

Determining the Migration Distance of a Vagile Vernal Pool Specialist: How Much Land is Required for Conservation of California Tiger Salamanders?

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ABSTRACT. Unlike most other vernal pool specialists, the California tiger salamander (*Ambystoma californiense*) is dependent upon vernal pools for its aquatic larval phase, but makes extensive use of the surrounding grasslands for its terrestrial adult phase. The current U.S. Fish and Wildlife Service guidelines consider all land within 2092 m of a California tiger salamander breeding pond as upland salamander habitat, based on the observation of a single *A. californiense* found this distance from the nearest breeding pond. Here we used data from 15,212 individual captures and 1,164 recaptures to calculate both the average migration distance and the 95% tail of the migration distribution. We empirically determined the density distribution of *A. californiense* around two breeding ponds, and used these data to model the percentage of the reproductive potential of the population as a function of distance from the vernal pool shoreline. Since this method required extrapolating beyond the range of our capture data, we then determined whether the resulting migration distances were within the ecophysiological limits of *A. californiense* based upon observed migration rates of individual salamanders and the number of rainy nights available for migration during each of five consecutive breeding seasons. Our results indicated that *A. californiense* are physiologically capable of migrating up to 2484 m each breeding season, and that 95% of the population occurs in upland habitat within 1867 m of the breeding pond. Both of these estimates are similar to and not significantly different from the current 2092 m buffer used to delimit *A. californiense* habitat. Using this buffer width, we generated a list of 89 other listed species that share critical habitat with *A. californiense*, and suggest that California tiger salamanders have the potential to be an umbrella species for conservation of vernal pool grassland species in central California.

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INTRODUCTION

The Recovery Plan for Vernal Pool Ecosystems of California and Southern Oregon (U.S. Fish and Wildlife Service, 2005) lists 36 rare, threatened, or endangered species that are vernal pool specialists. The California tiger salamander (*Ambystoma californiense*) is the only one of these that requires large amounts of terrestrial habitat in the surrounding grasslands in addition to the aquatic habitat provided by the vernal pools themselves. At the

same time, *A. californiense* is perhaps the most difficult of these species to observe when present, since they are fossorial for over 95% of their lives and only cross the terrestrial landscape on rainy nights (Trenham et al., 2000). This has led to many difficulties in determining the extent of critical habitat for this species. The current U.S. Fish and Wildlife Service guideline stipulates that all land within 1.3 mi (2092 m) of a breeding pond is considered *A. californiense* upland habitat. However, this guideline is based on the observation

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of a single individual that was 1.3 mi from the closest known breeding pond (U.S. Fish and Wildlife Service, 2004). The frequency of dispersal events of this magnitude was unknown, and it was not even known if an individual this far from a breeding pond would be capable of making it back to the breeding pond such that it should still be considered part of the population.

Previous studies on migration distances for California tiger salamanders have revealed migration distances that are much less than 2092 m in length. The more systematic of these attempts to determine the extent of California tiger salamander migration distances have utilized radio tracking (Trenham, 2001), interpond adult dispersal (Trenham et al., 2001), and drift fence arrays (Trenham and Shaffer, 2005). All of these studies yielded average migration distances between 94 and 431 m and maximum migration distances between 248 and 670 m. Somewhat less quantitative, site-specific monitoring projects have found salamanders 800-1200 m from the nearest known breeding ponds (U.S. Fish and Wildlife Service, 2004). However, these projects were neither designed nor equipped to calculate the frequency of migration distances, and we remain unable to state with any certainty the percentage of the breeding population that migrates long distances and whether any appreciable percentage routinely migrates in the range of 2092 m.

Although the California tiger salamander received full federal protection in 2004, it was not granted protection under the California Endangered Species Act until March 3, 2010. At that meeting, two of the California Fish and Game commissioners who voted to protect the salamander pointed out that it is peer-reviewed science that sways the commission in such instances. We thus require the strongest possible data on terrestrial habitat use to guide management of this declining fossorial

species that is difficult to study. Toward that end, we here present data on the locations of over 15,000 salamanders captured around two breeding pools over the course of five breeding seasons. This is the largest data set available on terrestrial habitat use by California tiger salamanders, or any other pond-breeding amphibian in California. Using this data set, we first calculate the density distribution of salamanders and their reproductive potential as a function of distance from the vernal pool shoreline (Searcy and Shaffer, 2008). The power of this method is that it utilizes all of the capture data from our large data set, although it also involves fitting an empirically-derived function to the data and extrapolating beyond the observed range of actual dispersal distances.

Given the biological and economic importance of accurately estimating the terrestrial habitat that is used by California tiger salamanders, we felt that it was critical to ground-truth estimates with observed migration distances of actual salamanders. We therefore made an additional calculation of the migration distances that are physiologically reasonable for salamanders based on the distribution of rainy nights when salamanders can be active and on our empirically documented distances that individual salamanders have been observed to travel in a single night. Our primary goal was to determine whether this ecophysiological limit is greater than or equal to the migration distances predicted by our extrapolation from drift-fence capture data. If so, then it suggests that these extrapolated distances are biologically credible and represent realistic estimates of upland habitat requirements of California tiger salamanders.

METHODS

Study System

We conducted our study at the Jepson Prairie

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Preserve in central Solano County, 9.6 km east of Travis Air Force Base. The site is essentially flat, with a total range in elevation of about 3 m across the entire 625-ha preserve. The dominant vegetation type is grassland, and like most California grassland it is now dominated by invasive annuals (Huenneke, 1989). There are two California tiger salamander breeding ponds on the preserve that are 925 m apart: Olcott Lake, which is 33 ha when full, and Round Pond, which is 3 ha when full. Both are shallow playa pools that fill between October and December, reach a maximum depth of about 0.5 m, and dry between April and July, depending on the rain year. California tiger salamanders are known to use the burrows of both California ground squirrels (*Spermophilus beecheyi*) and pocket gophers (*Thomomys bottae*) across their range (Loredo et al., 1996), but only gophers are found on the preserve, and the salamanders rely heavily on them for underground retreats.

We believe Jepson Prairie is characteristic of much of the historical habitat of the California tiger salamander. Given that *A. californiense* can be found along much of the undeveloped rim of the Great Central Valley and at a few intact localities on the valley floor (e.g., Jepson Prairie, and Grasslands State Park), we postulate that the species was historically distributed across much of the floor of the San Joaquin, and at least the southern Sacramento Valleys prior to conversion to agricultural uses. Over 80% of the original vernal pool habitat in the Great Central Valley is lost (Holland, 2011), and it is likely that much of the historic range of the California tiger salamander fell into this area. Habitat use at Jepson Prairie is thus likely representative of much of the former and current range of *A. californiense*.

Experimental Procedures

We constructed two drift fence arrays, each to

the northeast of its associated breeding pond (Figure 1). Each drift fence consisted of a 10-m length of 30-cm shade cloth partially buried in the ground such that salamanders migrating to and from the breeding ponds were directed by these fences it into one of the pitfall traps at either end. At Olcott Lake, the array consisted of ten lines of fences, each running parallel to the shoreline of the pond. The lines were placed at 10, 100, 200, 300, 400, 500, 600, 700, 850, and 1000 m distances from the shoreline, and formed concentric arcs radiating out from the pool. The fence 10 m from the shoreline was continuous, with each 10-m segment separated from the neighboring segment by a single pitfall trap. The other fence lines consisted of 10-m drift fences with a pair of pitfall traps at each end, separated by 90 m without a drift fence, providing 10% coverage of each arc. The array at Round Pond was similar except that it consisted of five fence lines at 10, 100, 200, 300, and 400 m from the shoreline. Together the two arrays consisted of 165 10-m fences (137 at Olcott Lake and 28 at Round Pond).

Buckets (3.8-liter) buried such that their upper lip was flush with the ground were used as pitfall traps. When the traps were open, the bucket lids were inverted and supported 3 cm above the opening by wooden legs to provide shade for the bucket.

California tiger salamanders are only active on the surface of the terrestrial habitat during two distinct periods each year: 1) a period of juvenile dispersal and adult breeding in the fall and winter, and 2) a period of metamorph emergence from the pond in the spring and early summer (Loredo and Van Vuren, 1996; Trenham et al., 2000). Our pitfall traps were open during both of these periods for five consecutive years from 2005 to 2010. During the fall/winter activity period, our traps were open every night that was predicted to have rain, since rainy nights are the only nights during

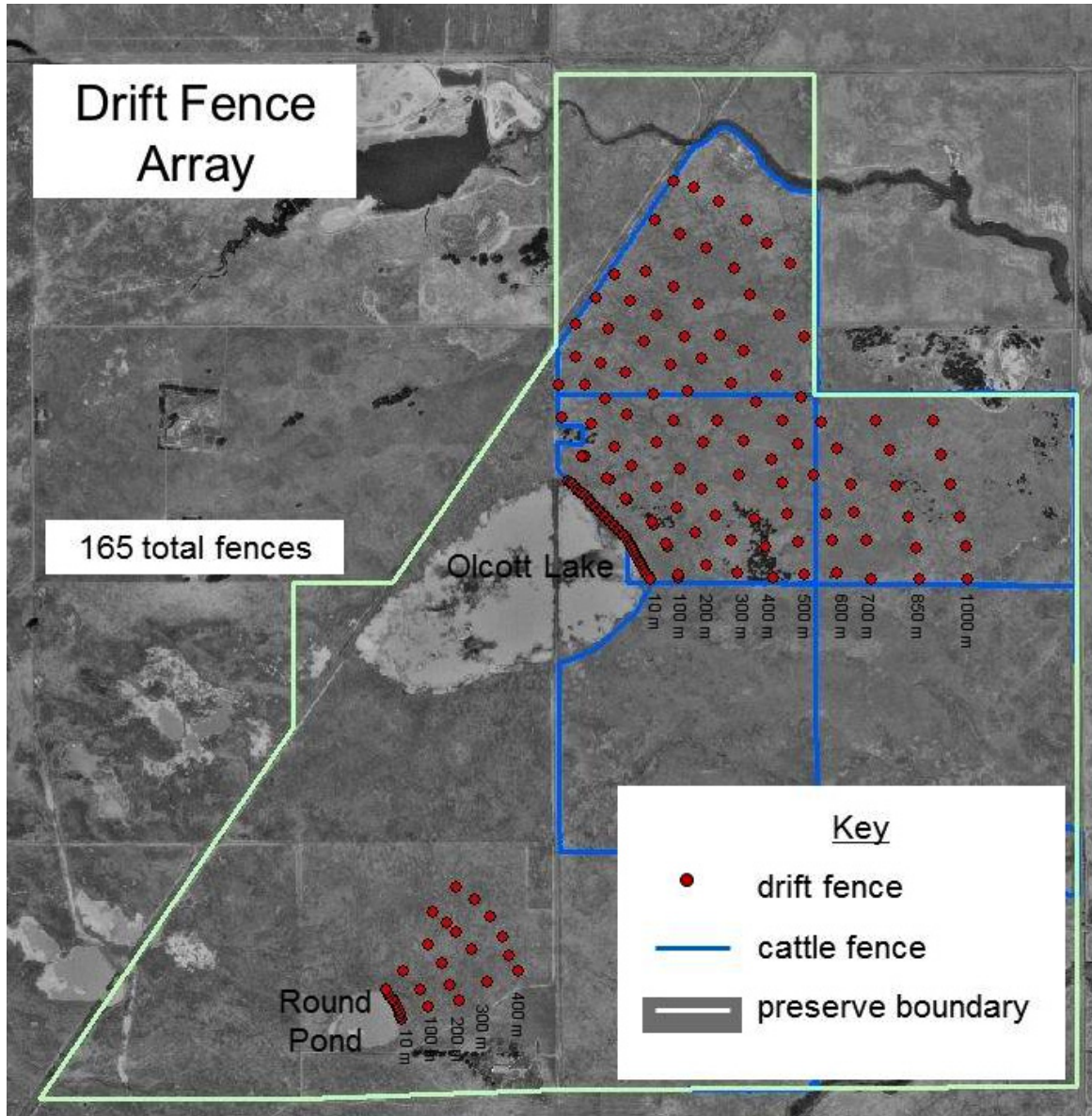


FIGURE 1. Map of the drift fence array at the Jepson Prairie Preserve. All of the drift fences are located to the northeast of the breeding ponds, because during an earlier study at Olcott Lake (Trenham and Shaffer, 2005), the highest density of salamanders was found in this region. Each drift fence is represented by a circle rather than a line, because the individual drift fences are small compared to the scale of the entire prairie.

which the vast majority of adults are active (Loredo and Van Vuren, 1996). Our traps were open from the first rains in October until the number of salamander captures dropped below five per night (always in late February).

During the spring/summer activity period, our traps were open every night from mid-May

until the ponds dried. During previous studies, no *A. californiense* metamorphs (terrestrial salamanders that recently metamorphosed from the larval condition) have been found prior to 19 May (Anderson, 1968; Loredo and Van Vuren, 1996; Trenham et al., 2000), and metamorph emergence by definition ends by the time the pond has dried. While it is possi-

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ble for metamorphs that emerged earlier in the season to still be active after the pond dries, this is a rare occurrence (Searcy and Shaffer, unpublished data). By the time we closed the traps each summer, fewer than ten metamorphs were being captured per night, compared with up to 550 per night during the height of emergence. We are confident that we sampled virtually the entire period of salamander activity in all five years.

When open, traps were checked every morning starting immediately before sunrise. For every salamander capture, we recorded its trap location, weighed the salamander, and, unless it was a metamorph, took a digital photograph of its dorsal surface from directly overhead (Figure 2). We then immediately released each salamander into the mouth of a nearby gopher burrow on the opposite side of the fence from where it was captured. Each salamander was classified into one of three age classes: metamorph, juvenile, or adult. Metamorphs were identified by their poorly defined spot pattern and time of emergence (spring or summer). Juveniles were identified by their adult color pattern, lack of other adult characteristics listed below, and small size. Adults were identified by their keeled tails, swollen vents (males), and obvious gravid condition (pre-breeding females). In addition, animals that were over 18.5 g (the largest confirmed weight for a juvenile), but did not have a keeled tail or swollen vent, were counted as adult females.

All digital photographs were entered into a pattern recognition program that was custom-designed for our use with California tiger salamanders (Conservation Research, Ltd.). For each photograph, the program extracted information on spot positions, and used this information to rank all other photographs previously entered into the database based on their probability of representing the same individual using two different algorithms. A



FIGURE 2. Two photographs representing an initial capture and recapture of the same adult salamander. Similar photographs were taken of every adult and juvenile salamander captured in the drift fence array in order to identify them based on the spot pattern found on their dorsal surface.

member of our research group then visually compared each photograph with the ten most likely matches generated by each of the two algorithms to determine if they were actually the same individual. Based upon a test set of sixty photographs representing thirty individuals, each of which was photographed and processed twice, we determined that visually comparing each photograph to the ten highest ranked matches should have detected all true matches. In the test set, most true matches were given a rank of one, and all received a rank of four or higher (28 rank-one, 1 rank-two, and 1 rank-four). Thus, no true recap-

tures should have been missed with this system.

Precipitation data were gathered from two different weather stations. For the 2005 to 2009 activity periods, data came from the Hastings Tract Station in Dixon, CA, which is 3.2 km from the drift fence array. In 2009, the Hastings Tract Station shut down and data for the 2009-10 activity periods came from the Westgate Subdivision Station in Vacaville, CA, 12.4 km from the drift fence array. Both stations generally yield very similar values for daily precipitation ($r = 0.925$).

Analyses

We estimated the maximum migration distance of California tiger salamanders using two methods.

Multiple linear regression model. This model consisted of seven terms, consisting of all possible factorial combinations of three independent variables: 1) pond (Olcott Lake or Round Pond), 2) year (2005-06, 2006-07, 2007-08, 2008-09, or 2009-10), and 3) distance from shoreline (10, 100, 200, 300, 400, 500, 600, 700, 850, or 1000 m). Pond and year were treated as categorical variables, while distance from shoreline was treated as a continuous variable.

The response variable in this model was density of reproductive value (Searcy and Shaffer, 2008). Density of reproductive value was calculated as a linear combination of the density of the three visually identifiable age classes (metamorph, juvenile, adult) weighted by their reproductive values. The density of each age class was calculated as the number individuals of that age class caught at each distance from the shoreline divided by the number of 10-m drift fences at that distance. Density was calculated separately for each of the two ponds and each of the five years. Reproductive val-

ues were calculated as the probability of individuals in each of the three age classes reaching maturity and were based upon survivorship values from Trenham et al. (2000), as calculated in Searcy and Shaffer (2008). Density of reproductive value was log-transformed to better fit the assumption of normality, and all model fitting was performed using JMP 8 (SAS Institute, Inc.).

After testing the full model for density of reproductive value, we concentrated on the relationship between density of reproductive value and distance from shoreline, since this relationship describes how far salamanders migrate from the average breeding pond during the average breeding year. Since the relationship between log-transformed reproductive value and distance from shoreline was linear, this relationship took the form of an exponential decay. We considered a theoretical pond with an area of 18 ha (the average of Olcott Lake and Round Pond) with this relationship describing the density of salamanders surrounding it. While 18 ha is much larger than the average vernal pool, using this pool size in our calculations actually makes our estimate of migration distance more conservative in the sense that it returns a minimal migration distance. Through integration, we determined the volume underneath this curve and calculated how large a terrestrial buffer one would have to create in order to include 50%, 90%, and 95% of this volume. These values represent the amount of terrestrial habitat surrounding a breeding pond necessary, on average, to protect that percentage of the breeding potential of a California tiger salamander population.

Distance = rate x time approach. Here, we calculated both the distance that a salamander could migrate in a single night (rate) and the number of nights available for such movement (time). The *rate* at which a salamander can move was determined from recapture data

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generated with the pattern recognition program. We searched through our database of recaptures, and used the rate of movement (in meters/night) of the salamander that made the longest observed migration. We did this to ensure that we were using a rate that a salamander could sustain over a long distance across many nights. While we could have used a higher rate that a salamander maintained over a shorter distance, this might represent a rate that would exhaust a salamander after a few nights and thus was not sustainable.

The *time* over which a salamander could migrate was based upon the length of the fall/winter activity period during each of the five years of the study. We defined the fall/winter activity period as beginning and ending on the first and last day in a rain season on which five or more adult or juvenile salamanders were captured. We then partitioned the fall/winter activity period into three sub-periods: an immigration sub-period, a breeding sub-period, and an emigration sub-period. The length of the breeding sub-period was set at 28 days, since this is the average length of time that adult salamanders spend in the pond (Trenham et al., 2000). We reasoned that during the breeding sub-period salamanders are in the water, and therefore those rain nights are not, on average, used for terrestrial movement activity. We somewhat arbitrarily placed the breeding sub-period in the middle of the fall/winter activity period to maximize the number of rain nights on either side of it, and tallied the number of rainy nights during both the immigration sub-period and the emigration sub-period. To ensure that we only included nights conducive to long, sustained migration events we considered a "rain night" to be one when it rained as much or more than the nights when the salamander making the longest observed migration was active. We took the number of such rain nights during either the immigration or emigration sub-period

(whichever was smaller) as the number of nights available for migration.

Finally, we modified this calculation to describe the migration of the average adult rather than the maximum possible adult migration. Here, the movement rate we used was the average rate of all of the adults that were captured twice during the same rain event such that all of the nights between the two captures were theoretically available for movement. We excluded from this set salamanders that were both initially captured and recaptured at the shoreline, since they presumably spent the intervening time in the pond and their movement in the water would not be characteristic of movement on land.

We also multiplied each migration rate by a correction factor that reflects the fact that by capturing a salamander during a migration night, we are not allowing it to complete its movement. We reasoned that, on the night of capture, we are on average capturing salamanders at the midpoint of their planned movement. Some individuals will be at the beginning of their migration for that night, and some at the end, but on average each salamander would have traveled twice as far on the night it was captured. Therefore, for all of the salamanders that were recaptured after a single night, we multiplied the movement rate by two. For all of the salamanders that were recaptured after two nights, we multiplied the movement rate by $4/3$ since these salamanders presumably migrated three quarters of their planned distance (full distance during the first night and half distance during the second night). Extrapolating upon this line of reasoning, the correction factor for each movement rate is $2n/(2n-1)$, where n is the number of nights between the capture events.

We also re-defined the beginning and end of the fall/winter activity period as the first and last days on which five or more adult sala-

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manders were captured rather than five or more adult or juvenile salamanders. By excluding juveniles, we narrowed the fall/winter activity period to the dates when adults really prefer to be active. We also re-defined the beginning and end of the breeding period as the average date on which all of the adults entered or exited the pond, respectively.

Finally, we re-defined movement nights as nights on which five or more adult salamanders were captured. These redefinitions resulted in the number of movement nights during the immigration and emigration sub-periods better representing the number of nights during which a large number of adults are actually making their breeding migrations rather than just those nights on which the climatic conditions would be favorable for them to do so.

RESULTS

Multiple linear regression model

Results show that protecting 95% of the reproductive value of a California tiger salamander population requires a 1867-m buffer (95% CI: 1391 to 3126 m), with correspondingly lower values for 90% (1501 m, 95% CI: 1132 to 2502 m) and 50% (562 m, 95% CI: 464 to 887 m) (Figure 3B). These values were obtained by integrating the function relating density of reproductive value to distance from shoreline ($y = 5.0998e^{-0.002317x}$, where x is the distance from shoreline and y is the density of reproductive value) (Figure 3A). This function was obtained from the multiple linear regression model describing density of reproductive value in terms of distance from shoreline, pond, and year. Both the full model and the distance term individually were highly significant ($p < 0.0001$). An exponential function was used rather than a linear one, because a Shapiro-Wilk Test revealed that the log-transformed density of reproductive value

fit a normal distribution ($W = 0.9886$, $p = 0.7414$). The data for this model consisted of 15,212 capture events, including 2190 adult captures, 3697 juvenile captures, and 9325 metamorph captures.

Distance = rate x time approach

Our estimate for the ecophysiological maximum migration distance for a California tiger salamander was 2484 m. This was based on an average of 13.2 nights being available for immigration/emigration during any given year (Table 1) and a maximum sustainable migration rate of 188.2 m/night. This was the movement rate of the salamander that made the longest observed migration across our pit-fall trap array. This salamander traveled 1129 m over six nights. Other salamanders moved at a faster rate over fewer nights: the fastest single-night rate was 352 m/night, the fastest two-night rate was 228 m/night, and the fastest rate over three nights was 223 m/night. Using these values would obviously result in a larger ecophysiological maximum migration distance, but they might represent speeds that are not sustainable over all of the rainy nights in a breeding season. We calculated the average of 13.2 nights being available for immigration/emigration by counting the number of nights with over 2 mm of rain that occurred during the immigration and emigration sub-periods. It rained at least 2 mm on each of the six nights over which the longest observed migration took place, suggesting that this amount of rainfall is adequate for long, sustained migrations to occur. Nights with less than 2 mm of rain were counted as unavailable for migration even if they received trace amounts of precipitation.

Finally, we calculated the average adult migration distance as 511 meters based on an average migration rate of 150.4 m/night and on the average adult spending 3.4 nights on immigration/emigration (Table 2). The average

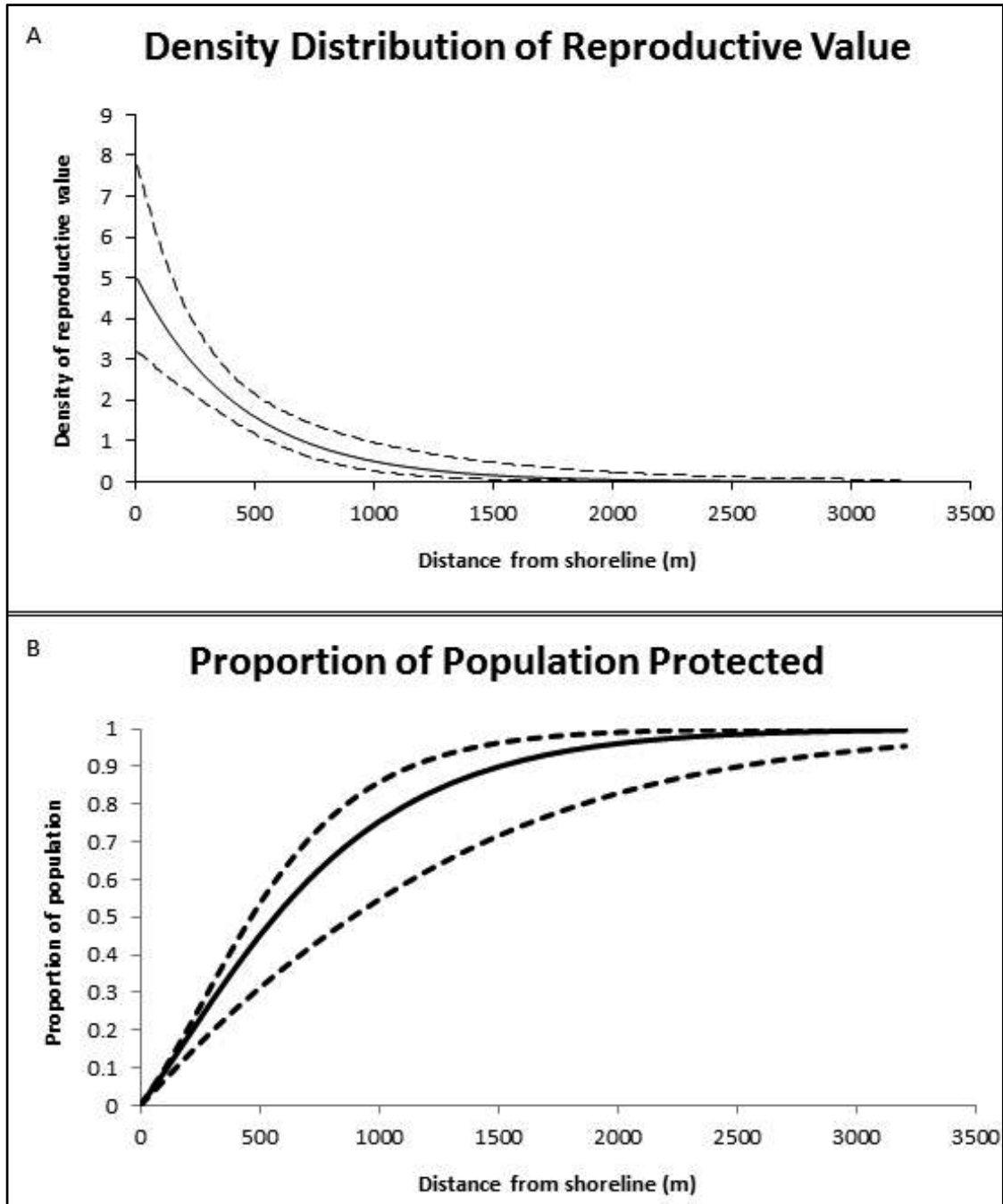


FIGURE 3. Method for calculating migration distances from the density distribution of reproductive value. A. Density of reproductive value as a function of distance from shoreline. B. Proportion of the reproductive potential of a California tiger salamander population that is protected based on the size of the terrestrial buffer. We treat this as the equivalent of the proportion of the California tiger salamander population that migrates a given distance or less from the breeding pond. These curves are derived from the integration of the density distribution of reproductive value function in A. Solid lines are best fit lines and dashed lines are 95% confidence intervals.

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TABLE 1. Maximum number of nights available for salamander migration across the five years of the study. Only nights with 2 mm of rain or more were counted as movement nights. The beginning of immigration and the end of emigration were the first and last day, respectively, on which five or more adult or juvenile salamanders were captured. The length of breeding was calculated as 28 days, the average number of days that an adult salamander spends in the breeding pond. Breeding was then placed in the middle of the fall/winter activity period so as to maximize the number of rain nights on either side of it. The number of movement nights during either immigration or emigration (whichever was smaller) was taken as the number of nights available for migration.

	2005-06	2006-07	2007-08	2008-09	2009-10
Beginning of immigration	8-Nov	3-Nov	11-Nov	2-Nov	14-Oct
Number of movement nights during immigration	11	19	14	15	16
Transition from immigration to breeding	19-Dec	2-Jan	30-Dec	25-Dec	22-Dec
Number of movement nights during breeding	15	0	15	3	8
Transition from breeding to emigration	16-Jan	30-Jan	27-Jan	22-Jan	19-Jan
Number of movement nights during emigration	10	11	14	15	20
End of emigration	28-Feb	25-Feb	25-Feb	23-Feb	24-Feb

number of nights during the immigration or emigration sub-periods during which five or more adult salamanders were captured was 3.4. We calculated 150.4 m/night as the average intended migration distance of adults recaptured during a single rain event. Forty adults were recaptured during a single rain event and their average observed migration rate was 89.5 m/night. These recapture events occurred between one and seven days after the initial capture (19 occurred after one day, 8 after two days, 8 after three days, 2 after five days, 1 after six days, and 2 after seven days). We multiplied the average observed migration rate of each of these 40 adults by the $2n/(2n-1)$ correction factor described in Methods to obtain the average intended migration distance.

DISCUSSION

Results and recommendations from Jepson Prairie

All of these results suggest that the extrapolations made from the multiple linear regression model are biologically reasonable and should be used as the basis for determining the migration distance of California tiger salamanders. The strongest argument for using this model is that it is based on data from more salamanders, averaged across more years of observation, than any previous estimate (e.g. Searcy and Shaffer, 2008; Trenham and Shaffer, 2005). Additionally, the estimates of migration distance based on this model are within the ecophysiological capabilities of California tiger salamanders. Specifically, the regression model predicts that 95% of the reproductive potential of an *A. californiense* population occupies terrestrial habitat within 1867 m of the breeding pond, while the maximum possible

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TABLE 2. Average number of nights during which adult salamanders migrated across the five years of the study. Only nights during which five or more adult salamanders were captured were counted as movement nights. The beginning of immigration and the end of emigration were the first and last day, respectively, on which five or more adult salamanders were captured. The beginning and end of breeding were the average day on which adult salamanders either entered or left the breeding pond, respectively. The number of movement nights during either immigration or emigration (whichever was smaller) was taken as the number of nights available for migration.

	2005-06	2006-07	2007-08	2008-09	2009-10
Beginning of immigration	29-Nov	14-Nov	11-Nov	2-Nov	12-Dec
Number of movement nights during immigration	2	3	5	5	3
Transition from immigration to breeding	16-Dec	11-Dec	19-Dec	2-Feb	5-Jan
Number of movement nights during breeding	4	1	7	3	4
Transition from breeding to emigration	28-Dec	1-Feb	12-Jan	10-Feb	24-Jan
Number of movement nights during emigration	9	6	8	4	6
End of emigration	28-Feb	25-Feb	20-Feb	23-Feb	24-Feb

migration distance based on the “distance = rate x time” approach is 2484 m. In addition, the estimate for the average migration distance (562 m) is not significantly different from the estimate for average migration distance obtained from the recapture events (511 m), again suggesting that the form of the multiple linear regression model is accurate.

Our confidence in the multiple regression model in turn provides a biological context lending support for the currently accepted maximum migration distance of 2092 m (U.S. Fish and Wildlife Service, 2004). It makes sense that the maximum migration distance observed (2092 m) would be slightly above the 95% cutoff from the multiple linear regression model (1867 m). Moreover, 2092 m is still less than the 2484 m migration distance that California tiger salamanders are physiologically capable of, so there is no reason to think that a salamander this distance from a breeding pond would be unable to return to breed even within a single breeding season. Given the large confidence intervals on our

95% cutoff (1386 to 3117 m) and the established benchmark of 2092 m, we recommend that this distance be maintained as a reasonable, biologically-justifiable migration distance for the species.

Finally, it is of interest to ask why some salamanders are apparently capable of moving over 2000 m, while the average salamander only moves 500 m. This can be understood by comparing the “distance = rate x time” estimates for average migration distance and maximum possible migration distance. The migration rates used to calculate these two distances are quite similar (150.4 m/night vs. 188.2 m/night), suggesting that most migrating salamanders are traveling close to the maximum sustainable migration rate. From a biological perspective, this may indicate that California tiger salamanders limit the number of nights spent traveling on the surface of the terrestrial environment, perhaps because they are vulnerable to predation, desiccation, or being caught out in the morning without finding an appropriate refuge. The substantial differ-

ence between the average and maximum migration distances comes from the number of movement nights used in their calculations (3.4 nights vs. 13.2 nights). This explains why some California tiger salamanders are capable of making such long distance migrations. There are a very large number of nights with proper conditions for movement if an individual utilizes all of them. However, most salamanders do not, which may indicate that repeated exposure or surface movement is costly.

Consistency with previous land use estimates

The migration distances calculated here are greater than those previously calculated for California tiger salamanders. Trenham and Shaffer (2005) made calculations most similar to our own, formulating a density distribution based upon captures at a smaller drift fence array at Jepson Prairie. They calculated separate density distributions for adult and juvenile salamanders and only the adult distribution was a negative exponential. Based on this distribution, they calculated that 95% of the adults were within 620 m of the shore-line. However, there are two shortcomings with their calculation. First, it is based on Riemann sums rather than integration. This method involves calculating an approximate value over each interval on the x-axis and since only a finite number of intervals can be included, this prevented Trenham and Shaffer (2005) from including the tail of the distribution. Second, they based their calculation on the area beneath a two-dimensional curve rather than the volume underneath a three-dimensional surface. However, the latter calculation is a more accurate representation of the area actually occupied by salamanders.

After making these corrections, 95% of the adults from Trenham and Shaffer (2005) were within 829 m of the shoreline, a roughly 25%

increase. This is still significantly less than the migration distance calculated here (outside the 95% CI), which may be due to the particular year in which their data were gathered (it was only a single year study), the focus on adults only, or the fact that they had very few drift fences more than 400 m from the shoreline of the breeding pond.

Trenham et al. (2001) looked at a different landscape (Hastings Natural History Reservation, Monterey County, CA) and the frequency with which California tiger salamanders switch breeding ponds between years. They used these data to develop a density distribution with a similar form to the one derived here (i.e., a negative exponential). The longest between-breeding-pond dispersal that they observed was 670 m and they did not integrate their density function in order to extrapolate longer migration distances. When we used the empirically-derived negative exponential from Trenham et al. (2001), we calculated that 95% of the population was within 1677 m of the shoreline, which is close to our value and within the confidence interval of our prediction.

Is our work representative of other vernal pool landscapes?

This leads us to consider how representative our data are of the distribution of California tiger salamanders on other vernal pool landscapes. The outstanding features of Jepson Prairie are that it: 1) is relatively flat with a total elevation range of only 3 m, 2) is dominated by grassland with almost no other vegetation types, and 3) has only two breeding pools, both of which are extremely large (>150 m in diameter). The landscape investigated by Trenham et al. (2001) at the Hastings Natural History Reservation, Monterey County, is at the opposite end of the spectrum: it has an elevation range of over 200 m, a mix of vegetation types, including grassland, oak sa-

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vanna, and oak woodland, and 17 documented breeding ponds, all of which are small (< 70 m diameter) and consist of a mix of artificial stock ponds and modified natural ponds. Given these differences, the similarity in migration distance calculated from the Hastings and Jepson data suggests that California tiger salamanders behave similarly across broadly divergent landscapes. This was, to us, rather surprising, and we initially predicted smaller migration distances at Hastings, given that California tiger salamanders have less endurance when walking over steeper slopes (Ohlin and Searcy, unpublished data), and that they do not disperse as freely through oak woodland, which makes up a substantial component of the Hastings landscape (Wang et al., 2009). In addition, given the strong correlation between breeding pond size and effective population size both in eastern Merced County, CA (Wang et al., in press) and at Hastings (Wang and Shaffer, submitted manuscript), the smaller breeding ponds at Hastings presumably support smaller effective population sizes, which could reasonably lead to smaller overall migration distances. However, the available data suggest that migration distances at Hastings and Jepson are quite similar.

Is the California tiger salamander an umbrella species for vernal pool habitat?

Shrader-Frechette and McCoy (1993) define an umbrella species as a species with such demanding habitat requirements that conserving it will automatically protect many other species. Since all of our calculations suggest that the 2092 m maximum migration distance used by the Fish and Wildlife Service to delineate terrestrial habitat for *A. californiense* is scientifically supported and probably applies across the range of the California tiger salamander, it becomes important to consider the implications of protecting this large amount of terrestrial habitat, particularly for other rare or endangered taxa. Based on this migration dis-

tance, each breeding pond will require at least 1375 ha of terrestrial habitat. Also, there are many landscapes in which the distance between breeding ponds is less than 2092 m, and thus the protected habitat surrounding different breeding ponds will overlap, leading to the protection of large continuous areas of terrestrial habitat. For example, in eastern Alameda and Contra Costa Counties, there are 480 California tiger salamander breeding ponds that utilize overlapping terrestrial habitats (Searcy and Shaffer, unpublished data). This protection of large continuous blocks of terrestrial habitat containing entire vernal pool complexes further emphasizes the important role that the California tiger salamander can play as an umbrella species for California's vernal pool grasslands.

As it turns out, 91 other rare, threatened, or endangered species are found within the aquatic and terrestrial habitat used by California tiger salamanders (i.e., occur within 2092 m of a California tiger salamander breeding pond), including 48 that are federally listed (Searcy and Shaffer, unpublished data). This is similar to the situation with another key umbrella species, the red-cockaded woodpecker (*Picoides borealis*). The red-cockaded woodpecker is an umbrella species for longleaf pine (*Pinus palustris*) forests in the U.S. Southeast where it coexists with 71 rare, threatened, or endangered species, 31 of which are federally listed (Simberloff, 1998). Another key umbrella species is the northern spotted owl (*Strix occidentalis*), which functions as an umbrella species for old-growth rain forest in the Pacific Northwest (Simberloff, 1998). A mating pair of northern spotted owls requires 800 ha (Simberloff, 1987), while a breeding population of California tiger salamanders requires 1375 ha.

Clearly California tiger salamanders have demanding enough habitat requirements and coexist with a sufficient number of other rare,

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threatened, and endangered species to put them on a par with other long-recognized umbrella species. Moreover, California tiger salamanders are found in nine of the 17 vernal pool regions referenced in the Recovery Plan for Vernal Pool Ecosystems of California and Southern Oregon (U.S. Fish and Wildlife Service, 2005) and coexist with 24 of the 33 vernal pool specialists that The Recovery Plan attempts to protect. California tiger salamanders are not found in the extreme southern and northern vernal pool regions of the state, and therefore do not provide protection for those vernal pool ecosystems. However, California tiger salamanders coexist with all but one of the vernal pool specialists that are not confined to these northern and southern regions, and this single exception, Bearded popcorn flower (*Plagiobothrys hystriculus*), is confined to a single locality (U.S. Fish and Wildlife Service, 2005). This makes *A. californiense* an almost ideal umbrella species for vernal pool grasslands in the latitudinal middle half of California.

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