ton (San Diego Natural History Museum), Charles H. Lowe (University of Arizona) for permission to examine snakes in the herpetology collections of their respective institutions. Leslie N. Ajimine assisted with histology.

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APPENDIX

Specimens examined by county from herpetology collections, Arizona State University (ASU), Natural History Museum of Los Angeles County (LACM), San Diego Natural History Museum (SDSNH), University of Arizona (UAZ). * includes one specimen from Sonora, Mexico. *Phyllorhynchus browni*, Gila: SDSNH 60992; Maricopa: ASU 00169–00170, 13682; Pima: ASU 03281, 04043, 04046, 04048, 04051, 04053, 24306, 26407, 26492–26493, 28383, 28385–28390, 28392–28394, 28396; LACM 02663, 27832–27836, 27838–27839, 34926–34927, 34929, 53084, 53086, 53088–53091, 53093, 64266–64267; SDSNH 17876, 32285, 32497, 32499, 34921, 37630, 39157, 39161, 40826–40827, 40830, 44125–44126, 49508, 52907; UAZ 25767, 25781, 25783, 25806, 25810, 32285, 34795, 35984, 38118, 41154, 41156, 41468, 41473, 41488, 41490, 41494, 41496, 41500, 42594, 42779, 44252; Pinal: ASU 26396–26398, 26399, 26401, 26405; LACM 58922; UAZ 25773; *Mexico: ASU 08266. *P. decurtatus*, Maricopa: ASU 00033, 00789, 04057, 14121; LACM 130799; UAZ 34909, 35910, 43148; Mohave: ASU 23613; UAZ 44868–44870, 44872–44873; Pima: ASU 04063, 13949, 13951, 24309; LACM 02666–02667, 102781, 102783–102784; SDSNH 39160, 49533; UAZ 25878, 25883, 32956, 33843, 37817, 40835–40836, 42709, 44246; Pinal: ASU 13909, 26402–26403; UAZ 34787, 35951, 40368; Yavapai: ASU 04059; Yuma: ASU 15856, 23612; LACM 09140; SDSNH 23918; UAZ 33842.

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Habitat Use and Migration Behavior of the California Tiger Salamander

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The California tiger salamander (*Ambystoma californiense*) is endemic to California and geographically isolated from other North American ambystomatids. Populations of this species have declined in recent years, and *A. californiense* is listed as a "species of special concern" by the state of California and as a Category I species on the federal Endangered Species List (Sorensen, 1994). The most important threat to the California tiger salamander is habitat loss and fragmentation, especially due to urban development and conversion of its habitat to agriculture (Sorensen, 1994). Other threats include predation by introduced species such as fish and bullfrogs (*Rana catesbeiana*), vehicular-related mortality especially during breeding migrations, and rodent control programs (Sorensen, 1994).

The California tiger salamander is found in the Central Valley and adjacent foothills and coastal grasslands (Storer, 1925), an area with a Mediterranean climate of cool, wet winters and hot, dry summers. It inhabits primarily annual grasslands and open woodlands of the foothills and valleys (Stebbins, 1985; Barry and Shaffer, 1994). California tiger salamanders are rarely seen except during their nocturnal breeding migrations which begin with the first seasonal rains, usually in November or December (Storer, 1925; Barry and Shaffer, 1994; Loredo-Prendeville, 1995). Breeding sites are usually ephemeral ponds that fill during winter and may dry by summer. Larvae grow rapidly; metamorphosis begins in late spring or early summer and is followed by the departure of juveniles from their natal ponds into terrestrial habitat (Storer, 1925; Holland et al., 1990; Loredo-Prendeville, 1995).

Terrestrial habitats used by the California tiger salamander are unknown. Ambystomatids in general are

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fossorial during the nonbreeding season. Adults of several ambystomatid species have been found in rodent burrows (Hamilton, 1946; Douglas and Monroe, 1981), but some species have also been found in what appear to be self-constructed burrows, either in association with rodent burrows (Gordon, 1968) or not (Semlitsch, 1981). These studies suggest a widespread commensal relationship between *Ambystoma* and small mammals, providing reason to expect such a relationship with the California tiger salamander. Use of ground squirrel burrows by California tiger salamanders has been suggested (Storer, 1925; Fitch, 1948), but verification is limited to one anecdotal account (Storer, 1925). Such a relationship would have important conservation implications because California ground squirrels, *Spermophilus beecheyi*, are considered a pest species, and numerous control programs are aimed at reducing or eliminating local populations (Marsh, 1987). Our purpose was to quantify habitat selection, migration distances, and movement rates of California tiger salamanders.

The study was conducted at a pond at Concord Naval Weapons Station (CNWS), Contra Costa County, California. The pond holds water year-round in years of normal or above average rainfall, but dries by late summer in drought years. Surrounding topography and vegetation consist of open, rolling grassland-covered hills with scattered oaks, *Quercus* spp. Other small ponds occur ≥750 m away. Much of CNWS supports dense populations of California ground squirrels (mean density = 32 squirrels/ha; Loredo-Prendeville et al., 1994) and burrow density within 100 m of the pond is 223 burrows/ha (unpubl. data). Field work spanned two summer seasons (May through July 1992 and May through August 1993) when juvenile salamanders metamorphosed and left the pond, and two winter seasons (December 1992 through March 1993 and December 1993 through April 1994) when breeding adults migrated to and from the pond.

Salamanders were captured with a drift fence and pitfall traps as they left the pond. Traps were checked every night in the summer and every rainy night or at least every other night during the winter. After capture, one to five salamanders per night were chosen at random to be tracked. The number of salamanders tracked per night was limited by logistical constraints. Salamanders were in traps usually ≤4 h before being released. Weather conditions during tracking varied during the study. Salamanders were placed on the outside of the fence and visually tracked by moonlight or with an intermittent flashlight beam until settlement. Salamanders did not seem disturbed by this method of tracking (Gordon, 1968). We defined settlement as when a salamander vanished below ground or underneath a surface object and did not emerge for at least 15 min. Each settlement site was characterized and the linear distance to the pond's edge was measured. Soil crevices were deep cracks in the soil surface that formed as the clay soil dried. Distance measurements were normalized by square-root transformation prior to statistical analysis. Movement rate of each salamander was determined by dividing the linear distance from the release site to the settlement site by the time elapsed in travel.

Ground squirrels (*Spermophilus* spp.) can be predators of various vertebrate species, including amphibians (Callahan, 1993), so we described the occupancy status of ground squirrel burrows utilized as settlement sites by salamanders. Burrows classified as occupied were those with signs of recent squirrel activity, such as fresh scat or newly excavated soil at the burrow entrance. Burrows that appeared unoccupied and that were within 1.5 m of an occupied burrow were considered occupied because ground squirrel burrow systems typically have several entrances, and those close to each other are likely connected underground (Fitch, 1948). Any burrows that could not be unambiguously categorized as occupied or unoccupied were excluded from the analysis. The ratio of occupied to unoccupied ground squirrel burrows available to salamanders was estimated by locating and classifying all burrows found within a 100 m radius of the pond.

TABLE 1. Proportional habitat use by adult (N = 59) and juvenile (N = 68) *Ambystoma californiense* upon emigration from a breeding pond in Concord, California, 1992–1994.

	Adults	Juveniles
Ground squirrel burrow	0.83	0.54
Soil crevice	0.05	0.46
Other burrow	0.10	0
Log	0.02	0

We tracked 68 juvenile salamanders during summer (1992, N = 33; 1993, N = 35) and 59 adult salamanders during winter (1992–1993, N = 42; 1993–1994, N = 17). Adults presumably had bred and were returning to their terrestrial habitat, although some may have returned subsequently to this or another pond. Most adult salamanders settled in ground squirrel burrows, although some entered other rodent burrows, or moved into crevices or beneath logs (Table 1). Juvenile salamanders also settled most often in ground squirrel burrows. Unlike adults, however, many juveniles settled in soil crevices (Table 1). Juveniles and adults differed significantly in proportional habitat use ($\chi^2 = 31.28$, df = 2, $P < 0.0005$; habitat types besides ground squirrel burrows and soil crevices were combined to increase expected frequencies). Juveniles usually entered the first burrow or large crevice they encountered, whereas adults often passed by crevices or burrows en route to their settlement site.

Both adult and juvenile salamanders settled in occupied as well as unoccupied ground squirrel burrows. Use of occupied versus unoccupied burrows was independent of age class ($\chi^2 = 0.44$, df = 1, $P > 0.50$), thus data from adults and juveniles were combined. Of the 57 ground squirrel burrows utilized by salamanders that could be unambiguously classified as to occupancy status, 68% were occupied and 32% were unoccupied. Among burrows within 100 m of the pond, 62% were occupied and 38% were unoccupied. A goodness of fit test showed no significant difference in use versus availability ($\chi^2 = 0.97$, df = 1, $P > 0.30$).

Adults moved a mean of 35.9 m (N = 59, SD = 24.6, range = 8–129) from the pond before settling, significantly farther ($t = 2.436$, $P < 0.02$) than the 26.0

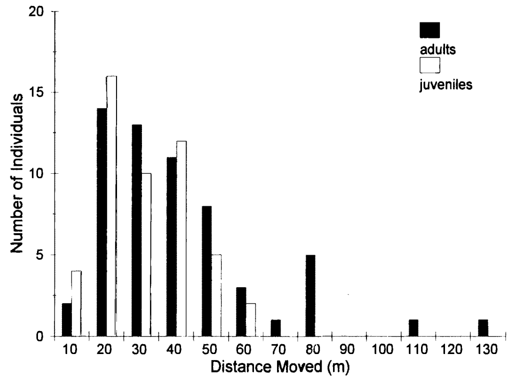

FIG. 1. Frequency distribution of distances moved by adult (N = 59) and juvenile (N = 49) *Ambystoma californiense* upon the first night's emigration from a breeding pond in Concord, California, 1992–1994.

m mean distance moved by juveniles (N = 49, SD = 13.1, range = 6–57). The distributions of distances moved were skewed toward shorter distances in both adults and juveniles; however, patterns differed in that no juvenile moved more than 60 m, whereas 14% of adults moved 70–130 m (Fig. 1).

Rate of movement also differed between adults and juveniles ($t = 4.688$, $P < 0.001$). Adults averaged 50.8 m/hour (SD = 28.9, range = 6.0–165.0), whereas juveniles averaged 30.9 m/hour (SD = 18.0, range = 0.25–66.7).

Our results show that burrows of California ground squirrels are an important habitat for both juvenile and adult California tiger salamanders. Because of hot, dry summers, salamanders probably require fossorial habitats, which offer greater protection from heat and desiccation than nonfossorial habitats such as rocks and logs. California tiger salamanders are unusual in that their range includes areas inhabited by no other salamanders (Stebbins, 1985). Presumably, the climatic conditions of these areas are too physiologically stressful for other salamanders.

Differences in habitat use between juveniles and adults might have resulted from seasonal differences in habitat availability as well as the inexperience of the new metamorphs with their surroundings. With the first few storms of winter, most soil crevices disappeared and were not available to adults. Further, emigrating juveniles lack familiarity with their surroundings and may face physiological stress. Salamanders are vulnerable to desiccation and juvenile California tiger salamanders migrate at night during the hottest, driest season, whereas adults migrate during the rainy season. Indeed, most juveniles migrated during dry weather, whereas most adults migrated during or immediately following rainstorms (Loredo-Prendeville, 1995). Thus some metamorphs may seek temporary shelter in soil crevices the first night, then continue moving on successive nights until reaching better quality habitat; alternatively, they may remain in crevices until the onset of the rainy season affords them conditions suitable for further movement. Soil crevices are important habitat for house-mice in Australia (Newsome, 1969) and may serve as important temporary habitat for many small vertebrates.

Physiological stress also may explain the shorter distances moved by juveniles, which are more prone to desiccation than adults because of higher surface area to volume ratios (Semlitsch, 1981). Juvenile ambystomatids often die due to heat or desiccation stress shortly after emigrating (Shoop, 1974; Semlitsch, 1981; Holland et al., 1990). Juvenile *A. talpoideum* also migrated shorter distances than adults (Semlitsch, 1981).

Migration distances reported here, which pertain only to movements the first night upon leaving the breeding pond, were less than mean distances moved by other *Ambystoma* that were followed for more than one night (100 to 280 m; Douglas and Monroe, 1981; Semlitsch, 1981). Thus, migration distances in the California tiger salamander may be several times the average documented for the first night in this study, and settlement sites documented here may be temporary.

Distance distributions for adults and juveniles were similar within 70 m but differed in that some adults moved farther distances (Fig. 1). Salamanders may move until they settle into the first suitable habitat, potentially explaining distributions skewed toward shorter distances (Murray, 1967). Adults perhaps move farther because of their near-exclusive use of ground squirrel burrows as well as their previous experience with the area. Adults probably travel faster than juveniles because they are larger and more familiar with their surroundings; adult ambystomatids use the same migration route among years (Stenhouse, 1985; Phillips and Sexton, 1989).

Our results suggest a commensal relationship between California ground squirrels and California tiger salamanders in which salamanders benefit from habitat provided by burrowing activities of squirrels. A similar relationship has been found between gopher tortoises, *Gopherus polyphemus*, which occur in relatively xerophytic habitats, and several species of small vertebrates associated with tortoise burrows, including the rare gopher frog, *Rana areolata* (Lips, 1991; Witz et al., 1991). Salamanders showed no avoidance of occupied ground squirrel burrows which suggests that squirrels are not a threat, perhaps due to the toxic skin secretions of salamanders (Brodie, 1977).

This commensal relationship has important conservation implications because California ground squirrels are controlled on over 4 million ha in California, keeping population sizes as low as 10–20% of carrying capacity (Marsh, 1987), while the California tiger salamander may soon be in danger of extinction throughout its range (Barry and Shaffer, 1994). Fewer ground squirrels probably means fewer ground squirrel burrows. Ground squirrels apparently must maintain their burrows, especially during the winter rainy season; once abandoned, a burrow soon collapses. Some burrows that were occupied during summer of 1992 were subsequently abandoned and had collapsed within 18 months. Ground squirrel burrows are important habitat for California tiger salamanders during initial migration from breeding ponds and possibly for permanent habitat as well, although we did not determine where salamanders eventually settled. Reduction of ground squirrel densities would reduce the availability of habitat for salamanders. Further, lower densities of burrows would mean that salamanders must travel farther to locate suitable habitat, potentially increasing the risk of mortality. Complete eradication of ground squirrels could entirely eliminate an important habitat of California tiger salamanders.

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Is the Venom Related to Diet and Tail Color During *Bothrops moojeni* Ontogeny?

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Snakes are strictly carnivorous reptiles, and many of them feed upon large prey which they swallow whole. Juveniles and adults, however, may exhibit a significant difference in body size, which can lead to an ontogenetic dietary shift (see Mushinsky, 1987). In this regard, many species of snakes feed on anurans and lizards while juveniles, and on birds and mammals as adults (e.g., Sexton, 1956–1957; Saint Girons, 1980). Moreover, juveniles of some snakes use the conspicuous tip of the tail to lure ectothermic prey (Greene and Campbell, 1972; Heatwole and Davison, 1976), losing this feature with growth, when the diet changes to endotherms (Neill, 1960; Henderson, 1970; Murphy et al., 1978; Jackson and Martin, 1980). Nevertheless, some sub-adult and adult snakes, always males, retain the conspicuous color of the tail (see Burger and Smith, 1950).

The occurrence of ontogenetic changes in diet and caudal luring are well documented for the family Viperidae, a group of snakes in which venom has an important role in prey capture (e.g., Mushinsky, 1987; Meier and Stocker, 1991). Because venom properties may vary ontogenetically (Fiero, 1972; Theakston and Reid, 1978; Gutiérrez et al., 1980; Lomonte et al., 1983; Meier, 1986; Furtado et al., 1991) it has been proposed that such variation could be caused by differences in the feeding habits of juveniles and adults (Gans and Elliot, 1968; Sazima, 1991).

To evaluate the possible specificity between venom and prey, we investigated the toxicity of juvenile and adult *Bothrops moojeni* venom in frogs and mice, which