Journal of Herpetology, Vol. 47, No. 4, 555–564, 2013

Movements and Habitat Use of Yosemite Toads (*Anaxyrus* (formerly *Bufo*) *canorus*) in the Sierra National Forest, California

CHRISTINA T. LIANG

USDA Forest Service, Pacific Southwest Research Station, Davis, California 95618 USA; E-mail: christinaliang@fs.fed.us

ABSTRACT.—**The Yosemite Toad (*Anaxyrus* (formerly *Bufo*) *canorus*) is a high-elevation species endemic to the central Sierra Nevada mountain range in California whose populations are in decline. There is limited information on their terrestrial movement and habitat use, which impairs our understanding of the ecology and habitat needs of this sensitive species. I present radio-tracking data collected from 35 adult toads in the Sierra National Forest during daylight hours in the late spring and summer of 2007–2009. Movements, microsite cover type, and terrestrial habitat are analyzed and interpreted with regard to life-history characteristics of *A. canorus*. Adult toads moved a mean distance of 270 m from aquatic breeding sites, and the maximum distance recorded was 1.26 km. Females moved significantly longer distances than did males and had a larger home range. Distance traveled was related to ordinal day as well as the interaction between day and sex. Adult *A. canorus* used terrestrial environments extensively and were found in the mixed-conifer forest in dry habitat. Burrows were the most commonly used cover type, but other protective cover such as logs, rocks, and tree stumps were also used. The locations occupied by adult toads in the terrestrial environment were structurally different than other surrounding areas; occupied sites had less canopy cover and fewer woody species than did unoccupied sites. The results of this study have implications for identifying population processes such as metapopulation dynamics, as well as for management purposes such as identifying sensitive habitat and establishing protective areas for *A. canorus* in the terrestrial environment.**

Movement is a fundamental action for animal species, and studying movement patterns is necessary to determine ecological features such as home-range size and the maximum distance an animal can travel. Movement information is also needed to identify habitat requirements and patterns of use within the animal's home range. This information is important both for management purposes and for ecological knowledge. Species' habitat and habitat use are critical components of management decisions such as the establishment of buffer zones around sensitive populations or breeding sites (Lee et al., 2004) or the establishment of movement corridors (Chetkiewicz et al., 2006). Movement is also important for identifying basic population processes such as how a population is structured spatially (e.g., a metapopulation [Harrison and Taylor, 1997]).

For amphibian species that move between terrestrial and aquatic environments, studying movement can be challenging. Many amphibian species spend a majority of time in terrestrial habitats (Marsh and Trenham, 2001; Semlitsch and Bodie, 2003), but species can be difficult to locate and observe in these areas. However, the relatively recent advances in tagging and tracking techniques have allowed for more studies of movement and habitat use in the terrestrial environment (Donnelly et al., 1994; Muths, 2003a). These studies are important in understanding the ecology of animals in areas where visual observations and sampling are often limited.

Understanding movement is especially important for species of concern such as the Yosemite Toad (*Anaxyrus* (formerly *Bufo*) *canorus*), a high-elevation species endemic to the Sierra Nevada mountain range in California. Populations appear to be declining for unknown reasons, and the species is a federal candidate for listing as threatened (USFWS, 2013). The toad is found in both wetland and terrestrial habitats, moving from breeding sites in wetland areas to upland foraging areas (Martin, 2008). *Anaxyrus canorus* breeds in the late spring in areas of shallow water such as wet meadows, edges of ponds and lakes, and slow-moving streams (Mullally, 1953; Karlstrom, 1962). Breeding typically lasts for 1–2 weeks, after which adults move into other parts of the wetland area or into the terrestrial environment (Kagarise Sherman, 1980; Kagarise Sherman and Morton, 1984). The species is sexually dimorphic, and adult females are generally larger than adult males in both length and weight (Karlstrom, 1962; Kagarise Sherman, 1980). There is minimal information regarding movements of adult toads away from breeding sites along with their associated use of habitat (Kagarise Sherman, 1980; Martin, 2008). The aims of this study were to (1) determine mean and maximum distances traveled by adult *A. canorus* away from aquatic breeding sites; (2) analyze differences in distance traveled by sex and by capture location (breeding meadow); (3) examine microsite cover type used by adult *A. canorus*; and (4) examine terrestrial vegetation communities in locations with and without *A. canorus*.

MATERIALS AND METHODS

Study Area.—I conducted this study in the Bull Creek watershed within the Dinkey Creek drainage in the Sierra National Forest (SNF). The SNF is on the western slope of the central Sierra Nevada mountain range and is within the southern part of the historic range for *A. canorus* (Karlstrom, 1962). The Bull Creek watershed is in the southern portion of the SNF at elevations of approximately 2,130–2,440 m in mixed-conifer forest dominated by red fir (*Abies magnifica*), white fir (*Abies concolor*), and sugar pine (*Pinus lambertiana*). Adult toads were captured in four breeding meadows in the Bull Creek watershed: two meadows (520M15, 520M20) in 2007, and an additional two meadows (520M14, 520M25) in 2008 and 2009 (Fig. 1).

Radio-Tracking.—Adult toads were captured by hand within the four breeding meadows from April through June of each year. Captured toads were measured with a metric ruler for snout–vent length (SVL), their mass determined using a field scale (Pesola 100 g spring scale), and they were implanted with a passive integrated transponder (PIT) tag (AVID Identification Systems, Norco, CA) for individual identification. The PIT tag was inserted under the skin along the dorsum and maneuvered into position near the base of the spine. Females were captured only after they had finished spawning and were no longer gravid; males were captured opportunistically.

I outfitted adult toads with radio transmitters and tracked individuals as they left the breeding meadows. Transmitters

DOI: 10.1670/12-054

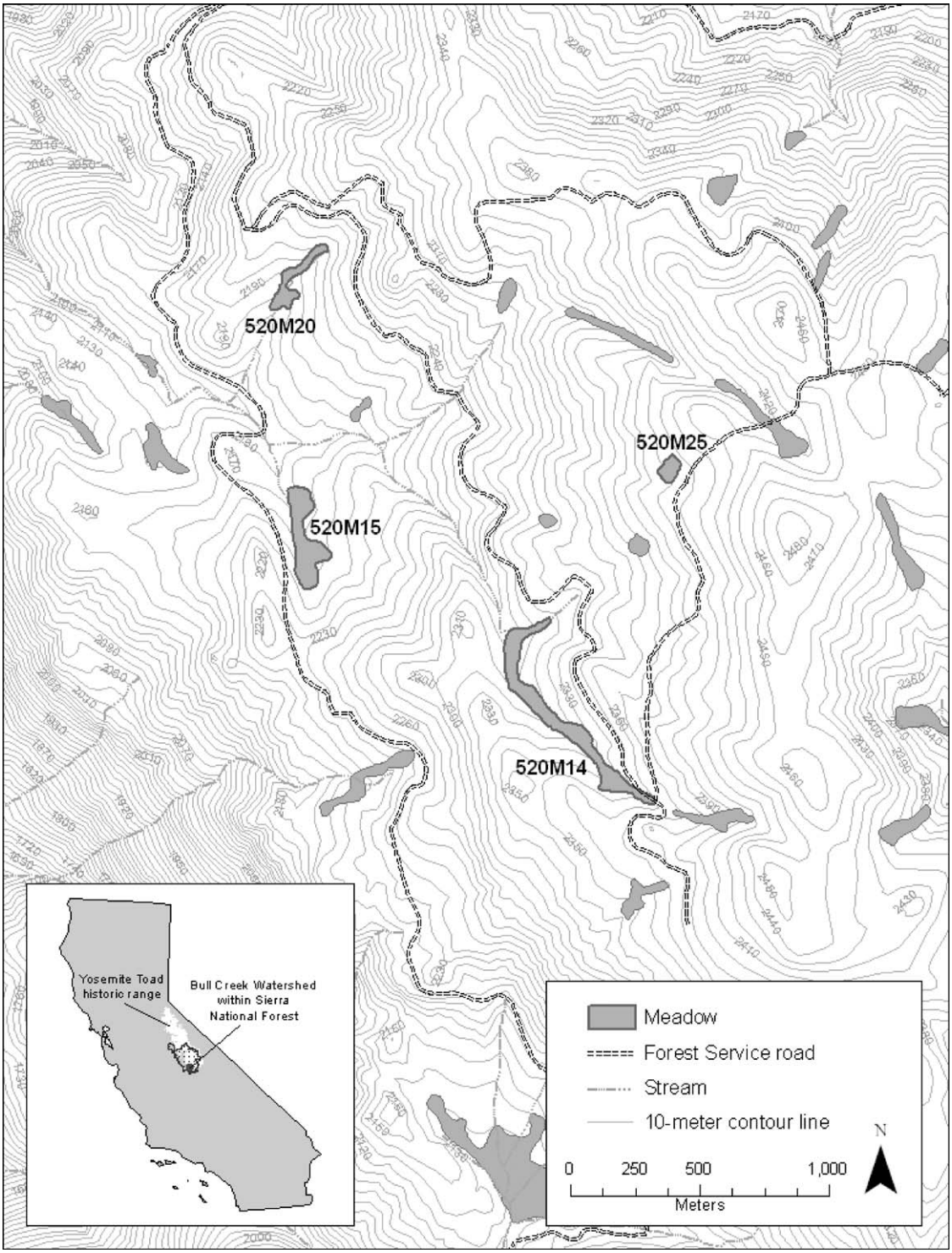

FIG. 1. Meadow locations within the Bull Creek watershed in the Sierra National Forest, California. Meadows 520M14, 520M15, 520M20, and 520M25 were used in the study.

from AVM Instrument Company (Colfax, CA; model G3-1V, expected battery life of 5–12 weeks) were used in 2007. Transmitters from Wildlife Materials (Murphysboro, IL; model SOPR-207, expected battery life of 18–21 weeks) were used in 2008–2009. I attached the transmitters to the adults using a tubing and wire belt system modified after Muths (2003a). Flexible, surgical grade polyethylene tubing (inside diameter = 0.58 mm, outside diameter = 0.99 mm) was placed through an opening in the transmitter casing with a nylon coated stainless steel wire threaded inside the tubing. The wire was crimped shut with a sterling silver bead and the wire ends were cut flush to the crimp. The belt was sized to fit over the widest part of the toad's thighs when the legs were fully extended and held together. The transmitter and belt apparatus was maneuvered over the legs and placed around the waist of the toad, with the transmitter situated on the dorsal side of the animal. The total

mass of the transmitter and belt was approximately 2 g. I attached transmitters only to toads that were ≥20 g to ensure that the transmitter and belt apparatus was ≤10% of the individual's mass (White and Garrott, 1990; Richards et al., 1994).

I used a Telonics TR-2 receiver and Telonics RA-2AK VHF (H type) directional antenna to track *A. canorus* during daylight hours every 1–19 days, which allowed enough time for independence of observations (Swihart and Slade, 1985). Toad locations were recorded with a GPS (Garmin eTrex Legend, accuracy ±3 m with 95% confidence). At each location, data were collected on environmental conditions (air and ground temperature, relative humidity, cloud cover, and wind), general habitat type, and microsite cover type. I removed transmitters in August and September before the battery life was expected to expire, or earlier if the transmitter began to send erratic signals.

Straight-line distance from the capture site in the meadow to every recorded location was calculated for each adult *A. canorus* using a geographic information system (GIS) (ESRI ArcGIS 9.3; http://www.esri.com). Home range for each individual was calculated using the minimum convex polygon method and Hawth's Analysis Tools v3.27 for GIS (http://www.spatialecology.com). I used *t*-test and one-factor ANOVA to compare differences in straight-line distance and home range between sex and among original capture location (meadow), using log-transformed values to meet the assumption of normality. I tested difference among meadows because the breeding meadows differ in total area, shape, and location, which could influence toad movement and distance traveled.

Distance was analyzed using a mixed model with sex, meadow, and ordinal day as fixed factors and toad as the random subject on which repeated measurements were taken. Year was not included in the model because it was highly correlated with toad. To analyze the within-subject variance–covariance structure, I assessed separate models for four types of covariance structure: compound symmetry, unstructured, autoregressive, and autoregressive with heterogeneous variances. I chose the model with the lowest Akaike's information criterion value for the covariance structure. Irregularly spaced time points were accounted for by using a multilevel model with time as a linear effect, shown in the following equations.

Level 1 (day):

$$\text{distance} = \beta_{0j} + \beta_{1j}(\text{day}) + e_{ij}$$

Level 2 (toad):

$$\beta_{0j} = \gamma_{00} + \gamma_{01}(\text{sex}) + \gamma_{02}(\text{meadow}) + \gamma_{03}(\text{sex}\times\text{meadow}) + u_{0j}$$

Level 2 (toad):

$$\beta_{1j} = \gamma_{10} + \gamma_{11}(\text{sex}) + \gamma_{12}(\text{meadow}) + \gamma_{13}(\text{sex}\times\text{meadow}) + u_{1j} \quad (1)\leftarrow$$

where *i* refers to the level 1 unit (i.e., day) and *j* refers to the level 2 unit (i.e., toad). In the level 1 model, the intercept (β_{0j}) and slope (β_{1j}) are random variables defined by the level 2 equations and the residual (e_{ij}) is the standard linear model residual term. In the level 2 model, the intercepts (γ_{00}, γ_{10}) and regression coefficients (γ_{0n}, γ_{1n} for $N = 1, 2, 3$) are the standard linear regression model variables. The residuals (u_{0j} , u_{1j}) are random variables with parameters $E(u_{0j}) = E(u_{1j}) = 0$, $\text{var}(u_{0j}) = \sigma^2$, $\text{var}(u_{1j}) = \sigma^2$, $\text{cov}(u_{1j}, u_{1j}) = \sigma_{u01}$.

Substituting the level 2 model into the level 1 model results in the following single equation, with the random variables in square brackets.

$$\begin{aligned}\text{distance} = {} & \gamma_{00} + \gamma_{01}(\text{sex}) + \gamma_{02}(\text{meadow}) + \gamma_{03}(\text{sex}\times\text{meadow})\leftarrow \\ & + \gamma_{10}(\text{day}) + \gamma_{11}(\text{sex}\times\text{day}) + \gamma_{12}(\text{meadow}\times\text{day})\leftarrow \\ & + \gamma_{13}(\text{sex}\times\text{meadow}\times\text{day}) + \left[u_{0j} + u_{1j}(\text{day}) + e_{ij}\right] \quad (2)\leftarrow\end{aligned}$$

To model the possible quadratic effect of time, I added a day × day term to (2).

$$\begin{aligned}\text{distance} = {} & \gamma_{00} + \gamma_{01}(\text{sex}) + \gamma_{02}(\text{meadow}) + \gamma_{03}(\text{sex}\times\text{meadow})\leftarrow \\ & + \gamma_{10}(\text{day}) + \gamma_{11}(\text{sex}\times\text{day}) + \gamma_{12}(\text{meadow}\times\text{day})\leftarrow \\ & + \gamma_{13}(\text{sex}\times\text{meadow}\times\text{day}) + \gamma_{20}(\text{day}\times\text{day})\leftarrow \\ & + \gamma_{21}(\text{sex}\times\text{day}\times\text{day}) + \gamma_{22}(\text{meadow}\times\text{day}\times\text{day})\leftarrow \\ & + \gamma_{23}(\text{sex}\times\text{meadow}\times\text{day}\times\text{day})\leftarrow \\ & \times\left[u_{0j} + u_{1j}(\text{day}) + u_{2j}(\text{day}\times\text{day}) + e_{ij}\right] \quad (3)\leftarrow\end{aligned}$$

I used model (3) to look at distance traveled by adult *A. canorus* as a function of sex, meadow, and time as ordinal day. Time was also included as a quadratic term to account for the possible nonlinear rate of movement whereby distance traveled varies during different time periods. I analyzed the data with R (version 2.11.1; http://www.r-project.org/) using the nlme package.

Microsite Cover Type.—I recorded microsite cover type where *A. canorus* individuals were located. Cover type was classified into nine categories: burrow, depression, downed wood, log, open/no cover, rock, stump, vegetation, water. The burrow category included both shallow burrows and more extensive underground burrows. The depression category was used for small concavities in the ground surface. Downed wood included smaller pieces of wood such as branches and bark, which were not as large as downed logs (log category). The open/no cover category was used when toads were exposed, in both terrestrial and wetland habitats. The rock category included rocks of all sizes, from small flat rocks to boulders. Stump was used for tree stumps in the terrestrial habitat. The vegetation category included herbaceous and woody cover. The water category included all standing or flowing water present in the study site, primarily meadow pools and streams.

Cover type data from each *A. canorus* individual was compared using a Friedman one-way repeated–measures analysis of variance by ranks, a nonparametric test similar to parametric repeated–measures ANOVA. Post hoc tests for multiple comparison analysis of ranked data were performed, analogous to Tukey's HSD for ANOVA. I analyzed the data with R (version 2.11.1, coin and multcomp packages), and the Friedman post hoc R code from Galili (2010) to perform the Wilcoxon-Nemenyi-McDonald-Thompson test (Hollander and Wolfe, 1999).

Vegetation Sampling.—I sampled vegetation in July 2008 and 2009 to compare terrestrial locations with and without *A. canorus*. Sampling in all locations was conducted within two weeks in both years and coincided with the presence of annual herbaceous vegetation. Occupied locations were identified by the daytime location of transmittered toads, and different toads were chosen for every location over both years. An equal number of males and females were selected randomly in 2009, but more males than females were available in 2008. Unoccupied locations were selected randomly from a set of grid points spaced 150 m apart that were established within the Bull Creek watershed for the U.S. Forest Service King's River Experimental Watershed (KREW) project (Hunsaker and Eagan, 2003). *Anaxyrus canorus* were presumed to be absent from these locations, but the absence of untransmittered toads could not be

verified. However, transmittered toads were not found in or near the locations assumed to be unoccupied. I sampled 38 occupied and unoccupied terrestrial locations: 26 were sampled in 2008 (13 occupied [3 locations occupied by females, 9 by males, and one location occupied by both male and females]; 13 unoccupied); and 12 were sampled in 2009 (6 occupied [3 locations occupied by females, 3 by males]; 6 unoccupied).

Vegetation sampling methods followed the protocol used by KREW personnel that was established to characterize the vegetation communities with regard to forest management actions at the landscape scale (protocol available at http://www.fs.fed.us/psw/topics/water/kingsriver/documents/KREW_Study_Plan_Sep2007.pdf). At each occupied and unoccupied location, I placed a 22-m transect in a random direction, starting at the toad location in occupied habitat and at the grid point in unoccupied habitat. I conducted three types of sampling: quadrat sampling for herbaceous plants, line-intercept sampling for shrubs and canopy, and belt transect sampling for trees. In quadrat sampling, a 1 × 1–m quadrat was placed on the left side of the transect axis (when facing from 0–22 m) at 2 m, 7 m, and 12 m. One side of the quadrat was the transect axis such that the quadrats were at 2–3 m, 7–8 m, and 12–13 m along the transect. I estimated percent cover for all herbaceous species within the quadrat along with percent cover of rock, gravel, soil, moss, and downed dead wood all under 1 m. Total coverage could exceed 100% because of species overlap. In line-intercept sampling, I recorded all woody species that intersected the transect at two levels: 2 m or below and above 2 m. Intersection below 2 m was determined by holding a meter stick perpendicular to level. Intersection above 2 m was determined using a densitometer. I recorded data at every meter along the transect from 2–21 m, resulting in 20 sampled points. In the belt transect sampling, I counted all free-standing woody species taller than 2 m within 5 m on both sides of the transect from 2–22 m, resulting in a 10 × 20–m survey area. I identified all vegetation to genus and then to species in most cases, following Hickman (1993).

To compare vegetation communities at locations with *A. canorus* to those without, I calculated Sørensen dissimilarity for all possible pairs of locations. Sørensen dissimilarity is a distance measure used to evaluate the dissimilarities of two communities, with low dissimilarity values indicating more similar communities and high values indicating different communities (McCune and Grace, 2002). For each transect, I calculated the mean Sørensen values comparing the transect to both *A. canorus* occupied locations and toad unoccupied locations for the three vegetation layers (herbaceous, shrub and canopy, and trees). *T*-tests were used to test for differences in the mean dissimilarity scores of the transects at locations with toads versus locations without toads. I analyzed the data with R (version 2.11.1 ecodist package).

Results

Radio-Tracking.—I radio-tracked 35 adult *A. canorus* individuals (16 females, 19 males) from 2007–2009. Six of the toads were captured and tracked in multiple years; two females and three males in two years, and one male in three years. Forty-two sets of tracking locations (18 females, 24 males) were used in the data analysis (Appendix 1). Female toads (mean length [SD]: 76 mm [5]; mean mass: 46.4 g [8.7]) were larger than males (mean length [SD]: 67 mm [4]; mean mass: 30.0 g [5.0]). Animals were tracked from 13 to 127 days (mean [SD]: 81.0 [28.7]). The number of locations per individual ranged from 5 to 38 (mean [SD]: 21.1 [9.6]). The length of time individual toads could be tracked was sometimes limited by transmitter failure or the shedding of the transmitter by the toad. Each individual was located on average every four days (mean [SD]: 4.0 [3.2]). Transmitters did not appear to interfere with toad activity, either during breeding (for males) or during movement in aquatic or terrestrial environments.

The maximum distance traveled was greater for females (1,260.9 m) than for males (865.2 m) (two-sided *t*-test $P = 0.013$, df = 30; Fig. 2). The mean distance traveled by females was twice as great as by males (two-sided *t*-test $P = 0.003$, df = 31). The average home range was more than 1.5 times as large for females than for males (Table 1) but the difference was not significant (two-sided *t*-test $P = 0.139$, df = 30). There were no significant differences between toads from different meadows for mean distance traveled (ANOVA $P = 0.275$, df = 3,38), mean maximum distance traveled (ANOVA $P = 0.454$, df = 3,38), or home range (ANOVA $P = 0.475$, df = 3,38).

The mixed model was used to analyze distance traveled based on sex, meadow, ordinal day, and interactions between all variables. The variance–covariance model with the lowest AIC value was the autoregressive with heterogeneous variances; this covariance structure was used in the mixed model. Day, day × day, and sex × day were all significant ($P < 0.01$); neither sex nor meadows alone were significant variables (Table 2). Most of the longer distance movements occurred within 60 days of leaving the breeding site.

Microsite Cover Type.—Adult *A. canorus* were most often located in burrows (Fig. 3), and results of the Friedman test showed that there was a difference in the use of cover type ($P < 0.00$). Post hoc analysis showed that burrow use was different from all other cover types except for vegetation and water ($P < 0.01$ for all significant comparisons). Downed wood was used less than the open/no cover, vegetation, water, and burrow cover types ($P < 0.05$ for all comparisons). All other cover type comparisons were not significant ($P > 0.05$).

Vegetation Sampling.—For all vegetation layers, mean Sørensen dissimilarity values indicated that vegetation communities in occupied locations were more similar to one another than to vegetation communities in unoccupied locations (Table 3).

Herbaceous, shrub, and tree species from 20 different families were identified. Locations where toads were present generally had more herbaceous plants such as *Lupinus* and *Lotus* species but included fewer woody plants and had less canopy cover. Locations without toads generally had more trees and shrubs such as red fir (*Abies magnifica*), white fir (*Abies concolor*), and bush chinquapin (*Chrysolepis sempervirens*). Woody species were found in the ground layer as well as the understory and overstory in locations without toads but not in locations with toads.

Discussion

Movements of Yosemite Toads.—Adult *A. canorus* moved an average distance of 270.2 m [261.7] (mean [SD]) from breeding meadows during this study, and the maximum distance traveled was 1,260.9 m. The maximum distance is greater than dispersal distances of 150–850 m reported previously for this species (Karlstrom, 1962; Kagarise Sherman, 1980; Kagarise Sherman and Morton, 1984; Morton and Pereyra, 2010), although distances greater than 1 km have been recorded for other toads such as *Anaxyrus* (formerly *Bufo*) *boreas* (Muths,

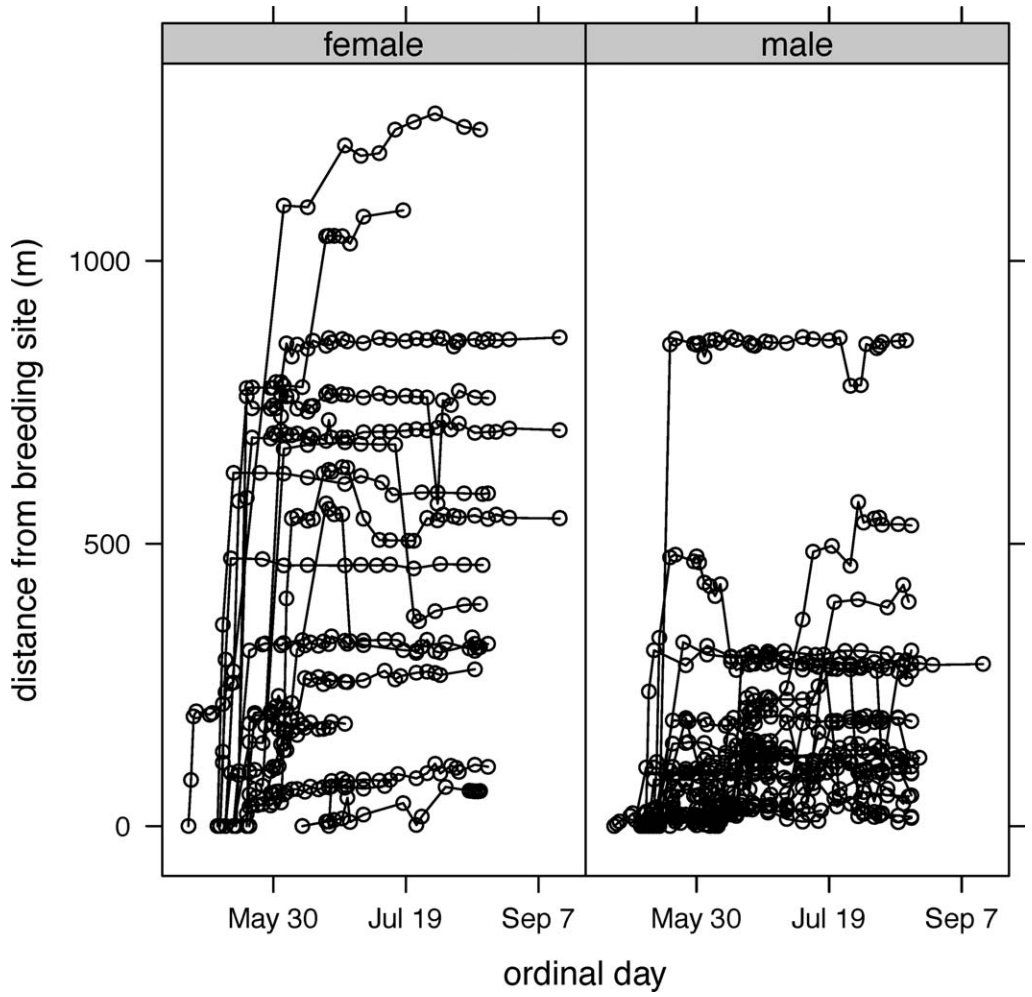

FIG. 2. Distances traveled by radio-tracked *Anaxyrus canorus* individuals.

2003b; Bartelt et al., 2004) and *Bufo bufo* (Sztatecsny and Schabetsberger, 2005). The only other radio-tracking study of adult *A. canorus*, conducted by Martin (2008) in 1995–1997 on 10 adult toads (4 females, 6 males) over 17 to 91 days, reported a maximum distance of 657.4 m and a mean distance of 278.6 m away from breeding pools. That study site was in the northern part of the species' range in the Highland Lakes area on the Stanislaus National Forest, at higher elevation (2,620 m) and in a subalpine forest ecosystem that is substantially different from the mixed-conifer forest ecosystem in the Bull Creek watershed. Notably with regard to the toad, the upland area of Highland Lakes includes an abundance of moderate to steep vegetated slopes with springs and seeps, whereas the upland area of Bull Creek is forested and drier with fewer water sources. In both radio-tracking studies, the mean distance traveled by adult *A. canorus* was very similar (278.6 m and 270.2 m), but the maximum distance reported in Martin (2008) was about half that at Bull Creek. Collectively these studies suggest that the mean distance traveled is representative of the species, but maximum distance might be affected by elevation, forest type, or terrain. In addition, environmental conditions such as the amount of snow-free days might affect the maximum distance traveled by toads. Snow remains on the ground longer in the Highland Lakes area compared to the Bull Creek area, melting later in the spring and arriving earlier in the fall–winter at the higher elevation, and this might impede longer distance travel.

TABLE 1. Mean distance traveled, mean maximum distance traveled, and mean home range for radio-tracked *Anaxyrus canorus* individuals by year and by sex.

Year	Sex	*N*	Mean distance (m) [SD]	Mean maximum distance (m) [SD]	Mean home range (m2) [SD]
2007	F	5	292.0 [299.3]	425.1 [416.1]	20,944 [29,433]
	M	4	109.1 [42.8]	142.1 [36.0]	3,824 [1,723]
2008	F	9	384.1 [282.6]	443.9 [303.1]	25,604 [25,028]
	M	13	182.6 [186.8]	294.3 [224.9]	13,086 [10,457]
2009	F	4	649.2 [317.2]	759.5 [345.3]	36,295 [18,474]
	M	7	146.5 [115.6]	210.4 [142.5]	15,141 [17,894]
2007 through 2009	F	18	417.4 [307.0]	508.8 [352.3]	26,685 [24,308]
	M	24	159.8 [150.8]	244.5 [188.2]	12,142 [12,499]
	both	42	270.2 [261.7]	357.8 [298.1]	18,375 [19,639]

TABLE 2. Results of the mixed model for analyzing distance traveled by radio-tracked *Anaxyrus canorus* individuals.

	Numerator df	Denominator df	*F*-value	*P*-value
(Intercept)	1	828	19.9195	<0.0001
Factor (sex)	1	34	2.9578	0.0946
Factor (meadow)	3	34	1.4406	0.2481
Day	1	828	40.6399	<0.0001[a]
Day × Day	1	828	30.5140	<0.0001[a]
Factor (sex) : factor(meadow)	3	34	0.9373	0.4334
Factor (sex) : day	1	828	11.1904	0.0009[a]
Factor (meadow) : day	3	828	0.6968	0.5541
Factor (sex) : day × day	1	828	0.4288	0.5128
Factor (meadow) : day × day	3	828	0.2237	0.8799
Factor (sex) : factor (meadow) : day	3	828	0.3955	0.7563
Factor (sex) : factor (meadow) : day × day	3	828	0.6057	0.6114

[a] Significant at the $P < 0.001$ level

Female *A. canorus* moved significantly greater distances and had larger home ranges than did males. Other amphibians including the closely related Western Toad (*A. boreas*) exhibit the same pattern, with females moving significantly farther from breeding sites than males (Rittenhouse and Semlitsch, 2007). The difference between female and male movements is likely related to both physiology and ecology. Females may have higher energy requirements for egg production and, thus, require larger foraging areas to meet their energetic needs (Muths, 2003b; Bartelt et al., 2004). Female toads are also larger than male toads and may have greater water storage capability, allowing for longer distance movement away from wetland areas or water sources (Bartelt et al., 2004). There may be less competition for resources related to foraging and overwintering in the areas farther from aquatic sources. Female *A. canorus* do not necessarily breed every year (Kagarise Sherman, 1980; Morton, 1982); therefore, the risks associated with longer distance movements are lower when not undertaken annually.

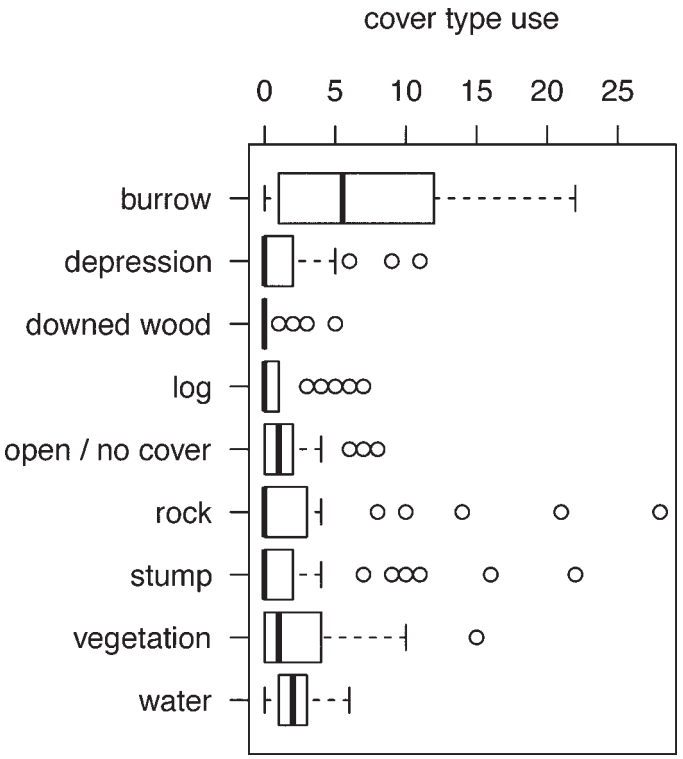

FIG. 3. Box plot for microsite cover type use by *Anaxyrus canorus* individuals.

In addition, female toads may not need to stay as close to breeding sites as would male toads. For males, remaining close to breeding sites and being among the first to arrive might be a competitive advantage when breeding begins in the spring (Bartelt et al., 2004). The benefits of arriving early at a site could be lower for females because mate choices may be few compared to later in the breeding period.

Ordinal day was a significant factor in *A. canorus* movement both as a linear and quadratic predictor. Toads left the breeding sites after breeding finished in May and June and moved into the terrestrial habitat or other areas of the meadows. Most long-distance movement was accomplished within a few days after leaving the breeding sites (shown in Fig. 2) although some toads did move long distances after that period. Martin (2008) also found that toads moved from breeding sites to upland foraging areas over short periods of time. The length of time that an individual spent in a given area was variable. Some individuals stayed in the same area for weeks and did not move any further after the initial travel away from the meadow. Other individuals moved between different upland areas during the tracking period. There was a significant interaction between ordinal day and sex in *A. canorus* movement. Females leave breeding areas as soon as they finish laying eggs while males stay in breeding areas for longer periods of time presumably to try to mate with as many females as possible. Kagarise Sherman (1980) found that males that mated successfully tended to stay at breeding sites longer. Females most likely leave the breeding site as soon as egg-laying is finished to avoid being approached by other males.

Long-distance movements by *A. canorus* appear to be undertaken after dark (Martin, 2008), but there is no tracking evidence that toads move long distances on a regular diel cycle (Martin, 2008; pers. obs.). Toads are active both nocturnally and diurnally (Martin, 2008; pers. obs.) and likely forage during the night in areas close to their daytime location. Although toads were only tracked during daylight hours in this study, it is unlikely that this bias skewed the results for total distance traveled away from breeding sites or for general post-breeding movement patterns.

Movement information is important for determining the type of spatial population structure in *A. canorus*. Amphibians are often thought to exhibit a metapopulation structure, which is a "population of populations" connected by dispersal (Levins, 1969). One of the requirements of a metapopulation is limited dispersal in which only a few individuals move between breeding sites (Hanski et al., 1995; Hanski, 1999), although this condition has rarely been tested for in amphibians (Smith and

TABLE 3. Mean Sørensen dissimilarity values for vegetation layers comparing locations with *Anaxyrus canorus* to (1) one another and (2) locations without *A. canorus*.

	Mean Sørensen dissimilarity between locations with toads [SD]	Mean Sørensen dissimilarity between locations with and without toads [SD]	*t*-value	df	*P*-value
Quadrat	0.46 [0.05]	0.52 [0.03]	–4.4854	31.58	0.0001[a]
Line-intercept (under 2 m)	0.65 [0.13]	0.75 [0.11]	–2.3733	34.93	0.0233[b]
Line-intercept (over 2 m)	0.38 [0.10]	0.56 [0.05]	–6.9979	27.50	<0.0000[a]
Belt transect	0.25 [0.07]	0.43 [0.07]	–7.7857	35.75	<0.0000[a]

[a] Significant at the $P < 0.001$ level
[b] Significant at the $P < 0.05$ level

Green, 2005). Some dispersal is required to connect the metapopulation, but high gene flow between breeding sites would lead to one panmictic population. This study shows that *A. canorus* do have the capability to travel distances between breeding meadows (average distance between known occupied meadows in the Bull Creek watershed is approximately 800 m), but most individuals do not move that far. However, at least one individual during this study (female F06-07) moved 1,089.3 m between breeding meadows. Therefore, it is possible that toads in this study area make up a metapopulation because the requirement of limited dispersal is met, although other requirements such as asynchronous dynamics need to be evaluated.

Movement information is also important for management, where 30.5-m buffers are often used to protect riparian and wetland species (Clinnick, 1985; Lee et al., 2004). These buffers may not be adequate to encompass both the wetland and upland terrestrial habitats used by *A. canorus* based on the average distance moved away from breeding meadows. New protective zones should be considered, and factors to consider when establishing a protective zone for anurans include time of year and sex (Goates et al., 2007), as supported by the results of the toad movement mixed model in this study. Landscape connectivity between terrestrial and aquatic habitats is another important factor in establishing protective zones for population persistence. Connectivity between aquatic breeding sites is also important if *A. canorus* populations exhibit a metapopulation structure. Movement corridors used by toads through all habitats will need to be identified and protected.

Microsite Cover and Use.—Toads survive in the terrestrial environment away from water sources by absorbing moisture from wet substrates and minimizing dehydration (Mullally and Cunningham, 1956; Karlstrom, 1962). They likely choose microsite cover that helps reduce rates of water loss (Karlstrom, 1962; Bartelt et al., 2004). Previous studies reported that *A. canorus* are often found in subterranean rodent burrows made by species such as mountain meadow voles (*Microtus montanus*) and pocket gophers (*Thomomys monticola*) as well as under surface objects and in willow thickets (Mullally, 1953; Mullally and Cunningham, 1956; Karlstrom, 1962). Toads in this study were located most often in burrows, both in shallow burrows where the toad could be seen by looking inside the burrow and in subterranean burrows where the toad was not visible. Toads were also located under or in a variety of other cover types such as logs, rocks, and tree stumps. The selection of microsite cover might be opportunistic based on availability, although this study did not quantify the number of cover sites in the environment. Individuals were often found in the same cover site for several days to weeks and possibly overwintered in these sites. They presumably stayed in these sites because of favorable microsite conditions including adequate thermal insulation and moisture for absorption. However, this study did not measure the environmental conditions of the microsites.

Adult *A. canorus* showed site fidelity, defined as the tendency to return to a previously occupied location, at both the general habitat scale and the microsite cover scale. Site fidelity to terrestrial sites as well as to aquatic breeding sites occurred on an annual basis. Site fidelity to breeding sites was strong, and the majority of individuals identified in multiple years, though not necessarily tracked, were found in the same meadow pools during the breeding period (pers. obs.; see also Kagarise Sherman, 1980). Site fidelity to upland terrestrial cover sites also was evident, because some of the individuals tracked in multiple years returned to the same upland areas. Two males were located at the same cover sites (rock and tree stump) in multiple years. Other individuals (2 females, 2 males) were located in the same areas in multiple years although they did not return to the same cover sites. Site fidelity to breeding sites has been documented previously for *A. canorus* (Kagarise Sherman, 1980; Morton 1982), and fidelity to cover types has been shown for other amphibian species (e.g., Smith and Green, 2005). Site fidelity is a common life-history strategy for increased survival in many species (Switzer, 1993), because it may lead to more efficient movement through the environment and familiarity with resources for breeding, foraging, and/or overwintering.

Terrestrial Habitat.—Relatively little attention has been paid to the terrestrial habitat used by *A. canorus*. Many of the previous studies focused on wetland areas because toads are associated with this habitat (Mullally, 1953; Karlstrom, 1962; Kagarise Sherman, 1980; Kagarise Sherman and Morton, 1984) and because toads are difficult to locate in the terrestrial environment without the aid of tracking devices. The radio-tracking study by Martin (2008) was the first to examine terrestrial habitat use and overwintering burrows and found that adult toads used the upland foraging habitat extensively after the breeding season. The present study confirms that adult *A. canorus* use the upland terrestrial environment regularly in addition to the wetland habitat. However, unlike the environment described in Martin (2008), the upland habitat in Bull Creek consists of drier forest with fewer water sources. Morton and Pereyra (2010) also reported that *A. canorus* were found in dry and rocky areas at the edges of talus slopes at their study site at Tioga Pass, which is at an elevation of 3,018 m on the eastern Sierran slope in the northern part of the species' range.

Martin (2008) also identified overwintering sites that were different from upland or meadow foraging habitats. In contrast, the present study did not detect toad movement toward distinct overwintering sites in the fall, and additional toad tracking data collected at Bull Creek in May to November 2012 but not

presented here, indicate that most toads in this study site do not move longer distances to other overwintering locations at the onset of winter. However, there is some individual variation in movement patterns.

The time spent in the upland environment underscores the importance of the terrestrial habitat in the life cycle of *A. canorus* and the need to better identify this habitat for management purposes. Within the terrestrial mixed-conifer forest in this study, toads were found in locations that were structurally different than locations that were unoccupied by toads. Although plant species were the same in both occupied and unoccupied sites, there were differences in the percent species compositions in all vegetation layers. Occupied sites were more open than were surrounding areas; there were fewer trees and shrubs and less canopy cover and woody litter in toad-occupied sites compared to random sites in the watershed. Selection of more open areas may be related to environmental (e.g., light and microclimate) conditions, availability of suitable cover sites, and prey communities. The open areas often had higher percent cover of herbaceous species in the ground layer, many of which prefer full sun (e.g., *Lupinus* and *Lotus* species). Wood (1977) found that hymenopterans compose almost 80% of *A. canorus* diet in the summer. Because *Lupinus* and *Lotus* species attract these insects (e.g., ants and bees; pers. obs.), the open areas may provide increased food resources relative to areas with fewer herbaceous plant species.

The occupied locations may be more similar to historic vegetation communities under pre-fire suppression conditions. Fire suppression in the past century has benefited shade-tolerant species such as white fir (*Abies concolor*) and red fir (*Abies magnifica*), which are the dominant tree species in the Bull Creek study area, and has led to an increase in tree densities (Kilgore and Taylor, 1979; Parsons and DeBendeetti, 1979; Stephens et al., 2009). Forest management practices that reduce woody biomass and result in more open areas may be beneficial for *A. canorus*. However, more study on the potential effects of ground disturbance on terrestrial cover sites used by the toad and consideration of the seasonality of forest management operations are needed before those management practices are implemented widely.

Summary and Conclusions.—This study found that adult *A. canorus* moved further than previously reported, up to 1.26 km away from breeding meadows. The average distance traveled was greater for females (417 m) than for males (160 m), and movement was related to ordinal day. Toads were located extensively in the dry upland environment as well as in the aquatic meadows.

Anaxyrus canorus movements and terrestrial habitat use vary in the different ecosystems throughout its range, based on the Martin (2008) study and this study. The maximum distance traveled in the subalpine forest in Highland Lakes was lower than in the mixed-conifer forest in Bull Creek. Seeps and springs are common in the upland environment used by toads in Highland Lakes, but water sources are not as abundant in the upland environment in Bull Creek. Additionally, separate overwintering sites do not appear to be used by *A. canorus* at the Bull Creek study site. However, the mean distance traveled by toads was almost identical in both tracking studies, and the post-breeding movement patterns were very similar.

Movement information is critical for effective management of *A. canorus*, which should take into account the timing of movement, distance moved by sex, and possible movement corridors between critical habitats (e.g., aquatic breeding sites and upland foraging habitat).

Olsen et al. (2007) suggest that targeted protection of sensitive habitat may be a better management approach for protection of species rather than a general buffer zone around aquatic features. This necessitates the identification of sensitive habitat in the terrestrial as well as the wetland environment for mobile species such as *A. canorus* that can travel over 1 km. This current study analyzed occupied terrestrial sites with regard to vegetation in a first step toward characterizing upland toad habitat. Further studies can be conducted on physical conditions and environmental resources, including availability of prey and microsite cover sites along with associated microsite conditions. Comparisons of these physical and environmental measurements in occupied and unoccupied sites will further delineate *A. canorus* habitat within the terrestrial environment.

Finally, adult *A. canorus* showed site fidelity to both terrestrial and wetland sites, which in general may increase survival or breeding success. However, if occupied sites deteriorate or are disturbed, it is not known whether toads will leave to find more suitable habitat. If they remain in the degraded habitat, survival or breeding success may be lowered.

Acknowledgments.—I thank M. Thornton, C. White, A. Lind, R. Grasso, C. Brown, K. Kiehl, L. Wilkinson, J. Adair, C. Hunsaker, S. Barnes, and P. Strand for assistance and support on this project. Funding was provided by the USDA Forest Service-Pacific Southwest Research Station, the Sierra National Forest, and the University of California, Davis. Research animals for this study were collected under a California Department of Fish and Game Scientific Collecting Permit (SC-008621). This research was approved by the Animal Care and Use Committee of the University of California, Davis (Protocols 12283 and 15318).

Literature Cited

Bartelt, P. E., C. R. Peterson, and R. W. Klaver. 2004. Sexual differences in the post-breeding movements and habitats selected by western toads (*Bufo boreas*) in southeastern Idaho. Herpetologica 60:455–467.

Chetkiewicz, C.-L. B., C. C. St. Clair, and M. S. Boyce. 2006. Corridors for conservation: integrating pattern and process. Annual Review of Ecology Evolution and Systematics 37:317–342.

Clinnick, P. F. 1985. Buffer strip management in forest operations: a review. Australian Forestry 48:34–45.

Donnelly, M. A., C. Guyer, J. E. Juterbock, and R. A. Alford. 1994. Techniques for marking amphibians. *In* W. R. Heyer, M. A. Donnelly, R. W. McDiarmid, L. C. Hayek, and M. S. Foster (eds.), Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians, pp. 275–284. Smithsonian Institution Press, Washington, DC.

Galili, T. 2010. Post hoc analysis for Friedman's Test (R code). R-statistics blog [Internet]. Available from: http://www.r-statistics.com/2010/02/post-hoc-analysis-for-friedmans-test-r-code. Accessed 7 June 2010.

Goates, M. C., K. A. Hatch, and D. L. Eggett. 2007. The need to ground truth 30.5 m buffers: a case study of the boreal toad (*Bufo boreas*). Biological Conservation 138:474–483.

Hanski, I. 1999. Metapopulation Ecology. Oxford University Press, Oxford.

Hanski, I., T. Pakkala, M. Kuussaari, and G. Lei. 1995. Metapopulation persistence of an endangered butterfly in a fragmented landscape. Oikos 72:21–28.

Harrison, S., and A. D. Taylor. 1997. Empirical evidence for metapopulation dynamics. *In* I. Hanski and M. E. Gilpin (eds.), Metapopulation Dynamics: Ecology, Genetics and Evolution, pp. 27–42. Academic Press, San Diego.

HICKMAN, J. (ed.). 1993. The Jepson Manual: Higher Plants of California. University of California Press, Berkeley.

HOLLANDER, M., AND D. E. WOLFE. 1999. Nonparametric Statistical Methods. 2nd ed. John Wiley, New York.

HUNSAKER, C. T., AND S. M. EAGAN. 2003. Small stream ecosystem variability in the Sierra Nevada of California. *In* K. G. Renard, S. A. McElroy, W. J. Gburek, H. E. Canfield, and R. L. Scott (eds.), First Interagency Conference on Research in the Watersheds, October 27–30 2003, pp. 716–721. U.S. Department of Agriculture, Agricultural Research Service, Benson, AZ.

KAGARISE SHERMAN, C. 1980. A Comparison of the Natural History and Mating System of Two Anurans: Yosemite Toads (*Bufo canorus*) and Black Toads (*Bufo exsul*). Unpubl. Ph.D. diss., University of Michigan, Ann Arbor.

KAGARISE SHERMAN, C., AND M. L. MORTON. 1984. The toad that stays on its toes. Natural History 93:72–78.

KARLSTROM, E. L. 1962. The toad genus *Bufo* in the Sierra Nevada of California. University of California Publications in Zoology 62:1–104.

KILGORE, B. M., AND D. TAYLOR. 1979. Fire history of a sequoia mixed conifer forest. Ecology 60:129–142.

LEE, P., C. SMYTH, AND S. BOUTIN. 2004. Quantitative review of riparian buffer width guidelines from Canada and the United States. Journal of Environmental Management 70:165–180.

LEVINS, R. A. 1969. Some demographic and evolutionary consequences of environmental heterogeneity for biological control. Bulletin of the Entomological Society of America 15:237–240.

MARSH, D. M., AND P. C. TRENHAM. 2001. Metapopulation dynamics and amphibian conservation. Conservation Biology 15:40–49.

MARTIN, D. 2008. Decline, Movement and Habitat Utilization of the Yosemite Toad (*Bufo canorus*): An Endangered Anuran Endemic to the Sierra Nevada of California. Unpubl. Ph.D. diss., University of California, Santa Barbara.

MCCUNE, B., AND J. B. GRACE. 2002. Analysis of Ecological Communities. MjM Software Design, Gleneden Beach, OR.

MORTON, M. L. 1982. Natural history of the Yosemite toad. National Geographic Society Research Reports 14:499–503.

MORTON, M. L., AND M. E. PEREYRA. 2010. Habitat use by Yosemite toads: life history traits and implications for conservation. Herpetological Conservation and Biology 5:388–394.

MULLALLY, D. P. 1953. Observations on the ecology of the toad *Bufo canorus*. Copeia 1953:182–183.

MULLALLY, D. P., AND J. D. CUNNINGHAM. 1956. Aspects of the thermal ecology of the Yosemite toad. Herpetologica 12:57–67.

MUTHS, E. 2003a. A radio transmitter belt for small ranid frogs. Herpetological Review 34:345–348.

———. 2003b. Home range and movements of boreal toads in undisturbed habitats. Copeia 2003:160–165.

OLSEN, D. H., P. ANDERSON, C. A. FRISSELL, H. H. WELSH JR., AND D. F. BRADFORD. 2007. Biodiversity management approaches for stream-riparian areas: perspectives for Pacific Northwest headwater forests, microclimates and amphibians. Forest Ecology and Management 246:81–107.

PARSONS, D. J., AND S. H. DEBENDEETTI. 1979. Impact of fire suppression on a mixed-conifer forest. Forest Ecology and Management 2:21–33.

RICHARDS, S. J., U. SINSCH, AND R. A. ALFORD. 1994. Supplemental approaches to studying amphibian biodiversity: radio tracking. *In* W. R. Heyer, M. A. Donnelly, R. W. McDiarmid, L. C. Hayek, and M. S. Foster (eds.), Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians, pp. 155–158. Smithsonian Institution Press, Washington, DC.

RITTENHOUSE, T. A. G., AND R. D. SEMLITSCH. 2007. Distribution of amphibians in terrestrial habitat surrounding wetlands. Wetlands 27: 153–161.

SEMLITSCH, R. D., AND J. R. BODIE. 2003. Biological criteria for buffer zones around wetlands and riparian habitats for amphibians and reptiles. Conservation Biology 17:1219–1228.

SMITH, M. A., AND D. M. GREEN. 2005. Dispersal and the metapopulation paradigm in amphibian ecology and conservation: are all amphibian populations metapopulations? Ecography 28:110–128.

STEPHENS, S. L., J. J. MOGHADDAS, C. EDMINSTER, C. E. FIEDLER, S. HAASE, M. HARRINGTON, J. E. KEELEY, E. E. KNAPP, J. D. MCIVER, K. METLEN ET AL. 2009. Fire treatment effects on vegetation structure, fuels, and potential fire severity in western U.S. forests. Ecological Applications 19:305–320.

SWIHART, K., AND N. A. SLADE. 1985. Testing for independence of observation in animal movements. Ecology 66:1176–1184.

SWITZER, P. V. 1993. Site fidelity in predictable and unpredictable habitats. Evolutionary Ecology 7:533–555.

SZTATECSNY, M., AND R. SCHABETSBERGER. 2005. Into thin air: vertical migration, body condition, and quality of terrestrial habits of alpine Common Toads, *Bufo bufo*. Canadian Journal of Zoology 83:788–796.

USFWS (U.S. FISH AND WILDLIFE SERVICE). 2013. Endangered status for the Sierra Nevada yellow-legged frog and the northern distinct population segment of the mountain yellow-legged frog, and threatened status for the Yosemite toad. Federal Register 78(80): 24472–24514.

WHITE, G. C., AND R. A. GARROTT. 1990. Analysis of Wildlife Radio-Tracking Data. Academic Press, San Diego.

WOOD, T. S. 1977. Food Habits of *Bufo canorus*. Unpubl. master's thesis, Occidental College, Los Angeles.

Accepted: 9 March 2013.

APPENDIX 1. Sex, meadow of origin, dates tracked, number of days tracked, number of locations, maximum distance traveled, and home range for radio-tracked *Anaxyrus canorus* individuals.

Toad-ID	Sex	Meadow	Dates tracked	Number of days tracked	Number of locations	Maximum distance (m)	Home range (m2)
F2-07	F	520M20	Apr–May 2007	13	7	216.5	3,096
F4-07	F	520M15	May–Aug 2007	93	22	570.3	23,177
F5-07	F	520M15	May–Jun 2007	26	7	179.8	5,340
F6-07[1]	F	520M15	May–Jul 2007	64	14	1,089.3	71,273
F7-07[2]	F	520M20	Jun–Aug 2007	67	17	69.4	1,834
M1-07[3]	M	520M20	Apr–May 2007	22	10	103.8	1,514
M3-07	M	520M15	May–Jun 2007	39	11	188.4	4,062
M4-07	M	520M15	May–Jul 2007	66	17	149.0	4,032
M7-07	M	520M15	May–Aug 2007	94	23	127.4	5,686
F1-08	F	520M20	May–Aug 2008	101	35	962.2	107,896
F2-08	F	520M20	May–Sep 2008	122	35	864.4	110,200
F3-08	F	520M20	May–Sep 2008	122	34	908.6	55,568
F4-08	F	520M15	May–Jun 2008	37	17	199.9	7,706
F5-08	F	520M15	May–Aug 2008	86	28	277.8	27,026
F6-08	F	520M15	May–Aug 2008	91	31	115.7	4,729
F7-08	F	520M15	May–Aug 2008	91	28	335.9	22,281
F8-08	F	520M25	May–Sep 2008	117	32	742.9	58,010
F9-08[1]	F	520M14	Jun–Jul 2008	23	7	83.5	548
M01-08[4]	M	520M20	May–Sep 2008	127	38	480.8	68,193
M02-08	M	520M20	May–Aug 2008	98	35	865.2	79,767
M03-08[3]	M	520M20	May–Aug 2008	99	33	230.0	20,082
M04-08	M	520M25	May–Aug 2008	95	29	191.6	16,410
M05-08[5]	M	520M25	May–Aug 2008	95	31	447.8	36,155
M06-08[6]	M	520M25	May–Aug 2008	95	31	295.6	22,303
M07-08	M	520M15	May–Aug 2008	94	32	244.2	24,569
M08-08	M	520M15	May–Aug 2008	91	30	303.8	19,369
M10-08	M	520M15	May–Jul 2008	57	22	101.5	3,700
M11-08	M	520M15	Jun–Aug 2008	76	23	309.0	25,811
M12-08	M	520M25	Jun–Aug 2008	74	22	400.7	17,707
M14-08	M	520M14	Jun–Aug 2008	73	22	742.6	36,528
M15-08	M	520M14	Jun–Aug 2008	73	23	200.3	16,338
F1-09	F	520M20	May–Aug 2009	99	15	474.0	12,387
F2-09[2]	F	520M20	May–Aug 2009	96	14	678.6	51,826
F3-09	F	520M15	May–Aug 2009	102	15	624.6	49,865
F4-09	F	520M15	May–Aug 2009	96	12	1,260.9	31,102
M1-09[3]	M	520M20	May–Aug 2009	101	16	92.1	3,799
M2-09[4]	M	520M20	May–Aug 2009	98	15	319.2	22,892
M3-09	M	520M15	May–Aug 2009	96	13	325.5	22,321
M5-09[5]	M	520M25	May–Jun 2009	35	5	107.3	824
M6-09[6]	M	520M25	May–Aug 2009	96	13	124.7	5,316
M7-09	M	520M14	May–Aug 2009	95	13	427.1	49,584
M8-09	M	520M14	May–Jul 2009	67	9	76.7	1,249
Total locations: F = 370, M = 516							

[1–6] = same individuals radio-tracked in more than one year.