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Terrestrial Habitat Use by Adult California Tiger Salamanders

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Although most aquatic-breeding amphibians spend much of their lives away from water, relatively little is known about terrestrial habitat requirements or movements for most species. Recent discussions of strategies to conserve amphibians have emphasized the importance of maintaining adequate buffers of suitable terrestrial habitat adjacent to aquatic breeding areas (Semlitsch, 1998). Unfortunately, available data are often insufficient to determine terrestrial habitat requirements and buffer widths with any confidence. For example, Dodd (1996) surveyed the published data on terrestrial movement by North American salamanders and frogs and found that most reports were based on incidental observations of a few unmarked individuals away from water.

The California tiger salamander, *Ambystoma californiense*, is considered a species of special concern by the state of California, and recently the U.S. Fish and Wildlife Service listed the remaining populations in Santa Barbara County as endangered (U.S. Fish and Wildlife Service, 2000). Although this salamander currently lacks formal protection throughout most of its range, recent development and management plans have included efforts to set aside sufficient habitat to maintain viable populations (S. Meyers, pers. comm.). Much is known about the aquatic habitat requirements of *A. californiense* (Fisher and Shaffer, 1996), and aspects of its adult life history and demography have been described elsewhere (Barry and Shaffer, 1994; Loredo and VanVuren, 1996; Trenham et al., 2000). In comparison, essential terrestrial habitats and buffer requirements are relatively poorly understood.

Loredo et al. (1996) visually tracked the nocturnal emigration of adult and newly metamorphosed *A. californiense* from the pond edge until they were no longer visible on the surface. They found that adults almost always settled in mammal burrows and that dis-

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tances between the pond and settlement sites ranged from 10–130 m. However, because these refuges could be temporary, these data are not necessarily appropriate for determining protective terrestrial buffer widths. My objectives were to radiotrack adult California tiger salamanders during the months following breeding to (1) quantify ultimate emigration distances achieved and estimate appropriate buffer widths, (2) to determine whether movements following initial settlement are related to precipitation, and (3) to quantify habitat selection relative to available vegetation types.

I radiotracked *A. californiense* at the Hastings Natural History Reservation (HNHR) and adjacent Oak Ridge Ranch, in the upper portion of Carmel Valley, Monterey County, California (36°N 23'; 121°W 33'). The landscape is generally steep and dominated by open grassland with scattered oaks and stands of mixed deciduous woodland. Grassland areas are dominated by *Avena* spp and *Bromus* spp. Wooded areas include mixtures of willows *Salix* spp, coast live oak *Quercus agrifolia*, valley oak *Q. lobata*, poison oak *Toxicodendron diversilobum*, and California buckeye *Aesculus californica*. Isolated oaks are typically valley *Q. lobata* or blue *Q. douglasii* oaks. I captured adult salamanders for radio implantation at two breeding ponds that were completely encircled by permanent drift fences with pitfall traps: Blomquist Pond and Laguna Conejo (Trenham et al., 2000). The area immediately surrounding each of these ponds is open grassland with scattered oaks.

I calculated the percentages of the landscape within 250 m of Blomquist Pond that were covered by grassland, continuous woody vegetation, or isolated oaks, using a digital aerial photograph of the area and GIS software. Hourly weather data were logged at a weather station located 500 m north of Blomquist Pond and the same elevation. In an attempt to minimize the impact of transmitters on movements, I selected the heaviest available individuals for radio tracking. I collected males for transmitter implantation as they attempted to enter or exit the drift fenced ponds, but I selected only females that were exiting the breeding pond and no longer appeared gravid. I radiotracked salamanders from February–July 1996 and December 1996–June 1997.

Following initial capture, I transported experimental animals 500–1000 m to the HNHR laboratory in covered coolers. To sedate salamanders, I placed them in a 0.03% solution of Benzocaine until they no longer righted themselves (Venable, 1985). I made a 1-cm incision penetrating the peritoneal cavity on the right side 1 cm posterior to the forelimb and inserted a Holohil® BD2G implantable transmitter. These transmitters weighed 1.8 g, and constituted no more than 5.5% of the mass of any animal at release. I closed the incision with six to eight stitches of 5-0 sterile silk suture material. Following at least 24 h of recuperation, I released animals at night at the point where I had captured them but on the opposite side of the drift fence. On rainy nights, or if the ground was damp from rainfall that day, I released salamanders on open ground. Under dry conditions, I released salamanders at the entry to the nearest California ground squirrel (*Spermophilus beecheyi*) burrow.

I attempted to locate each animal at least every other day and several times during rainy evenings. I de-

termined the position of each individual by direct overhead localization (Madison, 1997). Because the location of the signal could only be determined to a precision of roughly ± 0.5 m, I analyzed only movements of 1 m or more. The maximum distances from which radio signals could be detected varied from <5 m when animals were in deep burrows to a maximum of 50 m. I marked new locations with labeled flags, surveyed these points using a measuring tape and magnetic compass, and subsequently plotted them on a GIS map of the site. I also noted the general habitat type of each new location (grassland, woodland, or isolated oak).

During 1996, I excavated animals at least once to assess their condition. To minimize disturbance, and because animals excavated in 1996 healed rapidly, I did not excavate animals during tracking in 1997. Transmitters had a battery life of 3–4 months. Values presented are $\bar{x} \pm$ SD.

I followed a total of eight male and five female *A. californiense* beyond the drift fenced areas during their postbreeding emigration. Following the evening of their initial release, I never reencountered any of the radio-equipped salamanders above ground; all were underground and closely associated with burrows of ground squirrels. Although rocks, logs, culverts, and other potential refugia were available, these were never used by the tracked salamanders.

For individuals not released directly into burrows, the total straight-line distances moved on their first night averaged 60 m for males (range = 3–158 m, $N = 5$) and 44 m for females (2–94 m, $N = 4$). Most of these salamanders moved to another, or several other, burrow systems during the months that followed (total additional movement: $\bar{x} = 44$ m, 3–161 m, $N = 9$). Final distances from their points of release were always greater than the distances moved on the first night (Wilcoxon signed ranks test: $Z = -2.7$; $N = 9$; $P = 0.008$). No statistically significant differences between the sexes were detected for any movement parameters.

For eight *A. californiense* tracked for the entire life of their transmitter batteries, maximum observed distances from their points of release ranged from 16–248 m ($\bar{x} = 94 \pm 89$ m). Because all observed movements >15 m in length were away from the point of release, it is most likely that individuals that were lost or died during tracking would have ended up farther from the pond than my final radio fixes indicate. Including three additional individuals tracked for at least 50 m from their points of release, the average final distance was 114 ± 83 m. Assuming that the maximum distances that adult *A. californiense* move from their breeding ponds are normally distributed around a mean of 114 m (Shapiro-Wilk test of normality for maximum distances: $W = 0.88$, $N = 11$, $P = 0.11$), I estimated the upper bound of a 95% confidence interval for adult California tiger salamander emigration distances to be 173 m (Semlitsch, 1998). I detected movements of less than 1 m between 82% (681/828) of subsequent radio fixes, and movements of less than 10 m between 97% (806/828) of fixes (Fig. 1). Longer movements were generally separated by extended periods of little or no movement (days between movements >10 m: $\bar{x} = 14$ days, 1–38 days). When movements of 1 m or more occurred they were sig-

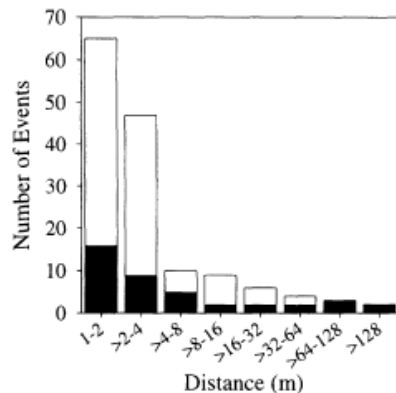


FIG. 1. Histogram of distances moved during post-breeding emigration, excluding movements made within 24 h of release, by radiotracked adult California tiger salamanders ($N = 13$). Movement distances correspond to the straight-line distance between consecutive relocations, and only movements of at least 1 m were included ($N = 147$). The black portion of each bar corresponds to movements that were detected following intervals where measurable precipitation was detected.

nificantly longer if detectable precipitation had fallen since the salamander was last relocated (Mann-Whitney U : $Z = -2.30$, $P = 0.021$, $\bar{x}_{\text{rain}} = 20.9 \pm 41.0$ m, $\bar{x}_{\text{no rain}} = 3.7 \pm 5.1$ m). All detected movements greater than 64 m occurred during intervals with detectable precipitation (Fig. 1). Mean maximum distances tracked for males were almost twice as far in 1996 ($\bar{x}_{96} = 139 \pm 89$ m, $N = 5$; $\bar{x}_{97} = 71 \pm 80$ m, $N = 3$), when the interval during which tracking occurred was considerably wetter than in 1997, with nearly five times the total rainfall (11.6 vs. 2.4 cm) and more than twice as many nights with measurable precipitation (13 vs. 6 nights).

Of the 11 individuals released at Blomquist Pond, seven crossed a creek at least once during emigration. Although several salamanders occupied burrows adjacent to creeks for some time, none of these animals showed any indication of movement along creeks or riparian vegetation. The area within 250 m of Blomquist Pond is covered by 74% open grassland, 25% continuous woody vegetation, and 1% large isolated oaks. Out of a total of 720 individual fixes, 82%, 12%, and 6% were in each of these vegetation types, respectively, suggesting that salamanders preferentially use open grassland and isolated oaks ($\chi^2 = 7.9$, $df = 2$, $P = 0.019$). None of the salamanders located in areas of continuous woody vegetation was ever more than 3 m from an adjacent area of open grassland.

The results of this study reinforce the general conclusions that mammal burrows are critical habitat elements for adult *A. californiense* and that burrows located some distance from breeding ponds are used (Jennings, 1996; Loredo et al. 1996). Although previous authors have suggested that California tiger salamanders aestivate in burrows (Barry and Shaffer, 1994), continued movement within the burrows indicates that some individuals are active at least into summer. Adult movements on the night of release

were somewhat longer in the present study than those reported by Loredo et al. (1996), possibly because salamanders did not always remain in the first burrow that they entered that night (pers. obs.). Although two individuals remained in their initial burrow for the entire life of their transmitter, most salamanders made one or more additional moves away from the breeding pond, and these movements often occurred on rainy nights. Total emigration distances observed here for *A. californiense* adults were similar to those observed in radiotracking studies of *A. tigrinum* (0–286 m, Madison and Farrand, 1998) and *A. maculatum* (15–210 m, Madison, 1997).

Because in a typical year adult *A. californiense* females and males spend an average of only 12 and 45 days at Blomquist Pond, respectively, sufficient suitable terrestrial habitat is clearly critical to the persistence of local populations (Trenham et al., 2000). Based on data from tracking studies of six other species of ambystomatid salamanders, Semlitsch (1998) estimated that 95% of movements could be encompassed by a 164-m wide terrestrial buffer. The results of this study suggest a similar buffer around *A. californiense* breeding ponds. However, because individuals that moved long distances from the pond were more likely to be lost because of the increasingly large search area required, and because I only followed salamanders for a maximum of four months, the 173 m buffer width may underestimate the terrestrial habitat necessary to encompass adult movements.

In his review of ambystomatid tracking studies, Semlitsch (1998) also noted that most salamanders were relocated in closed-canopy habitats and in tunnels located 2.5–7.5 cm beneath the surface. In comparison, California tiger salamanders were most often relocated in open grassland habitats, and the individuals that I dug up were in tunnels 20 cm to 1 m beneath the surface. Because tracked salamanders moved through all available types of habitat in the area around Blomquist Pond, the apparent preference for grassland and isolated oak habitats is probably driven by the fact that ground squirrels most often construct burrows in open habitats (Jameson and Peeters, 1988). The depth of these burrows reduced the distance over which transmitter signals could be detected, but such burrows are probably critical for salamander survival through the hot dry summers of central California, where daytime temperatures commonly exceed 37°C and monthly rainfall averages less than 1 mm. Because burrows collapse rapidly if not maintained, *A. californiense* probably require sites with active populations of burrowing mammals (Loredo et al., 1996).

I conclude that any plan to maintain local populations of California tiger salamanders should include pond(s) surrounded by at least 173-m wide buffers of terrestrial habitat with burrowing mammals. However, it should be noted that single isolated breeding ponds, even if surrounded by optimal terrestrial habitat, might not support populations indefinitely (Pechmann and Wilbur, 1994; Semlitsch and Bodie, 1998).

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Discrimination of Femoral Gland Secretions from Familiar and Unfamiliar Conspecifics by Male Iberian Rock-Lizards, *Lacerta monticola*

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Intraspecific communication by chemical signals is widespread among vertebrates (Stoddart, 1980), including reptiles (Halpern, 1992; Mason, 1992; Cooper, 1994). In many lizards, secretions from skin (Mason and Gutzke, 1990), cloaca (Cooper and Trauth, 1992), or femoral pores (Alberts, 1990, 1993) play an important role in pheromonal communication. The femoral pores are epidermal structures located on the ventral surface of the thigh of many saurians and are connected to glands that produce copious amounts of holocrine secretion (Mason, 1992). Femoral secretions are composed primarily of proteins (Cole, 1966; Fergusson et al., 1985; Alberts, 1990, 1991, 1993), which have low volatility, suggesting that perception could occur by the vomeronasal organ (Halpern, 1987) rather than by nasal olfaction (Wilson, 1970). Components of low volatility are likely to work in the absence of the signalers because of their durability (Alberts and Werner, 1993). Femoral pores are larger in males than in females, are regulated by androgens, and present a peak of activity in the breeding season (Mason, 1992). Additionally, the ventral location of the femoral pores suggests that secretions are passively deposited on the substrate as lizards move through their home ranges (Fergusson et al., 1985). Therefore, femoral gland secretions could advertise residence in a home range and could convey information about social status and competitive ability of the sender, thus reducing costs of agonistic encounters.

When discrimination between conspecifics occurs, the relative concentrations of chemical components should be variable among individuals (Beecher, 1989). The electrophoretic patterns of femoral gland proteins differ consistently among individuals of the desert iguana, *Dipsosaurus dorsalis* (Alberts, 1990), which are able to detect and respond differentially to their own femoral gland secretions and those of unfamiliar conspecifics (Alberts, 1992). Male green iguanas, *Iguana iguana*, use chemical cues from femoral gland secretions to discriminate between familiar and unfamiliar conspecific males (Alberts and Werner, 1993).

The vomeronasal organ is well developed in Squamates, and within this group, *Lacertidae* is one of the families in which it is best developed (see Halpern, 1992). Although there are several studies that have suggested the role of femoral gland secretions of lacertids in pheromonal communication (e.g., Gómez et al., 1993), there is a lack of direct empirical support.

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