Had we collected only a single year of data from the "good" 2005–2006 breeding season, we would have severely underestimated population dispersion in dry years. Similarly, if we had collected data only from Round Pond, we would have underestimated upland dispersion at the largest, and perhaps most important breeding sites like Olcott Lake. As it stands, with two years of data, we can document statistical interactions and develop hypotheses on the causal role of annual precipitation and pond size in driving them; ongoing, additional sampling will allow us to test these hypotheses in the future.

4.4. Migration distance

Finally, our data indicate that, compared to other urodeles, California tiger salamanders migrate surprisingly long distances from their breeding ponds. Among salamanders, only the red-spotted newt (Notophthalmus viridescens), has a longer documented migra-

tion distance (mode = 800 m; Healy, 1975). We found the median migration distance for *A. californiense* to be 556 m, roughly twice that of the next highest ambystomatid (the marbled salamander, *Ambystoma opacum*, is the next highest with a median migration distance of 297 m (Gamble et al., 2007)). Considering each age class separately, median migration distances for *A. californiense* were 49 m, 615 m, and 667 m for metamorphs, juveniles, and adults, respectively. It is not clear what ecological processes may underlie these enormous migration distances in the California tiger salamander. Possibly their grassland habitat does not contain as high a density of resources as the more mesic, forested habitat of most other salamanders (Kovar et al., 2009), and they migrate farther to achieve a lower terrestrial population density. Alternatively, it could simply be easier to migrate through grassland than through forest (Stevens et al., 2004). Tiger salamanders, and particularly populations and species from the western US and Mexico, are grassland specialists, but all previous studies of tiger salamander migrations have occurred in eastern tiger salamanders (*Ambystoma tigrinum*; Madison and Farrand, 1998; Semlitsch, 1983) rather than those occupying the relatively sparse shortgrass prairie habitats further west. If the key to the long migration distances seen in California tiger salamanders is the grassland habitat, then we predict that prairie populations of the barred tiger salamanders (*Ambystoma tigrinum mavortium*), for example, should show similarly long migration distances. The very low levels of genetic differentiation seen across the central prairie populations (Shaffer and McKnight, 1996) are consistent with this interpretation, but field ecological studies are badly needed.

5. Conclusion

Although this study focuses on a grassland amphibian, some of the results were qualitatively similar to those from forest-dwelling species, and certain generalizations may be emerging. For example, recruitment was found to fluctuate between years (Pechmann et al., 1991) and population size was found to differ between breeding ponds (Gill, 1978). There was also spatial (Kovar et al., 2009) and temporal (Johnson et al., 2007) heterogeneity in distance distributions among populations. Unlike forest-dwelling species, however, these grassland salamanders were found to seek out drier microhabitats rather than moister ones (Montieth and Paton, 2006), and to make exceptionally long breeding migrations (Semlitsch and Bodie, 2003). It is not certain that adaptations to grassland habitat drive these differences, but at least for the exceptionally long migration distances, we suspect that this is the case.

Detailed observations, such as those presented here, on microhabitat use are critical for conservation efforts for this endangered species, as they reveal both the extent of terrestrial buffers that need to be conserved around breeding ponds and some of the subtle environmental factors, such as slightly elevated areas that are protected from inundation, that should ideally characterize these buffers. These results may be representative of the habitat use of other grassland amphibians, which as a group are severely understudied. Without detailed habitat use information across multiple sites and multiple years, it would be impossible to determine the most utilized habitat types, and thus to identify the best remaining critical habitat to conserve.

Acknowledgements

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2012.08.033.

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